LAING

BUREAU OF LAND MANAGEMENT

WATERFOWL/WETLAND WORKSHOP

ANCHORAGE, ALASKA

14-16 AUGUST, 1991

WATERFOWL AND WETLANDS WORKSHOP - ALASKA

Bureau of Land Management
Internationl Airport Inn, Anchorage, AK
14-16 August 1991

First Day - Wed 14 Aug

8:30 Opening remarks on workshop format: Alaskan wetlands DU rep and BLM rep

9:00 An overview of North American wetlands: Status and classification - Emphasis on the Pacific Flyway - Mickey Heitmeyer

9:30 Extent and complexity of Alaskan wetlands

9:50 Break

10:20 Wetland structure and function - Fritz Reid

11:00 Conceptual model of marsh ecology and its utility to wetland management - Jeff Nelson

11:30 Questions/Comments on morning session

11:45 Lunch Break

13:30 Modified hydrological regimes: their impact on wetland productivity - Fritz Reid

14:00 Invertebrates in wetland communities - Fritz Reid

14:40 Break

15:00 Northern wetland communities: Waterfowl species and population trends - Tom Rothe / Dirk Derksen

Second Day - Thu 15 Aug

8:00	Addresses by Cy Jamison and Ed Spang
9:00	Basic life history strategies of waterfowl: Energetic and nutritional needs - Mickey Heitmeyer
10:15	Break
10:45	Waterfowl foods - Fritz Reid
11:30	Lunch
13:00	Cross-seasonal effects, the importance of Alaskan, Californian, and Mexican habitats - Mickey Heitmeyer
14:00	BLM work session
16:00	Dinner
18:00 -22:00	Optional field inspection of estuarine and palustrine wetlands

Third Day - Fri 16 Aug

8:30	USFWS waterfowl/wetland surveys - Bob Leedy/Russ Oates
9:00	California waterfowl habitat evaluation using remote sensing techniques - Dick Kempka
10:15	Break
10:45	Habitat inventory and evaluation in the Prairie Pothole Region - Dick Kempka
11:15	Satellite inventory and monitoring: A complete Pacific Flyway perspective - Dick Kempka
12:00	Lunch
13:30	Step-wise approach to habitat enhancement/restoration - Tom Rothe

14:00 Cooperative Partnerships

Current legislative and funding opportunities - Scott Sutherland

Ducks Unlimited's Habitat Programs / IWWR - John Nagel / Jeff Nelson

Wildlife 2000 / WETT - Mike Mathiot / Craig Altop

U.S. Forest Service / Taking Wing Program - Rob Olsen

15:15 Break

15:40 Partnerships for Alaskan wetlands and stewardship of the waterfowl resource - Ed Spang / Bishop Buckle

16:00 Meeting wrap-up

Reference List for Wetland/Waterfowl Workshop

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5 Impacts of Hydrologic Alteration on Management of Freshwater Wetlands

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Impacts of Hydrologic Alteration on Management of Freshwater Wetlands

Leigh H. Fredrickson and Frederic A. Reid

Abstract: Wetlands are dynamic systems that are characterized by daily, seasonal, and long-term fluctuations in water levels. Man's activities in the 48 conterminous states, Hawaii, and the Canadian provinces have severely impacted a vast area of these habitats either by destruction or through modification of natural hydrological functions. Constriction of river channels, and subsequent conversion of floodplain habitats to croplands, change hydrological regimes throughout major river basins and cause a decrease in the productivity of remnant isolated wetlands by stabilizing water levels. In an attempt to counteract the effects of habitat loss and hydrological change, intensive wetland management is widely practiced in North America. Unfortunately, implementation of commonly used manipulations may further stabilize wetlands developed for intensive management. To diminish these detrimental effects, it is essential that we have an understanding of wetland values and functions, as well as knowledge concerning life history strategies of plant and animal foods that supply seasonal requirements for target organisms. Recommendations for desirable development features and guidelines for intensive management to maintain productivity require strategies that replicate natural hydrological regimes.

Freshwater wetlands are among the most productive habitats in the world, with average net primary production reaching 2,500 $g/m^2/yr$ (Whittaker and Likens 1973). The long-term productivity of these habitats are maintained by the perpetual destruction and creation of wetlands within the same general region. Glaciers, floods, fire, and changes in permafrost are common forces important in freshwater wetland formation and maintenance.

Unfortunately, productivity of our national wetland resource has been severely impacted because the natural hydrology that resulted in wetland formation, and to which myriad plants and animals have adapted, has been compromised. Developments such as dams for hydropower and flood control, diversions to speed water flow, levees for flood protection, wetland drainage for commercial districts and agriculture, and filling wetlands for marinas have modified wetlands across the continent (Tables 1 and 2).

Table 1. Agricultural developments that modify wetlands

Development	Modification	Hydrology or water quality
Rowcrops	Drainage	—Increases speed and volume of runoff, remaining basins receive more water faster —Decreased periodicity of headwater or backwater flooding, but increased intensity —Isolation of individual basins and disruption of wetland complexes —Smaller size of wetland fragments —Disproportionate loss of small ephemeral or seasonal wetlands
	Cultivation	—Increase erosion and turbidity —Increase toxins —Seasonal loss of vegetation increases rate and volume of flooding
Conservation practices	Terraces and contour farming and riparian buffer strips	—Reduce runoff and erosion —Lessen flow peaks in streams and/or wetlands

These destructive processes have been so complete within the 48 conterminous states that all watersheds have been degraded to some degree and few wetlands have retained either their natural hydrology or productivity. Because of these modifications in natural hydrological regimes, intensive wetland management is essential in many regions if wetlands are to retain their values and productivity. To be effective, management must be based on an understanding of untampered wetland functions and values in order to emulate natural hydrological conditions that will assure the long-term productivity of the remaining wetlands. A description of the essential components in wetland productivity sets the stage for an understanding of how various wetland developments designed for either wildlife, commercial, or navigational purposes have impacted wetlands. The goal of this paper largely focuses on the abiotic components of hydrology and fire and their role in maintaining viable wetland habitats. The effects of modified hydrology and the need for intensive management to compensate for man's modifications are discussed.

R. Baskett, P. Covington, R. Drobney, B. Dugger, J. Kelley, M. Laubhan, P. Magee, G. Pogue, and J. Taylor kindly provided constructive criticism. Our thinking about the dynamic nature of wetland systems was stimulated by many individuals, but most noteworthy are M. Heitmeyer, C. Klimas, and M. Weller. Support was provided by Gaylord Memorial Laboratory

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Basic Wetland Concepts

Wetlands are transitional habitats between terrestrial and aquatic systems, that serve as a functional sieve (van der Valk 1981, Fredrickson 1982). Abiotic components that influence wetlands include: climate; soils; fire; water quantity, quality, and chemistry; hydroperiod; and hydrological regime (Fig. 1). Biotic components include those within a wetland basin and those that are more peripheral to the system. Diseases, predators, and upland wildlife that occasionally use wetlands are biotic components that have some influence on wetlands. Within the wetland basin, there are com-

Table 2. Non-agricultural developments that modify wetlands.

Development	Modification	Change in hydrology or water quality
Reservoir	Modify overbank flooding	—Natural peak flows removed, lower downstream flow over longer time period, reduced turbidity and sediment load, inundates riverine wetlands upstream
Reservoir with hydropower	Modify overbank flooding	—Natural peak flows removed, lower downstream flow over longer time period, reduced turbidity and sediment load, inundates riverine wetlands upstream —Dramatic daily and seasonal fluctuations may occur
Levees	Constriction of river channel Modify overbank flooding	—Intensifies extremes of flooding and drought —Increase turbidity, decrease sedimentation and surface area —Increase flow
Channels	Speed flow of water	—Water rises and drops quickly —Increased bank erosion —Increased flow velocity
Urbanization and marinas	Drain and filling wetlands	—Isolation of wetlands —Stabilization of water regimes —Increases speed and volume of runoff, remaining wetlands receive more water faster —Industrial and municipal pollutants, nutrient loading, eutrophication
Highways/railroads	Modify flow patterns	—Increase and/or decrease water depths —Toxic inputs

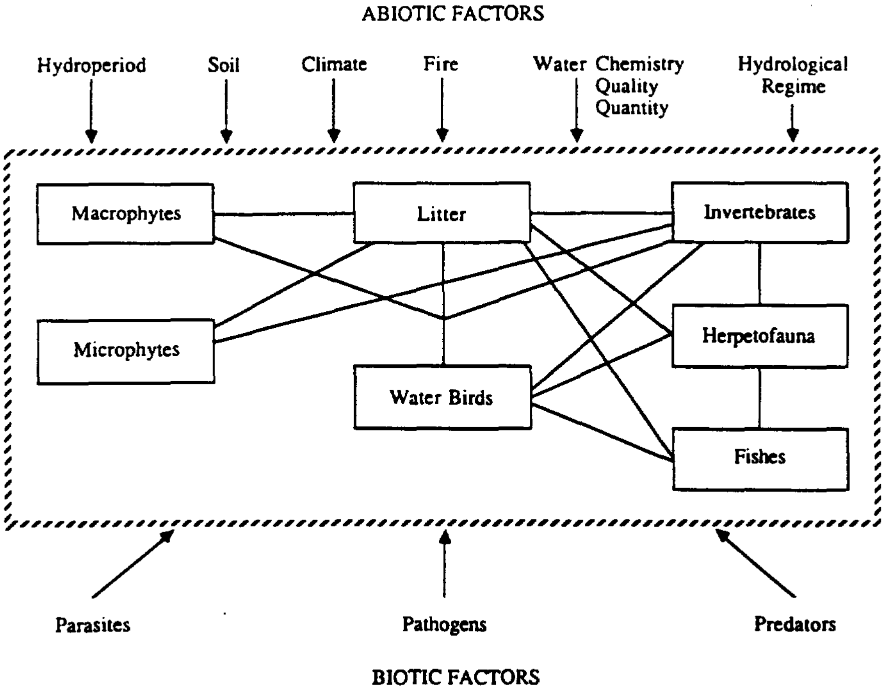

Fig. 1. Wetland seive model of the interrelationships among biotic and abiotic factors (after van der Valk 1981, Fredrickson 1982).

plex interactions among microorganisms, one-celled plants, macrophytes, invertebrates, and vertebrates. These biotic components are strongly influenced by abiotic factors, many of which have been severely impacted by man. Man's most dramatic impact has been the modification of the hydrological components that regulate wetland productivity.

Untampered Wetland Systems

Innoko River Complex: A Natural System

Examination of a natural, free-flowing river system is instructive in developing an understanding of the subtle effects that modifications have on natural wetland hydrology. The Innoko River system in western Alaska is such an example. A mountain range intercepts weather movements from the Bering Sea, with a resulting precipitation pattern that is highly variable among and within years. The rapid flush of water from the mountainous areas, during snow melt or periods of heavy precipitation, to more level terrain surrounding the Innoko River at lower elevations has produced a vast interconnected wetland system (Fig. 2*a*). Silt deposition along the main channel has formed natural levees that have been stabilized by willows (*Salix* spp). Behind these natural levees are interconnected floodplain lakes that drain into the main river channel through small streams that breach the levees along the main channel. When water is high in the main river channel, the water acts as a natural stoplog structure, controlling the floodplain

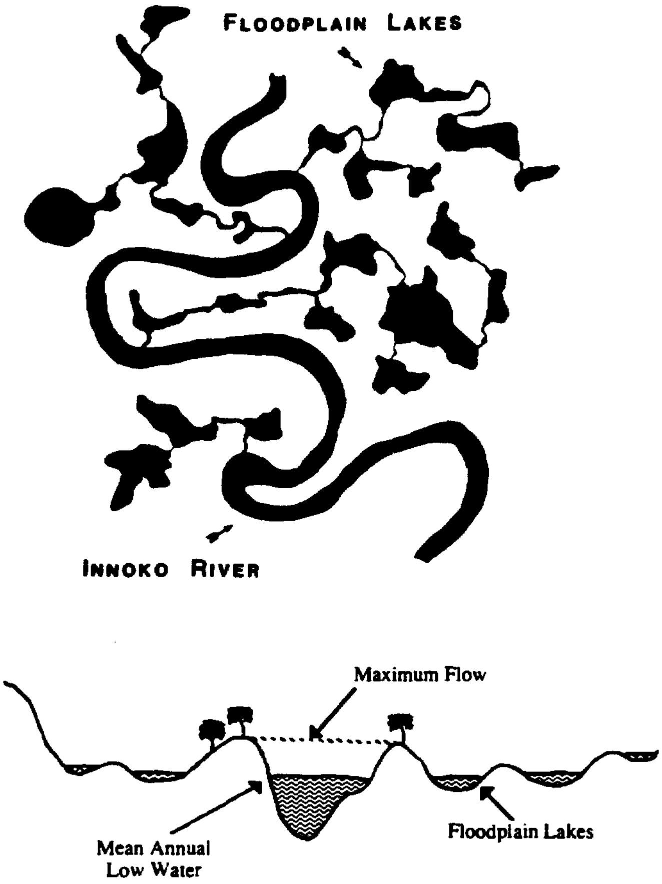

Fig. 2. Innoko River system, Alaska showing (a) aerial view of river and floodplain lake drainage pattern and (b) cross-section relationship of water levels in the river and floodplain lakes.

water level and rate of drawdown in the small streams that drain the interconnected lakes (Fig. 2*b*). As water drops gradually in the main channel, a slow drawdown occurs. Lush green browse develops on mudflats and attracts molting white-fronted geese (*Anser albifrons*). Interspersed among the mudflats are sites that are vegetated with robust emergents, such as the sedge (*Carex rostrata*). Higher water temperatures at these latter sites promote a great abundance of invertebrates. As water recedes, these invertebrates are concentrated and made available for waterbird use. Thus, the vast area of wetlands behind the natural levee along the main river channel provides an ideal feeding ground for arctic waterbirds, and supplies key nutritional components for breeding and molting (Myers et al. 1987).

In the case of the Innoko River, an upstream reservoir or other channel modification would compromise the productivity of the system. Retention of water within a reservoir would keep the floodplain lakes at a drawdown stage. Rapid release of water for hydropower would be devastating to the production of diverse food resources because of erratic fluctuations in water levels.

Managing Pristine Environments

Management of pristine environments should be passive. Emphasis should be placed on investigations or monitoring that results in understanding the dynamic processes of natural production, wetland function, and wildlife use. Unfortunately, resource agencies frequently emphasize intensive management activities within pristine habitats that should be reserved only for the rehabilitation of degraded habitats. As a current example, practiced or planned "habitat improvements" in Alaska include island construction, pothole blasting, hay infusions, fertilization, and impoundment of tidal wetlands. These actions are reasonable solutions to enhance degraded wetlands in some of the 48 contiguous states, but such activities disrupt the natural function of untampered Alaskan and northern Canadian wetlands. Understanding dynamic processes aids biologists in generating appropriate options to proposed perturbations including roads, dams, and oil exploration and transport. Furthermore, an understanding of functions in untampered environments provides clearer guidelines to manage modified environments.

Modified Wetland Systems

The principal cause of wetland loss in the 48 conterminous states has been conversion to agriculture, accounting for >85% of total losses (Tiner

1984). Recent losses of palustrine wetlands by conversion of forested and herbaceous habitats to agriculture have had significant impacts on wetland wildlife (Frayer et al. 1983). Field expansion, land leveling, and irrigation with ground water have been accelerated in the agricultural areas of much of the Midwest. As fields were leveled, small wetlands were destroyed and more ground water was pumped for irrigation. These practices further stabilized the remaining wetlands and stream systems by facilitating more rapid water drainage from fields and by lowering ground water levels (Table 1). In addition, the capacity to recharge ground water systems was reduced because fewer wetlands remained and near drought conditions often times occurred between periods of peak flow following storm events. As a result, ground water levels dropped, and wetland management has become more difficult and costly. Thus taxpayers spent huge sums of money for cross purposes. Millions of tax dollars or tax-break incentives were used to promote crop production on drained wetlands or on activities that further degraded wetlands. At the same time, millions of tax and hunting license dollars were spent to restore lost or degraded wetlands and to rebuild depleted wildlife populations. The true paradox, however, was that crop subsidies were paid amid continual grain surpluses.

Alteration of Flooding Regimes

The physical processes that drive the productivity of natural wetlands center around hydrologic events within each watershed. Timing, depth, duration, and frequency of flooding constitute a flooding regime. Changes in any of these factors cause alterations in the hydrologic cycle of wetlands. The 4 general categories of hydrologic alterations include: 1) stabilization, 2) shift in flood timing, 3) increased flooding, and 4) decreased flooding (Klimas 1988).

Stabilization of hydrological regimes usually corresponds to a prolonged inundation of substrates that were periodically exposed. Inundation may involve seasonal, annual, or multi-year flooding that stabilizes ephemeral, seasonal, or semi-permanent waterbodies. Modification of natural flood chronology and periodicity results in shifts in flood timing. Loss of natural floodplain wetlands along large Midwestern rivers has caused increased tributary flows following rainfall. Such floodwaters may inundate forest stands during the growing season and deposit heavy silt loads that cause tree mortality. Before waterway modifications, many of these sites remained seasonally dry except during unusual storm events. Increased flooding may result from changes in the 4 factors of flooding regime. For example, heightened flood peaks in levee-contricted floodplains adjacent to large rivers and increased flooding of semi-permanent glacial wetlands adjacent to agricultural fields with high run-off are common. Although flood control reservoirs, levees and drainage tiles generally result in decreased flooding, severe floods may still occur (Klimas 1988, Reid et al. 1989).

Most wetland management has been partially sensitive to these long-term averages and general flooding patterns. Unfortunately the constraints imposed by development of artificial configurations (i.e., levees, water control structures, water delivery and discharge systems) of many man-made wetlands compromise effective management. These constraints, in combination with a lack of knowledge pertaining to life history requirements of target organisms or their principal foods, generally results in management that emulates the average condition within months or years rather than the dynamic pattern of precipitation and associated flooding that characterizes the short- and long-term fluctuations of natural systems. Thus, stable patterns of hydrology are created across annual periods on many intensively managed areas. Variability in the timing of flooding or dewatering has an important influence on changes in plant species composition and availability of foods for wildlife, but use of this practice is rare in wetland management. Federal managers are regularly reassigned to areas within different biomes, thus they must constantly adapt their management activities to local variations in hydrological and temperature regimes. Types and timing of precipitation and length of growing season varies greatly among latitudes (Fig. 3) even in the Midwest. All are important factors in developing general management scenarios.

The Misconception of Stable Water

Waterbird response to fluctuating water regimes in the North American prairies is well known because of the well studied relationships between duck populations and drought cycles. In comparison, these relationships are more ambiguous in wetland systems outside the prairie pothole region. Because the goal of many management scenarios is to counteract the effects of seasonal or long-term droughts, a general tendency is to restrict water level fluctuations in managed wetlands. This misconception is based on the fact that most wetland wildlife requires water for most stages in their life cycles. In contrast less is known about the specific requirements of waterbirds and the manipulations that provide the necessary food and cover. Studies that address species biology or management often tend to focus on behavior, bioenergetics, or time-activity budgets but fail to address information on the dynamic nature of habitat conditions. These approaches lead to naive advice concerning the subtle differences in habitat conditions that determine the type and extent of use by wildlife. Furthermore many wildlife management studies are conducted by graduate students, whose short-term

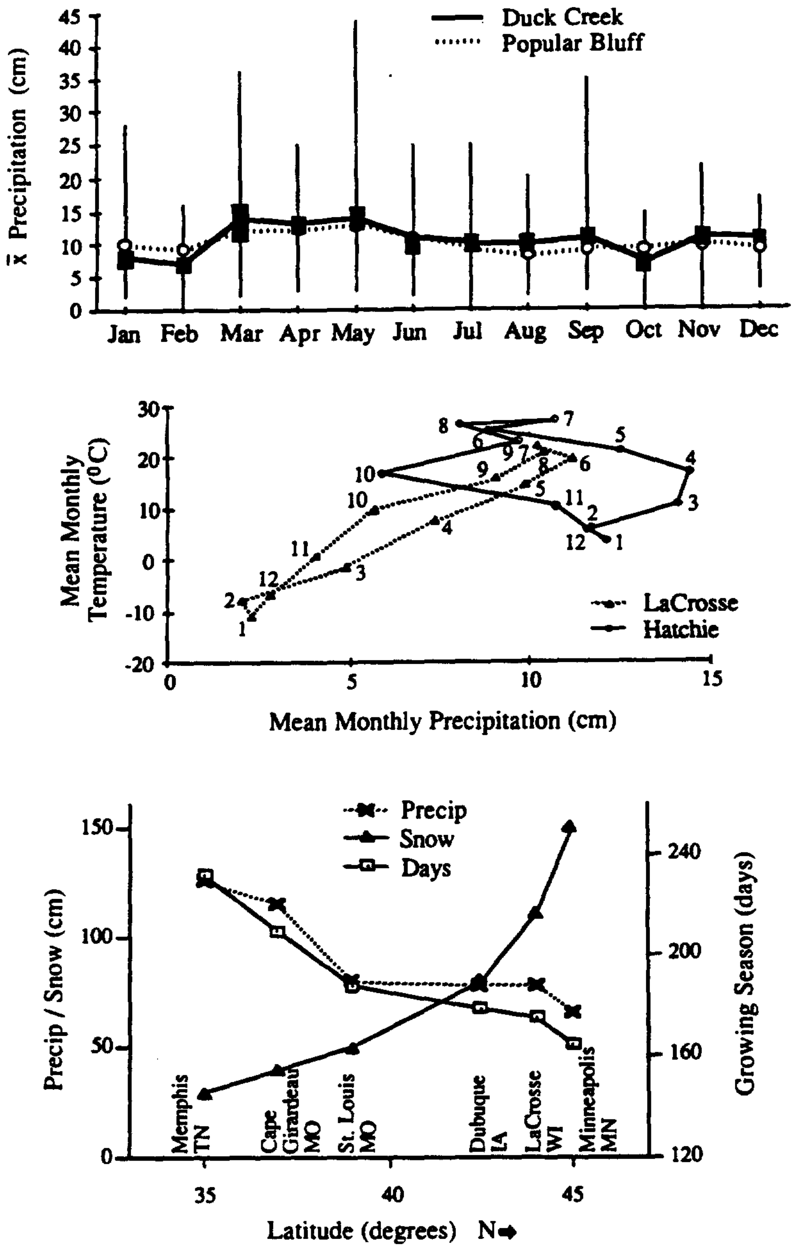

Fig. 3. Climatic patterns found in midwestern region of North America. (a) Variations in annual precipitation in southeastern Missouri (Duck Creek Wildlife Area 1960–78). Monthly ranges and averages of rainfall. (b) Climatographs for 2 wetlands (Hatchie National Wildlife Refuge, Tenn., and Upper Mississippi Fish and Wildlife Refuge, LaCrosse, Wisc.) in the Mississippi Flyway that represent conditions across 10° latitude. (c) Length of growing season and amount and form of precipitation across 10° latitude (35–45° N) in the Mississippi Flyway.

studies of 1 or 2 years duration lack continuity over longer time periods and provide only a "brief glance" at the complexities of wetland systems during a short segment of long-term wetland fluctuations or cycles.

This brief glance at wetland conditions often results in incorrect interpretation. Where the capability of intensive wetland management is possible, advice often centers on assuring water during the annual cycle. This practice frequently results in the maintenance of water levels at a set elevation. A more realistic strategy is to identify the wetland types required and to focus on the natural hydrologic regimes that make them productive. All natural basins have seasonal and long-term fluctuations in water levels. Fluctuations within and among seasons and years maintain the productivity as well as the structure and function of wetlands during the long-term cycle. In the real world of management biopolitics, decisions on maintaining dynamic fluctuations must be carefully balanced in order to maintain public support of management programs without habitat degradation. Public support of these more complex programs requires efforts to educate laymen with the basic facts of wetland management.

Managing Modified Wetland Systems

Southern Forested Wetlands

Rainfall in southeastern Missouri is highly variable among years and ranges from about 190 cm in the wettest years to only 64 cm in the driest years. Precipitation generally increases from fall into early winter and then is somewhat lower during mid-winter. There is a general tendency for heavy rainfall in April and May with lesser amounts between mid-July and September. The monthly range of precipitation clearly indicates that a major storm event can occur during any month of the year. Precipitation patterns in southeastern Missouri (Fig. 3*a*) result in 3 distinct flooding patterns that influence productivity and determine plant species composition at different sites along a flooding gradient. The gradual increase in precipitation each fall corresponds with a reduction in evapotranspiration caused by lower ambient temperatures and tree scenescence. Surface water begins to collect in small pools, a process called puddling (Heitmeyer et al. 1989). As these pools become larger, they gradually join to form even larger pools until the entire floodplain is inundated, a process termed backwater flooding. About every 6.5 years there is a major storm event when 25 cm or more of rain falls within a 24-hour period and the entire basin may be flooded in a matter of hours. This flash or headwater flooding carries and moves nutrients through the basin and often changes the drainage patterns of small intermittent and permanent streams. During severe flooding, channels of major rivers also change throughout the continuous mosaic of floodplain wetlands.

The area of southern hardwood forests in the Mississippi Alluvial Valley has been reduced from about 10 million ha to <2 million ha (Reinecke et al. 1989). Furthermore about half the remaining forested areas are between levees on major streams where flow velocities are high, water levels rise more quickly and remain higher longer, and depth of flooding is great. The integrity of the forest is further compromised because many tracts outside the levees are distributed as small islands in a vast sea of agriculture. Areas outside levees generally tend to be drier than normal because the depths, duration, and extent of flooding are less than under natural conditions.

These modifications in flooding regimes result in gradual changes in plant species composition. Areas surrounded by levees often exhibit a gradual shift in species composition to plant communities that are more water tolerant (Fredrickson 1979*a* and *b*, Klimas 1990). Trees such as pin oak (Quercus palustris) or nuttall oak (Q. *nuttallii*) are gradually replaced with more water tolerant forms such as overcup oak (Q. *lyrata*), bald cypress (*Taxodium distichum*), and water tupelo (*Nyssa aquatica*). In contrast, pin oak sites that become drier are more likely to be replaced by more xeric species such as hickories (*Carya* spp).

Changes in the vigor and condition of trees in greentree reservoirs are evident throughout the South. These changes likely are related to modifications in the timing, depth, and duration of flooding (Table 3). Normally greentree reservoirs are flooded rapidly in early to mid-fall to provide resources for waterfowl and opportunities to hunters. The timing of early flooding is very different from natural hydrological regimes (Figs. 3 and 4). Water levels in greentree reservoirs are normally held at full pool during the waterfowl hunting season. At the close of the duck season most greentree reservoirs are drained rapidly to protect the trees from flood damage or mortality. Thereafter water levels fluctuate with local precipitation. Tree mortality is common on sites within greentree reservoirs having deep flooding or poor drainage. Leaf chlorosis, branch-tip dieback, limited acorn production, and butt swelling are all indicative of stabilized water regimes among years and seasons (Black 1984). Furthermore stabilized flooding regimes influence nutrient cycling and invertebrate production (Wylie 1985, Batema 1987). The species composition and total biomass of invertebrates changes with the depth and duration of flooding (Batema et al. 1985, Magee 1989). As managed forests deteriorate, wildlife use also diminishes.

Table 3. Effects of development and intensive management practices in greentree reservoirs.

Development	General practice	Hydrological/ biological effects	Enhanced practice
Levees	Levees not on contours	—Wetter conditions inside levees —Shift in tree species dominance —Yields less area available for waterbird foraging —Increased beaver activity causing tree mortality	—Contour levees —Avoid overdevelopment of remnant forests —Beaver control
	Rapid early fall flooding for opening of duck season	—Earlier than natural flooding —Deeper flooding than in natural system —Repetitive flooding schedule among years —Modifies nutrient cycling	—Delay flooding until after senescence —Flood gradually —Vary time of flooding among years —Keep dry some years
	Maintain stable water levels	—Tree Damage a. Butt swelling b. Reduced acorn production c. Branch tip dieback d. Chlorosis of leaves —Reduced waterfowl use	—Replicate natural flooding regimes a. Change water levels throughout winter b. Never schedule the same depth or duration in consecutive years c. Avoid permanent inundation
	Rapid drawdown following duck season	—Export soluble nutrients —Remove potential for using macroinvertebrate resources —Severe ice damage to trees in some years	—Delay drawdown until spring migration begins —Use only slow drawdowns —Vary timing of drawdown among years
Water control structures	Screw gates	—Lack ability for precise control —Water level either at capacity or dry	—Replace with stoplog structures
Multiple impoundments	All units connected hydrologically	—Lack of independent water level control	—Develop header ditch and drainage system for independent control —Multiple intake and outlet structures

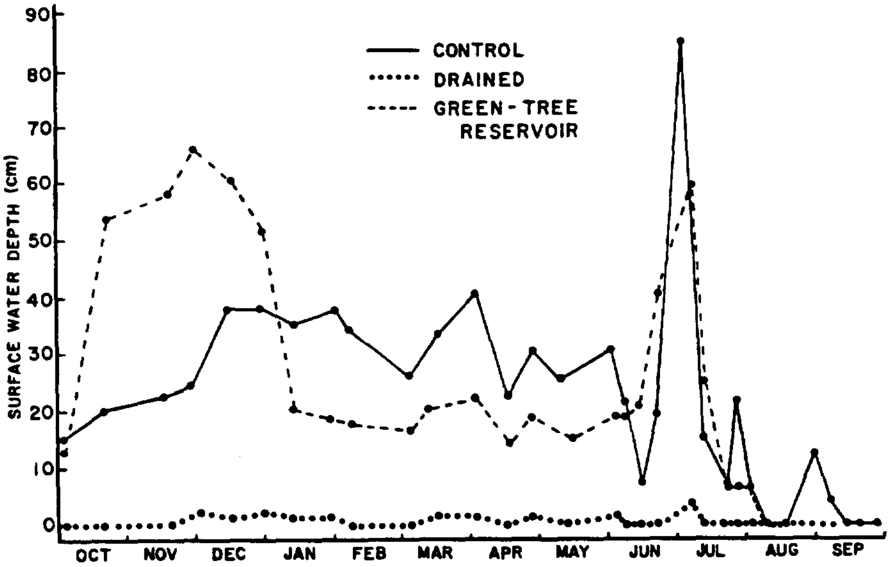

Fig. 4. Seasonal water depth in a greentree reservoir (Duck Creek Wildlife Area), a drained site, and a naturally flooded lowland hardwood forest (Mingo National Wildlife Refuge) in southeastern Missouri (after Fredrickson 1979*b*).

Moist-soil Impoundments

Moist-soil management is an increasingly common practice across the nation as managers attempt to grow native foods for wildlife in restored herbaceous wetlands. Although this management practice has been successful in many areas, the results of this intensive management are not free of adverse effects. Soil disturbance such as plowing or discing is a common moist-soil management practice to enhance the production of annual seeds. Such activities require relatively dry soil conditions that are usually associated with high ambient temperatures in summer. Soil manipulations under these conditions prevent seed germination, decrease organic matter, and facilitate conditions suitable for denitrification. If seed production is desired but drought conditions exist, seasonal irrigation is essential (Kelley 1986). Repetitive yearly management practices, including similar dates for flooding or drawdown, discing, or plowing result in a gradual decrease in the potential for food production (Fredrickson and Taylor 1982).

Table 4. Effects of development and intensive management practices on marsh systems.

Development	General practice	Hydrological/ biological effects	Enhanced practice
Levees	Steep-sided Not on contours Large units	—Burrowing animals cause damage —Flooding depths too deep or too shallow —Difficult to drain or flood	—Levee slopes of 4 to 1 or greater —Contour levees —Multiple units
Water control structures	Large expanse structures	—Flood important habitat for other waterfowl —Lack fine control of water levels	—Small structures with good water level features
	Screw gates	—Lack precise control —Water level at capacity or dry	—Replace with stoplog structures
	Maintain stable water level	—Monocultures develop	—Fluctuate water levels within and among years —Replicate natural fluctuations
Multiple impoundments	All units connected hydrologically	—Lack of independent water level control —Potential for drastically increasing soil salinities where evapotransportation is high	—Develop header ditch system for independent control —Multiple intake and outlet structures

Glacial Marshes

Some marshes in the prairie pothole region, the arid west, and throughout the East are man-made or man-modified wetlands with developments for intensive management. Unfortunately, many designs prevent managers from replicating natural hydrological regimes (Table 4). Water levels may be too high or are held constant. In other cases basins cannot be drained, and few systems are designed to permit subtle manipulations in water levels (as little as 1 cm) to which wetland plant and animal communities respond. In many cases expensive water delivery systems and control structures are detriments to good management. The most common effect of stabilized water regimes is the development of dense monocultures of robust emergent vegetation. These dense stands destroy the good cover-water interspersion characteristic of the productive hemi-marsh stage (Weller and Fredrickson 1974). Once monocultures are established in a basin with stabilized water regimes, disruptions of the dense stands are difficult.

Guidelines to Enhance Wetland Productivity

Water Control Structures

The most important design consideration in developing a wetland is a well conceived water control system. Effective management requires the capability to deliver and discharge water effectively, and to control water depth precisely. This is only possible when water control structures of the proper type and size are placed in the correct location. Many managers are placed at a great disadvantage if water control structures on their areas have been placed incorrectly, have become silt filled, or were the wrong types of structures for the site. In many cases dams simply establish a flow line and water depths are determined at the time of construction (Table 5). Radial gates are essential where high erratic flows pass through wetlands. Screw gates work well for water delivery, but they should never be installed as outlet structures because water levels are difficult to control. On smaller units (i.e., ≤100 ha) the least costly and most effective structure is a stoplog design. Stoplogs of various dimensions provide for a multitude of water level manipulations.

Replicate Natural Hydrological Regimes and Wetland Complexes

In general, water depths on most management areas are too deep because there are restrictions placed on proper manipulations by the physical

Table 5. Characteristics, costs and operational difficulties associated with different types of water control structures.

Structure	Characteristics	Cost	Operation/ management
Dam	Impounds water Floods habitat Changes downstream hydrology	High	Simple
Radial gate	Allows passage of high volume Difficult to control water level	High	Somewhat complex
Radial gate with stoplogs	Effective water level control	High	Complex
Screw gate	Either open or closed Poor for water level control	Moderate	Complex
Small stoplog structure	Effective water level control but volume of water moderate to low	Low	Simple

configuration or there is a misunderstanding of the desired water depths for most species. Of >150 bird species that use moist-soil impoundments in Missouri, only 23 regularly use water depths >25 cm and, of these, all but 7 generally use waters <25 cm (Fredrickson and Reid 1986). Another 43 species use water ≤25 cm and 26 species use water ≤5 cm. Manipulations that maximize resource availability should coincide with migrant arrival or certain life cycle events of resident species.

In most cases a single wetland cannot provide the resources to satisfy all life history requirements of a species. Thus, different wetland types in close juxtaposition are important to optimize wildlife response (Ryan and Renken 1987, Fredrickson and Heitmeyer 1988, Reid 1989). In the Mississippi Alluvial Valley, wood ducks and mallards tend to concentrate their activities within a 10–30-km radius (Delnicki and Reinecke 1986). In man-made complexes, 5–7 different impoundments allow for the implementation of a slightly different flooding and drawdown strategies that result in the production of diverse food resources (Fredrickson and Taylor 1982; Fredrickson and Reid 1986).

Soil Disturbance

Periodic soil disturbance must be used in systems lacking the dynamics of natural flooding to maintain early successional vegetation stages. Because man-made systems generally are stable, the availability of multiple impoundments allows timely rehabilitation of impoundments that have become unproductive without losing wildlife values for the entire area. Maximum use of time and management funds are possible when the timing and type of resources required by target wildlife are known. Such information provides the potential to convert resources of limited value to food and cover of high value. For example, impoundments covered with robust plants that do not produce seeds have limited value to most shorebirds. Discing of these plants in late summer initiates the decomposition process. If this plant litter and bare soil is flooded shallowly, invertebrate response is stimulated. The combination of shallow flooding and abundant invertebrates may attract large numbers of shorebirds and early migrant waterfowl. In addition, the soil disturbance and damp conditions result in germination and production of high quality green browse such as blunt spikerush (*Eleocharis obtusa*) (Kelley 1986). Most perennials decrease in abundance because of the discing while the response by seed producing annuals is usually great during the following growing season (Reid et al. 1989). Thus a manipulation during one growing season has the potential to provide benefits during future growing seasons. However, if the timing of discing is scheduled without consideration for the needs of shorebirds and fall migrating waterfowl that use browse, the opportunity to produce high quality habitats for insectivorous shorebirds and grazing waterfowl might be lost.

Fire

Man has influenced the dynamic nature of wetlands by suppressing fires for >50 years. Fire is an integral component of many natural wetland communities. The historical influence of fire on prairie and boreal forest habitats is obvious. Undoubtedly fire swept by southwesterly winds removed woody growth from prairie habitats, but forest remnants of burr oak (*Quercus macrocarpa*) exist to the north and east of large wetland complexes. Likewise in Alaska's interior boreal forests, fire scarred snags protrude from waterbodies and evidence of fire is abundant in zones of grasses and sedges surrounding many wetlands.

Fire can be an especially valuable tool at remote locations or where extensive physical developments are impractical or too expensive. The northern boreal forest is undoubtedly a system where fire management can play an important role, and its value as a tool in arid or high altitude environments is also great. Fire sets back succession and releases nutrients to promote vegetation growth. Timing and frequency of controlled burns should vary to encourage diverse plant communities.

Summary

Wetland managers should remember the following points when developing and implementing wetland management plans:

1. Emulate natural hydrology.
2. Use abiotic factors (water and fire) whenever possible to enhance management.
3. Rarely manipulate a unit the same way in consecutive years. Change the: a) time of flooding, b) depth of flooding, and c) duration of flooding.
4. Develop independent water delivery and discharge for each unit.
5. Deliver water to the system at the highest elevation.
6. Discharge water from the system at the lowest elevation.
7. Use stoplogs rather than screw gates as outlet structures.
8. Use contour levees.
9. Rarely flood the majority of a unit deeper than 25 cm (10 in).
10. Always match manipulations with biological events such as molt, migration, or reproduction.
11. Develop and manage wetlands as complexes or mosaics.
12. Control human disturbance.

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Use of Wetland Habitats by Birds in the National Petroleum Reserve - Alaska

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Use of Wetland Habitats by Birds in the National Petroleum Reserve—Alaska

by

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Abstract

Distribution, abundance, and use of wetland habitats by migratory birds were studied at two interior and three outer Arctic Coastal Plain sites in the National Petroleum Reserve in Alaska (NPR-A) in 1977 and 1978. Comparative data were collected in the same years from a Beaufort Sea coastal site near Prudhoe Bay.

Species composition of breeding birds varied between sites, especially between coastal areas and sites near foothills of the Brooks Range. Seasonal fluctuation in population densities were common with numbers greatest in June during breeding and August during migration. Population densities also differed between sites, perhaps due to variation in wetland composition and ratios of water cover to upland tundra.

Use of wetlands by loons, waterfowl, and shorebirds was quantified to assess relative values of seven classes of freshwater habitats. Wetlands with emergent *Arctophila fulva* were used most by these water birds. Breeding birds were especially dependent upon wetlands with emergent hydrophytes, although they used various types of wetlands during different activities and life stages. Most broods were found in wetlands with *A. fulva*, which afforded protective cover and substrate for aquatic invertebrates used as food by water birds. Wetlands and lakes without emergents were generally less attractive to breeding birds, but were especially important to molting geese.

Based on water bird distribution and densities and their dependence on Arctic Coastal Plain wetlands in NPR-A, petroleum exploration and production activities onshore and in the Beaufort and Chukchi seas may have significant adverse effects if not closely regulated and prohibited in some areas.

The 94,697-km^2 Naval Petroleum Reserve Number 4 in northern Alaska was established by Presidential declaration in 1923. Periodic oil and gas exploration sponsored by the U.S. Navy has occurred since about 1943. In 1976, management responsibility of the Reserve was transferred to the Department of the Interior and the area was renamed the National Petroleum Reserve in Alaska (NPR-A).

Much of the recent seismic testing and petroleum exploration in NPR-A has been in the Arctic Coastal Plain physiographic province (Payne et al. 1951), which has one of the largest and most stable collections of wetlands in North America (Wellein and Lumsden 1964). About one-half of NPR-A is within the Arctic Coastal Plain province of Alaska's North Slope. The dominant physical feature of this province is the extensive area of surface water in the form of wet meadows, ponds, lakes, and fluvial systems. Hussey and Michelson (1966) estimated that lake and marsh coverage on the Arctic Coastal Plain was 50%, or about 23,000 km^2, in NPR-A. These wetlands support large numbers of breeding and postbreeding loons, waterfowl, gulls, terns, and shorebirds. Interspersed upland tundra habitats are used by passerines, ptarmigan, and raptors.

Concern for these valuable wetlands and the avifauna that use them was expressed by Bartonek et al. (1971) and Brooks et al. (1971) when intensive onshore oil exploration and development were initiated in the Prudhoe Bay area of Alaska. King (1970) and Bergman et al. (1977) emphasized the importance of the Arctic Coastal Plain to waterfowl and shorebirds and recommended protection from oil development.

Bailey (1948) gave one of the earliest accounts of Arctic Coastal Plain birds. Gabrielson and Lincoln (1959), supplemented by Kessel and Gibson's (1978) update, provide the most complete records for the region. Pitelka (1974) summarized bird records for the Barrow area and coastal plain in northernmost NPR-A, and Kessel and Cade (1958) described the avifauna of the Colville River which bounds NPR-A to the east and to the south in the foothills. Maher (1959) presents one of the few reports from the foothills, at Kaolak River in western NPR-A, but studies to the east by Irving (1960) at Anaktuvuk Pass and by Sage (1974) in the Atigun and Sagavanirktok river valleys describe upland and riparian bird assemblages that extend through the foothills onto the coastal plain along drainages.

Bird communities near Prudhoe Bay on the eastern coastal plain have been studied by Norton et al. (1975) and Bergman et al. (1977). Schamel (1978) and Divoky (1978) described bird use of barrier islands in the Beaufort Sea near Prudhoe Bay and Johnson (1979) studied bird use of a Beaufort Sea lagoon. Salter et al. (1980) summarized distribution and abundance of Arctic Coastal Plain birds in northern Yukon and Northwest Territories in Canada.

Relatively little quantitative data are available on the use of various freshwater wetland habitats by birds on Alaska's Arctic Coastal Plain. Such information is essential if these species and their wetland habitats are to be protected with existing and new petroleum development in the Arctic. The present study was designed to (1) obtain data on distribution and abundance of water birds at selected locations in NPR-A, (2) determine the types of wetland habitat at selected sites and those used by breeding birds, and (3) provide recommendations for management of water bird habitats in relation to oil exploration and developemnt in NPR-A.

Study Areas

NPR-A sites studied in 1977 included Meade River delta, Singiluk, and East Long Lake. In 1978, field work was again conducted at East Long Lake and at Square Lake and Island Lake. Study sites were selected to represent the following major habitat types in NPR-A: (1) river delta (Meade River delta site), (2) large lake regime (Island Lake and East Long Lake sites), and (3) near-foothills (Singiluk and Square Lake sites). A sixth site, established in 1970 at Storkersen Point near the Prudhoe Bay oil fields (Bergman et al. 1977), was used in 1977 and 1978 to provide data representative of the eastern coastal plain.

All sites in NPR-A are 15.54 km^2 (3.22 x 4.83 km). Study areas were selected to include a diversity of wetland types; boundaries for each area followed section lines shown on topographic series maps published by the U.S. Geological Survey.

Conditions characteristic of all six study sites include continuous permafrost (Ferrians 1965), tundra vegetation (Britton 1957), cool summers (Wise et al. 1977), low regional and local relief (Sellman et al. 1975), poor drainage (Walker 1973), extensive wetlands, and ice-wedge polygons (Black and Barksdale 1949). All sites are in the unconsolidated Gubik Formation of Quaternary age (Black 1964) but surficial deposits vary considerably between sites.

The Meade River delta site (70° 48′N, 156° 22′W) is 55 km southeast of Barrow and 14.5 km upriver from Dease Inlet, at the head of the delta (Fig. 1). Relief is less than 10 m except in river-associated sand dunes. The site is floodplain and low terrace deposits of sand and silt grading into Eolian sand in the southern part of the area. Cool temperatures, easterly winds, and low humidity are the dominant summer climatological features in the delta (Wise et al. 1977).

Island Lake and East Long Lake study sites are in an area of large, NNW-SSE oriented lakes (Black and Barksdale 1949) near Teshekpuk Lake (Fig. 1), which is the largest on

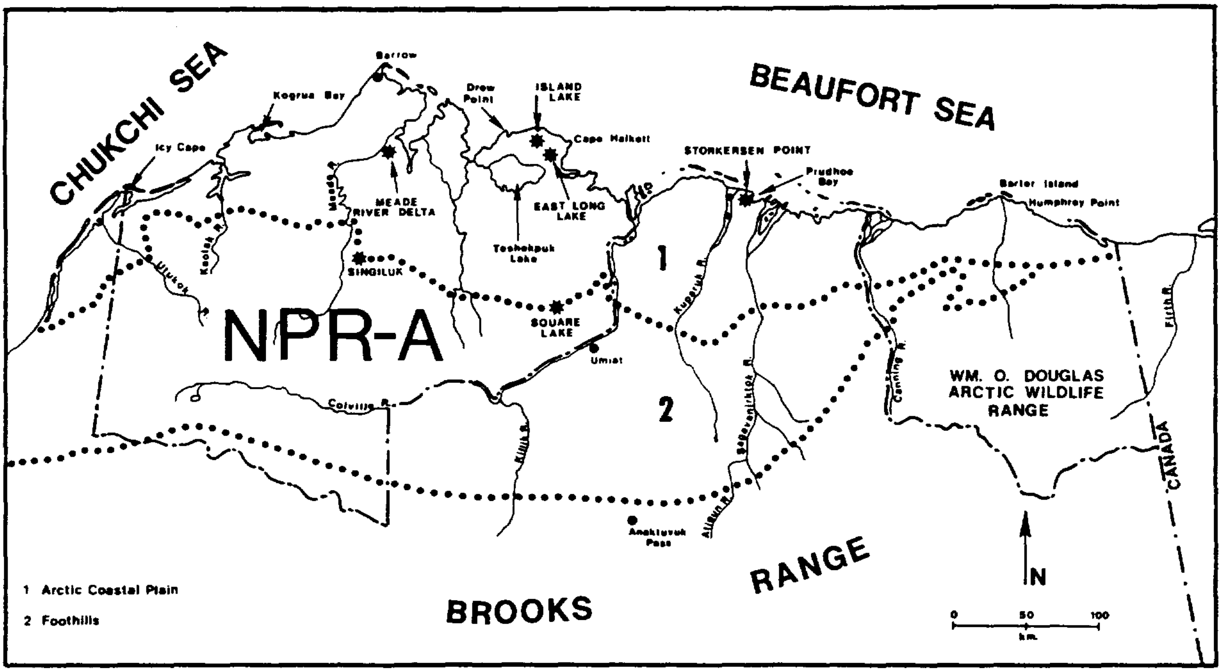

Fig. 1. Location of the five NPR-A and Storkersen Point study sites. Arctic Coastal Plain and Foothills provinces are identified.

the Arctic Coastal Plain. The Island Lake (70° 49'N, 153° 15'W) and East Long Lake (70° 39'N, 152° 43'W) study sites are 12.8 and 25.7 km south, respectively, of Lonely Distant Early Warning (DEW) site. This DEW site also was the location of the petroleum operations camp for NPR-A. Maximum elevation within the Island Lake study area is 6.7 m, although banks along larger lakes are up to 10 m in height. These two sites are located in areas of marine silt that contain fossil shells and bones of marine mammals. Maximum elevation at the East Long Lake site is 4.6 m along the banks of a small Beaded Stream. Island Lake had mean minimum and maximum ambient temperatures of -2.2° and 6.0°C, respectively, from 4 June to 13 August 1978. The mean minimum temperature at East Long Lake was 1.2°C and the average maximum was 10.3°C for the same time period. Extensive climatological data for this large lake area are found in Wise et al. (1977).

Singiluk (70° 05'N, 156° 20'W), 138 km south of Barrow, and Square Lake (69° 40'N, 153° 02'W), 47 km northwest of Umiat (Fig. 1), are in the interior of the Arctic Coastal Plain near foothills of the Brooks Range. These study areas are characterized by flat to gently rolling terrain with upland heath-tussock communities dominated by *Eriophorum* spp. (Britton 1957). Woody plants such as *Salix* spp. were more abundant, especially along streams, at these sites than at those farther north. Singiluk is at the southern margin of Eolian sand which forms a mantle over older marine deposits. The Square Lake site is in an area of upland silt which forms a boundary between the coastal plain and the Brooks Range foothills. Elevation is 22.9 to 30.5 m at Singiluk and from 91.4 to 121.9 m at Square Lake, and regional relief is greater at both sites than at the other study areas. Singiluk and Square Lake had warmer temperatures and less fog and wind than our sites nearer the Beaufort Sea. Wise et al. (1977) provided detailed climate data for Umiat, which are applicable to the Square Lake study site.

The Storkersen Point (70° 24'N, 148° 43'W) study site is on the Beaufort Sea coast between the Kuparuka and Sagavanirktok rivers, adjacent to the Prudhoe Bay oil field (Fig. 1). The area is characterized by small lakes, which are oriented with their long axis (generally NNW to SSE) perpendicular to prevailing winds (Sellman et al. 1975), and relief from sea level at coastal lagoons to 10 m a few km inland. For a more complete description of the study area and weather see Bergman et al. (1977).

Procedures

Wetland Classification and Composition

Ponds and lakes in the five NPR-A study sites were classified according to Bergman et al. (1977) who developed this system at the Storkersen Point study area near Prudhoe Bay. This system employs emergent vegetation, basin geomorphology, and water chemistry to define eight wetland categories. Flooded Tundra (Class I) includes shallow waters formed during spring thaw when melt water overflows stream basins or is trapped in vegetated tundra depressions (Fig. 2). Shallow-*Carex* (Class II) ponds have a gently sloping shore zone surrounded by and usually containing emergent *Carex aquatilis* with a central open water zone (Fig. 3). Shallow-*Arctophila* (Class III) wetlands have a central zone of emergent pendant grass (*Arctophila fulva*) and shoreward stands of *A. fulva* or *C. aquatilis* (Fig. 4). Deep-*Arctophila* (Class IV) wetlands are large ponds or lakes without emergents in the central zone and *A. fulva* near the shore (Fig. 5).

Deep-open (Class V) lakes have abrupt shores, sublittoral shelves, and a deep central zone (Fig. 6). Basin-complex (Class VI) wetlands are large, partially drained basins that may contain any of the other seven types. Because two of the NPR-A study areas (Island Lake and East Long Lake) were entirely within huge Basin-complex wetlands, we determined composition of all study areas on the basis of component wetlands within these basins. Beaded Streams (Class VII) are small fluvial systems composed of a series of pools linked by channels formed in ice-wedges (Fig. 7). Coastal Wetlands (Class VIII) are ponds or lagoons directly influenced by sea water (Fig. 8). See Bergman et al. (1977) for a more detailed description of these wetlands, and Table 1 for a comparison with the U.S. Fish and Wildlife Service national wetland classification system (Cowardin et al. 1979). All wetlands within the study areas were classified in the field and types were recorded on aerial photographs of 1:24,000 or 1:36,000 scale. Wetland area for each class was then determined by tracing the perimeter of individual wetlands on photos with an electronic planimeter.

Bird Surveys

Weekly censuses were conducted in the 15.54-km^2 study areas from June to mid-August in 1977 and 1978. Large birds including loons, waterfowl, hawks, owls, gulls, terns, and jaegers were counted in the 15.54-km^2 study areas. Shorebirds and passerines were recorded in five to seven subplots of 0.16 km^2 (0.2 x 0.8 km) located within the boundaries of study areas.

Large birds were counted by two or three observers walking abreast in four 0.80-km strips through the 15.54-km^2 (3.22 x 4.83 km) study area. Shorebirds and passerines were censused during single passes through the 0.16-km^2 plots. Age and sex of morphologically distinct species were recorded.

Additional observations were made during aerial surveys of the Colville River delta and groundwork on the west shores of Teshekpuk Lake (Fig. 1) in July 1976.

Use of Wetlands

Use of wetlands by water birds was recorded systematically during the weekly bird surveys at each of the 15.54-km^2 study sites in 1978. Differential use of wetland classes was

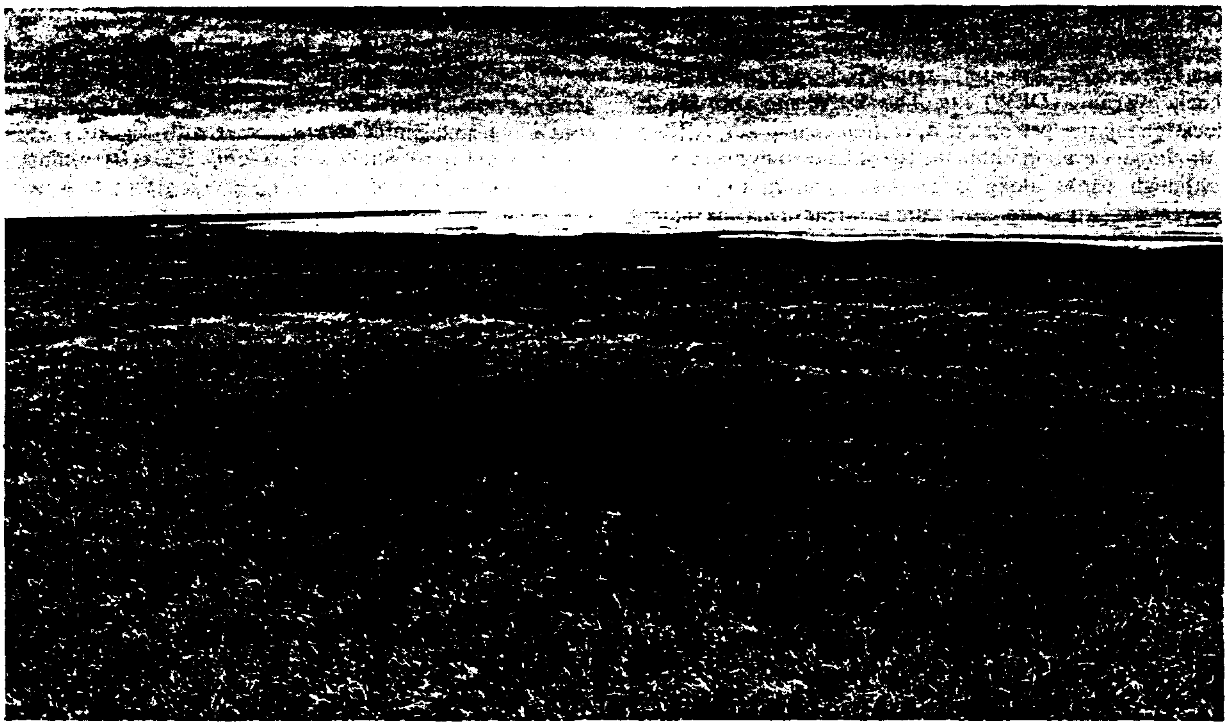

Fig. 2. Flooded tundra (Class I) in a shallow depression dominated by water-tolerant *Carex aquatilis*. Water seldom persists beyond June.

tested using chi-square contingency tables. The number of birds observed using wetlands on surveys was compared to the number of birds expected on those wetlands. Expected values were calculated by multiplying the total number of birds seen by the percent of the total surface area covered by each wetland class. Significant chi-square tables were further tested with analysis of cell residuals (Everitt 1977). For some species there were not sufficient sightings at each study area for statistical treatment.

Results

Wetland Composition

Wetland coverage in our NPR-A study areas ranged from 31.5% at Singiluk to over 85% at Island Lake (Table 2). All but one of the NPR-A study sites were dominated by the presence of Class I (Flooded Tundra) wetlands, which accounted for 43.0 to 63.3% of the total wetland areas

Table 1. *Comparison of nomenclature used in Arctic Coastal Plain and National Wetland classification systems. When Bergman et al. (1977) wetlands contain more than one category of the Cowardin et al. (1979) hierarchial system, components are shown in parentheses.*

	Cowardin et al. (1979)			
Class (Bergman et al. 1977)	System	Subsystem	Class	Subclass
Flooded Tundra (Class I)	Palustrine	None	Emergent wetland	Persistent
Shallow-*Carex* (Class II)	Palustrine	None	Emergent wetland	Persistent
			(Unconsolidated bottom)	(sand, organic)
Shallow-*Arctophila* (Class III)	Palustrine	None	Emergent wetland	Non-persistent
Deep-*Arctophila* (Class IV)	Palustrine	None	Emergent wetland	Non-persistent
	(Lacustrine)	(Limnetic littoral)	(Unconsolidated bottom)	(sand organic)
Deep-open (Class V)	Lacustrine	Limnetic	Unconsolidated bottom	Organic (sand)
Basin-complex (Class VI)	—[a]	—	—	—
Beaded Stream (Class VII)	Riverine	Lower Perrenial	Emergent wetland	Non-persistent
Coastal (Class VIII)	Estuarine	Intertidal	Emergent wetland	Persistent

[a] Class VI basins may contain the other seven wetland types of the Bergman et al. (1977) classification system. There is no equivalent unit in the Cowardin et al. (1979) classification system.

Fig. 3. Shallow-*Carex* (Class II) pond with open pools, emergent *Carex aquatilis*, and a low relief shoreline. Note the dry tundra in the foreground.

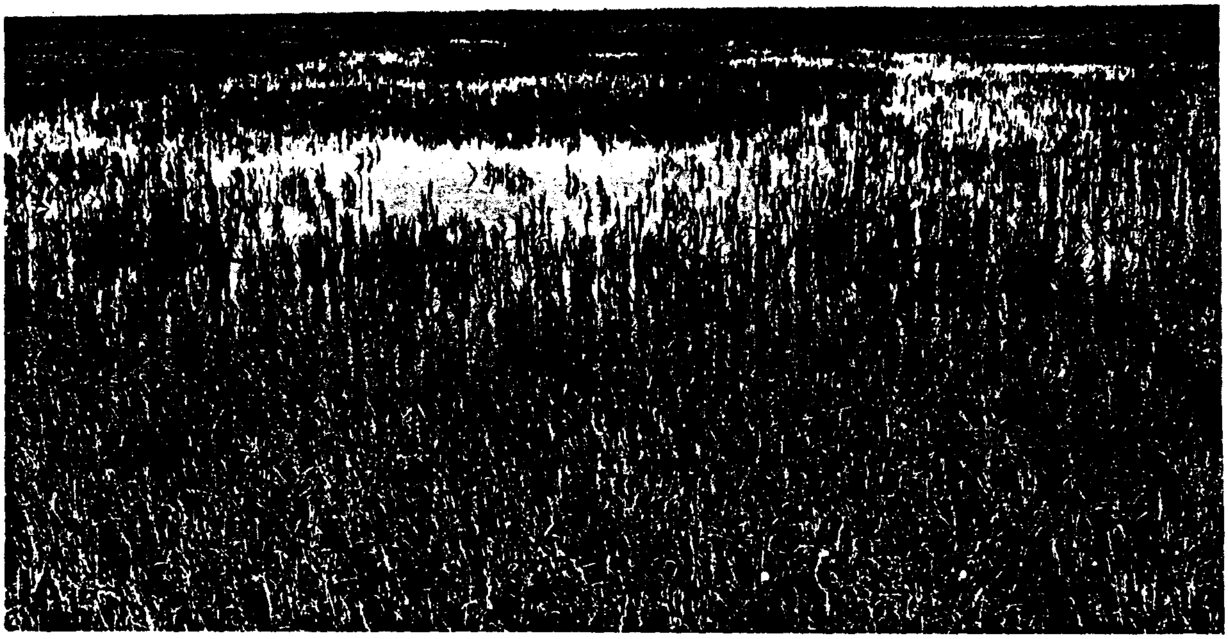

Fig. 4. Shallow-*Arctophila* (Class III) pond near East Long Lake containing central and shoreward stands of *Arctophila fulva*. (Photo by E. J. Taylor)

Fig. 5. Deep-*Arctophila* (Class IV) lake at the Square Lake study area. Note the sparse stand of *Arctophila fulva* in the foreground. The campsite is on the abrupt shore (7.6 m) in the background.

Fig. 6. Deep-open (Class V) lake near Cape Halkett. Water-filled polygons (Classes II and III wetlands) are in the foreground and smaller coalesced lakes in the upper left.

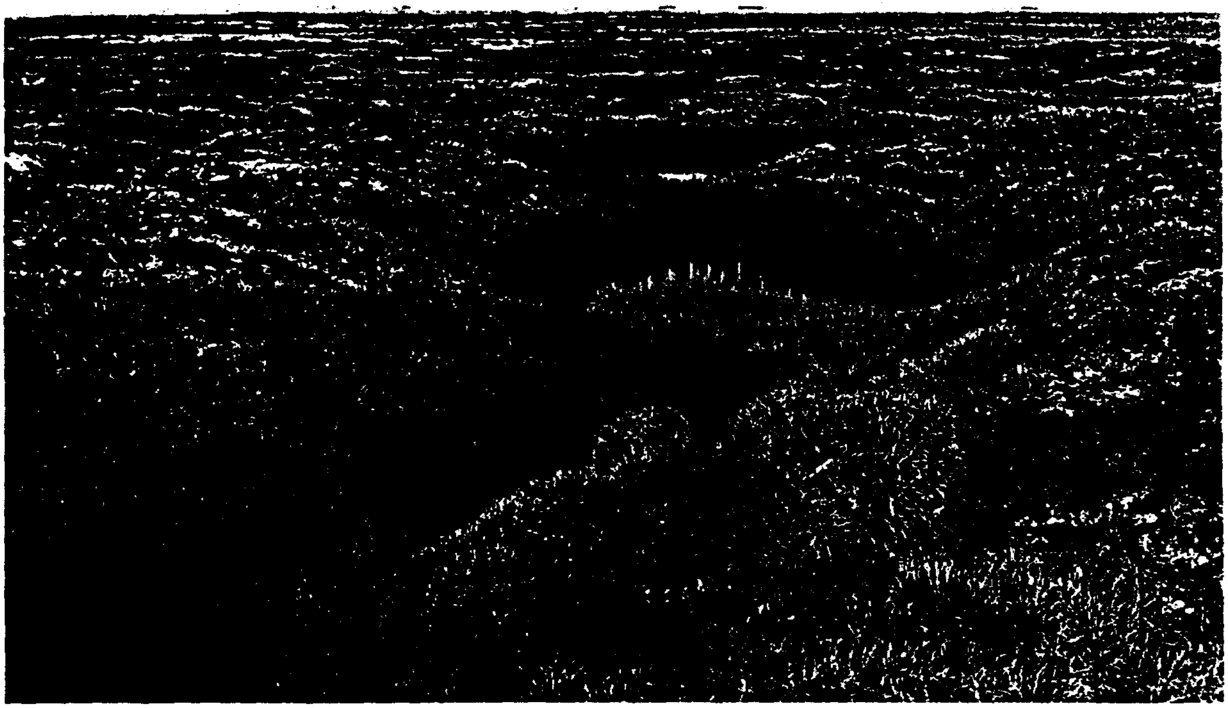

Fig. 7. Beaded Stream (Class VII) following ice-wedge troughs and intersections. Adjacent high center polygons are well drained, supporting lichens and shrubs.

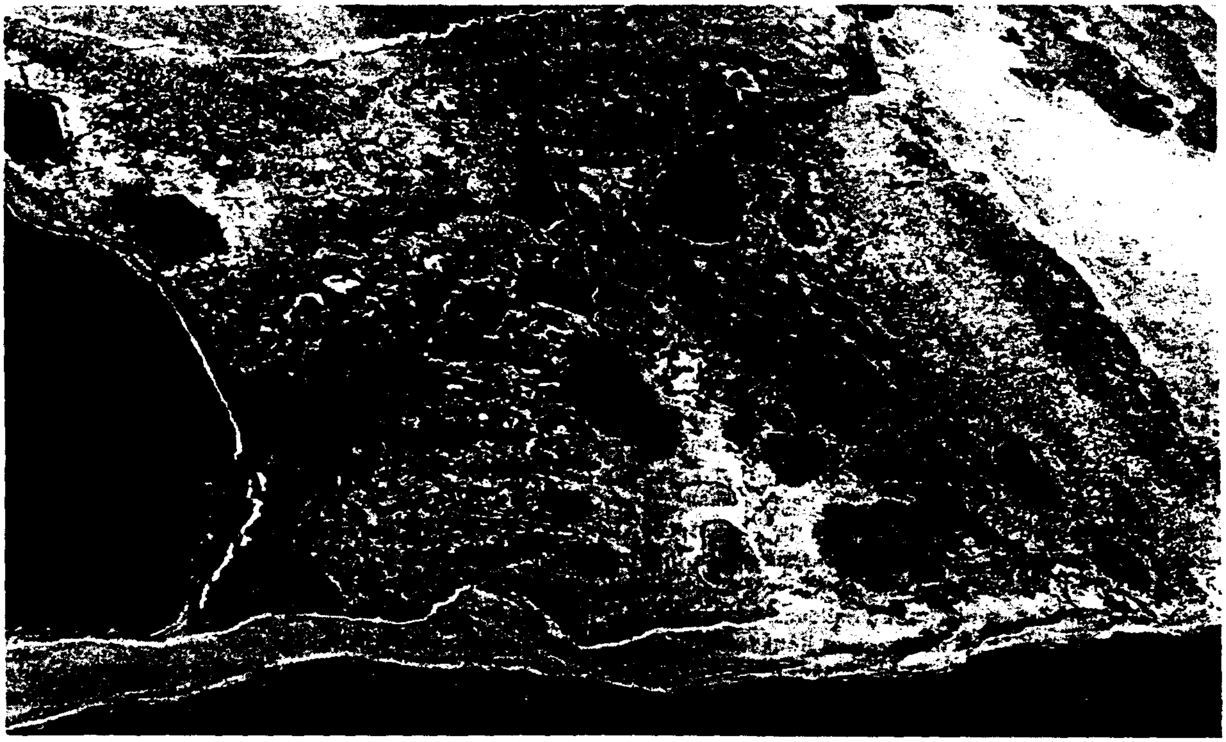

Fig. 8. Coastal wetlands (Class VIII) adjacent to the Beaufort Sea near Storkersen Point. Note driftwood line in upper portion of photo.

Table 2. *Percentage composition of wetland habitat at Arctic Coastal Plain study sites*[a].

Wetland class	East Long Lake	Island Lake	Meade River	Square Lake	Singiluk	Storkersen Point
I Flooded Tundra	48.1	63.3	51.3	43.0	46.6	51.2
II Shallow-*Carex*	16.2	14.5	15.7	7.1	2.1	32.4
III Shallow-*Arctophila*	6.1	7.9	1.4	1.4	0.5	4.5
IV Deep-*Arctophila*	4.7	0.8	1.7	48.4	45.5	2.9
V Deep-open	24.1	13.4	29.8	0.0	2.1	6.6
VII Beaded Stream	0.8	0.1	0.1	0.1	3.2	2.4
Wetland surface area (ha)	790.5	1,334.2	756.9	839.5	489.5	650.3
Percent of study site in wetlands	50.8	85.8	48.7	54.0	31.5	41.8

[a] Each study site was 15.54 km^2 (1,554.0 ha).

(Table 2). These meadows or polygonal complexes are most frequently found in the broad depressions of large Basin-complexes (Class VI). Class VIII wetlands were only present about 1 km north of the Storkersen Point study area and along other stretches of the Beaufort Sea coast.

Large Lake Regime

Wetland composition at Island Lake and East Long Lake was characterized by the presence of large, oriented Class V (Deep-open) lakes and huge drained or partially drained basins (Fig. 9). These basins may be discrete or, more often, a complex of overlapping basins of various ages. Hussey and Michelson (1966) mapped drained basins, according to age, in an area south of Barrow, Alaska, and suggested that basin formation is a result of the quantity and distribution of ground ice. Lakes at Island Lake and East Long Lake are among the largest on the Arctic Coastal Plain. Island Lake was 7.7 km long with a surface area of 1,720 ha and East Long Lake was 7.8 km long with a surface area of 1,951 ha.

Maximum water depths in Island Lake and East Long Lake were 1.5 and 2.0 m, respectively. Shorelines of these large lakes have been classified (Derksen et al. 1979*b*), and shoreline configuration and lake evolution have been discussed by Weller and Derksen (1979). About 70% of the Island Lake study area is within a large drained basin, which accounts for the high percentage of Class I wetlands (Table 2) at this site.

River Delta

The Meade River delta study site and surrounding area had numerous river channels, oxbows, shallow ponds, and larger lakes (Fig. 9). Second generation wetlands (Hussey and Michelson 1966) made up 50% of the area. Approximately 15% of the study area may have been influenced by the effects of thaw and drainage near the river. Wetland composition within the study area was similar to that of Island and East Long Lakes (Table 2). Class V (Deep-open) lakes were common, but basin size was considerably smaller than basin sizes at Island Lake and East Long Lake. Perched ponds (Walker and Harris 1976) and lakes breached by river channels (Walker 1978) were also prominent adjacent to the study area.

Near-Foothills

Lake density in the southern Arctic Coastal Plain near foothills of the Brooks Range is low compared to coastal tundra from Barrow to the Colville River delta (Sellman et al. 1975). These lakes do not exhibit orientation of the elongate axis (Black and Barksdale 1949; Fig. 9), although C. Sloan (personal communication) identified orientation of troughs within the shallower irregular basin from color infrared LANDSAT imagery. Nearly all large lakes in this region had beds of *Arctophila fulva* along littoral shelves (Fig. 5), resulting in the designation of few Deep-open lakes and high proportions of Deep-*Arctophila* (Class IV) wetland at Singiluk (45.5%) and Square Lake (48.4%). Lakes at these study sites were ice-free about 2 weeks earlier than those closer to the coast such as the Meade River delta.

Coastal

Bergman et al. (1977) described wetlands at Storkersen Point on the Beaufort Sea coast. Class II wetlands were abundant (210.6 ha) at this site compared to NPR-A sites (Table 2). A Beaded Stream bisected the study area and formed a delta northwest of the northern boundary of the area. Class V lakes were smaller than those in the large lake regime in NPR-A. Drained basins were present, but were not as large or numerous as those near Teshekpuk Lake.

Water Bird Populations and Habitat Use

The following water bird group accounts describe relative abundance between sites and variations over the breeding seasons, then provide habitat use patterns in relation to available wetland types.

Common Loon

All four species of loons are found on the Arctic Coastal Plain, with all but the common loon *(Gavia immer)* found nesting on our study sites. Common loons were not seen at our study sites in NPR-A, although one bird was observed near the Beaufort Sea coast at Storkersen Point on 26 July 1978 (Table 3). Bergman et al. (1977) also noted common loons along the coast near Storkersen Point in 1972 and

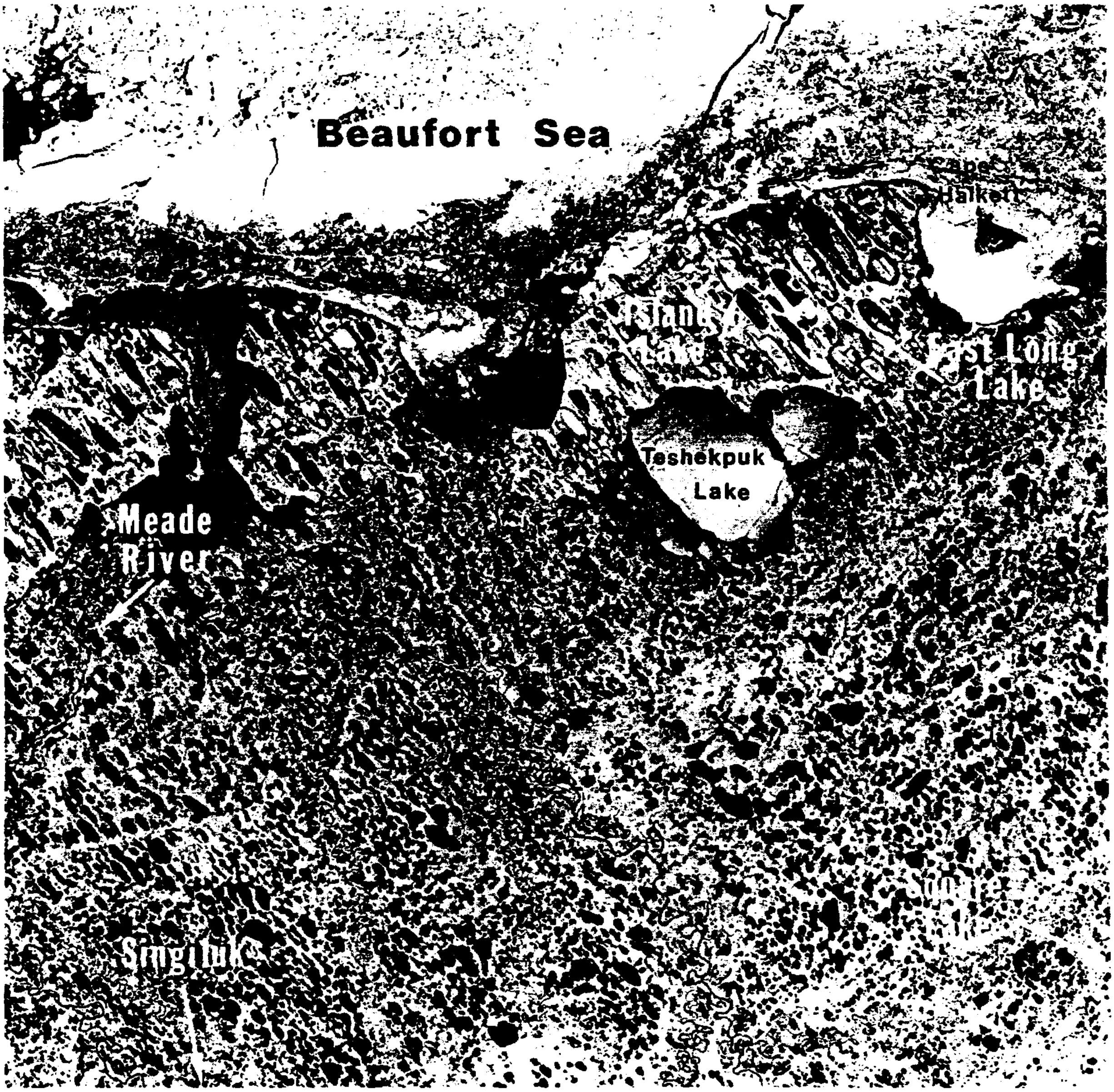

Fig. 9. LANDSAT image from 11 July 1977 showing location of NPR-A study sites. Note the pack ice in the Beaufort Sea and ice cakes on Teshekpuk Lake and large lakes southwest of Cape Halkett.

1975. No other records of this species are available for the Arctic Coastal Plain. Sage (1974) observed a pair of common loons on a lake in the foothills of the Brooks Range, although there was no indication of nesting.

Yellow-billed Loon

Yellow-billed loons *(Gavia adamsii)* were the least abundant of the three loons that breed on the Arctic Coastal Plain, and were recorded in surveys only at Square Lake ($\bar{x}$ density = $0.1/km^2$). A pair of yellow-billed loons and two chicks were seen on large lakes near the Singiluk study area in July 1977. Yellow-billed loons were seen regularly along the Meade River in July and August 1977, pairs were seen in both years at East long Lake, and one bird was seen near the Island Lake study area in 1978. Nests and broods were not found at Meade River, East Long Lake, or Storkersen Point. Sage (1971) found no evidence of yellow-billed loons on rivers or nearer than 110 km to the Arctic Ocean, but we discovered several nests on Class V lakes in the Colville River delta in 1976. Sjolander and Agren (1976) reported

Table 3. *Species composition, status[a], and mean seasonal densities (birds/km^2)[b] of birds observed at Arctic Coastal Plain study sites in 1977 and 1978[c].*

	Large Lake Regime					Delta		Near Foothills				Coastal		
	East Long Lake			Island Lake		Meade River		Singiluk		Square Lake		Storkersen Point		
	Status	1977	1978	Status	1978	Status	1977	Status	1977	Status	1978	Status	1977	1978
Common loon *(Gavia immer)*	—			—		—		—		—		CV		
Yellow-billed loon *(G. adamsii)*	CV			CV		CV		UB		UB	0.1	CV		
Arctic loon *(G. arctica)*	CB	1.5	1.2	CB	0.8	CB	2.1	UB	0.6	CB	1.5	CB	1.9	1.6
Red-throated loon *(G. stellata)*	CB	1.3	0.5	UB	0.1	UB	0.2	—		CV		CB	0.5	0.6
Whistling swan *(Olor columbianus)*	UB	0.2	0.2	RV		UB	0.2	RV		RV	0.2	UB	0.3	0.1
Canada goose *(Branta canadensis)*	RV	3.7	1.4	RV	6.6	—		CV		CV		UB	—	—
Black brant *(B. bernicla)*	CB	5.4	9.1	CB	9.6	CB	0.3	—		—		UB	0.3	0.7
White-fronted goose *(Anser albifrons)*	CB	1.1	1.0	CB	0.9	CB	0.7	CB	2.7	CB	0.8	CB	1.0	2.2
Lesser snow goose *(A. caerulescens)*	UB			RV		RV		CV		—		M		
Mallard *(Anas platyrhynchos)*	CV			—		CV		—		—		CV		
Pintail *(A. acuta)*	UB	17.1	6.5	RV	2.3	UB	5.1	CB	3.2	UB	1.1	RV	14.1	6.2
Green-winged teal *(A. crecca carolinensis)*	—		—			CV		—		UB		CV		
American wigeon *(A. americana)*	CV			CV		CV		CV		CV		CV		
Northern shoveler *(A. clypeata)*	CV	0.1	—	—		CV		CV		—		CV		
Greater scaup *(Aythya marila)*	CV			—		CV		UB	0.5	CB	0.8	CV		
Common eider *(Somateria mollissima)*	M			CV		—		—		—		RV		
King eider *(S. spectabilis)*	CV	—	0.3	CV	0.3	CV	0.1	UB	0.2	CB	0.2.	CB	2.4	1.9
Spectacled eider *(S. fischeri)*	CB	0.6	0.5	CB	0.1	CB	0.3	CV		—		UB	0.2	0.2
Steller's eider *(Polysticta stelleri)*	—			—		—		CV		—		—		
Oldsquaw *(Clangula hyemalis)*	CB	3.2	3.3	CB	2.3	CB	1.1	CB	3.5	CB	4.6	CB	2.3	1.8
White-winged scoter *(Melanitta deglandi)*	—									CB	1.0			
Surf scoter *(M. perspicillata)*	CV			—		—				CV		CV		
Red-breasted merganser *(Mergus serrator)*	—			—						CV		CV		
Marsh hawk *(Circus cyaneus)*	—			—		—		—		—		CV		
Rough-legged hawk *(Buteo lagopus)*	CV			—		—				CV				
Golden eagle *(Aquila chrysaetos)*	—					CV				CV		CV		
Gyrfalcon *(Falco rusticolus)*	—			—		—		—		CV		—		
Peregrine falcon *(F. peregrinus)*	CV			—		—		—		CV		CV		

Table 3. Continued.

	Large Lake Regime					Delta		Near Foothills				Coastal		
	East Long Lake			Island Lake		Meade River		Singiluk		Square Lake		Storkersen Point		
	Status	1977	1978	Status	1978	Status	1977	Status	1977	Status	1978	Status	1977	1978
Willow ptarmigan *(Lagopus lagopus)*	UB			—		UB	0.1	CB	1.1	CB	3.8	UB		
Rock ptarmigan *(L. mutus)*	—			—		—		—		RV	0.1	CV	0.1	—
Sandhill crane *(Grus canadensis)*	—			CV		CV		—		CV		CV		
American golden plover *(Pluvialis dominica)*	CB	3.5	1.6	CB	0.6	UB		UB	1.3	CB	4.1	CB	5.4	4.7
Black-bellied plover *(P. squatarola)*	CB	4.4	1.1	CB	1.7	UB	6.3	UB	3.2	CB	2.8	CB	1.9	1.9
Semipalmated plover *(Charadrius semipalmatus)*	—			—		—		—		CV		CV		
Whimbrel *(Numenius phaeopus)*	—			—		—		—		CV		CV		
Bar-tailed godwit *(Limosa lapponica)*	CV	—	0.1	—		—		UB	11.2	RV	1.2	CV		
Buff-breasted sandpiper *(Tryngites subruficollis)*	UB			CV		—		—		UB	0.3	CB	0.6	3.7
Stilt sandpiper *(Micropalama himantopus)*	CV			CV		—		—		CB	3.3	RV		
Long-billed dowitcher *(Limnodromus scolopaceus)*	UB	4.0	1.5	CV	0.4	UB	3.7	CV		UB	5.8	RV	1.2	0.8
Ruddy turnstone *(Arenaria interpres)*	UB	—	0.2	UB	0.3	UB	0.2	—		—		UB	1.1	2.4
Pectoral sandpiper *(Calidris melanotos)*	CB	36.3	18.5	CB	13.0	CB	22.9	CB	24.1	CB	11.6	CB	24.3	20.1
Red knot *(C. canutus)*	—		—			—		—		—		CV		
Dunlin *(C. alpina)*	CB	12.8	16.0	CB	12.8	CB	21.1	UB	0.5	CV	0.2	CB	15.5	15.7
Sanderling *(C. alba)*	—			—		—		—		—		CV		
White-rumped sandpiper *(C. fuscicollis)*	—			—		—		CV		—		CV		
Baird's sandpiper *(C. bairdii)*	RV	0.1	—	—		—		—		—		UB	0.9	2.8
Least sandpiper *(C. minutilla)*	—			—		—		CV						
Semipalmated sandpiper *(C. pusilla)*	CB	6.3	3.1	CB	1.4	CB	7.0	CB	6.9	CB	15.5	CB	11.6	17.2
Western sandpiper *(C. mauri)*	—			—		—		—		CV	0.1	CV		
Red phalarope *(Phalaropus fulicarius)*	CB	32.5	25.7	CB	13.7	CB	20.6	UB	4.0	RV	0.3	CB	26.5	26.4
Northern phalarope *(P. lobatus)*	CB	13.3	9.8	RV	1.0	RV	4.2	CB	9.7	CB	16.8	UB	1.6	3.6
Common snipe *(Gallinago gallinago)*	—			—		—		—		RV	0.3	—		
Parasitic jaeger *(Stercorarius parasiticus)*	UB	0.4	0.4	UB	0.4	UB	0.4	UB	0.3	UB	0.4	UB	0.5	0.5
Pomarine jaeger *(S. pomarinus)*	M			M	0.1	M	0.2	CV		M	0.1	M		
Long-tailed jaeger *(S. longicaudus)*	RV	0.2	0.1	RV		UB	0.2	UB	0.4	UB	0.3	RV	0.2	0.1
Glaucous gull *(Larus hyperboreus)*	UB	0.7	0.4	UB	1.4	UB	1.1	CV		UB	0.3	UB	0.6	0.5

Table 3. Continued.

	Large Lake Regime					Delta		Near Foothills				Coastal		
	East Long Lake			Island Lake		Meade River		Singiluk		Square Lake		Storkersen Point		
	Status	1977	1978	Status	1978	Status	1977	Status	1977	Status	1978	Status	1977	1978
Bonaparte's gull *(L. philadelphia)*	—			—		—		CV		—		CV		
Sabine's gull *(Xema sabini)*	UB	0.3	0.3	RV		CB	0.7	CV		CV		CV		
Arctic tern *(Sterna paradisea)*	UB	0.8	0.5	RV	0.1	UB	0.7	UB	0.9	UB	1.3	RV		
Short-eared owl *(Asio flammeus)*	CV			CV		CV		CV		UB		CV		
Snowy owl *(Nyctea scandiaca)*	RV			CV	0.1	CV		CV		CV		RV		
Say's Phoebe *(Sayornis saya)*	—			—		—		—		—		CV		
Horned lark *(Eremophila alpestris)*	—			—		—		—		—		CV		
Barn swallow *(Hirundo rustica)*	—			—		—		—		—		CV		
Common raven *(Corvus corax)*	—			—		—		CV		RV		CV		
Bluethroat *(Luscinia svecica)*	—			—		—		—		CV		—		
Ruby crowned kinglet *(Regulus calendula)*	—		—			—		CV		—		—		
Yellow wagtail *(Motacilla flava)*	—			—		—		UB	0.8	UB	0.4	—		
Rusty blackbird *(Euphagus carolinus)*	—			—		—		—		CV		—		
Redpoll *(Carduelis sp.)*	—			—		CV	0.3	UB	0.1	CB	1.5	UB		
Savannah sparrow *(Passerculus sandwichensis)*	CV			—		CV		UB	12.0	UB	2.7	—		
Tree sparrow *(Spizella arborea)*				—				—		CV	0.4	—		
Lapland longspur *(Calcarius lapponicus)*	CB	64.2	47.6	CB	24.3	CB	24.1	CB	42.3	CB	42.5	CB	20.4	36.7
Snow bunting *(Plectrophenax nivalis)*	CV			CV		CV		—		—		UB	0.6	1.1
Species Breeding	25			16		23		23		27		25		
Species Total	45			36		40		41		53		62		

[a] Status: CB = Common Breeder; UB = Uncommon Breeder; M = Migrant; RV = Regular summer visitor; CV = Casual or accidental visitor; = Not present.

[b] Means were determined from weekly surveys, June through August.

[c] Meade River and Singiluk sites were studied in 1977, East Long Lake and Storkersen Point in 1977 and 1978, and Island Lake and Square Lake in 1978.

that only one yellow-billed loon pair nested on each lake in an area 80 km southeast of Barrow. By comparison, several pairs of arctic *(Gavia arctica)* and red-throated *(Gavia stellata)* loons nested in single basins at Storkersen Point (Bergman and Derksen 1977) as well as our NPR-A sites (this study). It appears that breeding densities of yellow-billed loons are lower because they defend larger territories than either arctic or red-throated loons.

Little information is available on habitats used by yellow-billed loons. Sage (1971) found a breeding pair on a lake that had dense stands of emergent *Arctophila fulva* and a pair on a lake with no emergents. All of our observations of this species were on Class V (Deep-open) lakes or on large flowing bodies of water such as the Meade River. An open moat around a large ice cake in Teshekpuk Lake was used by yellow-billed loons for feeding in mid-July 1976.

Arctic Loon

Bailey (1948), Gabrielson and Lincoln (1959), Palmer (1962), and Pitelka (1974) identified the arctic loon as a common species nesting on the Arctic Slope. Our weekly surveys showed that arctic loons were the most abundant loon at all study sites in 1977 and 1978, and it was considered a common breeder. Mean seasonal densities ranged from 0.6/km^2 at Singiluk to 2.1/km^2 at Meade River (Table 3), which was comparable to the range of densities at Storkersen Point (Bergman et al. 1977). Petersen (1979) found much higher (9.6/km^2) densities of breeding arctic loons on the Yukon-Kuskokwim River Delta, Alaska, on the Bering Sea where milder climate and longer summers are more attractive to nesting birds. Arctic loons are also found on the upper and middle Colville River (Kessel and Cade 1958) and much farther inland along the upper Kaolak River (Maher 1959) and Sagavanirktok River (Sage 1974) valleys in the Brooks Range foothills.

Wetlands that contained *Arctophila fulva* (Classes III, IV, and VII) were preferred habitats for arctic loons (Table 4). Bergman and Derksen (1977) found 66% of all arctic loon nests in Deep-*Arctophila* (Class IV) wetlands. Class IV wetlands are relatively shallow and ice-free earlier and used significantly ($P<0.01$) more than Class V (Deep-open) lakes in June (Table 4). However, nesting (July) and post-nesting (August) use of Class V lakes was significant ($P<0.05$) at all sites. Differential use of Beaded Streams (Class VII) by arctic loons between sites (Table 4) may be due to the presence of *Arctophila fulva* in individual pools (beads), which would provide protective cover and a greater abundance and diversity of invertebrates (Bergman et al. 1977). Arctic loons did not use Class I (Flooded Tundra) wetlands, nor did they show preference for Class II (Shallow-*Carex*) wetlands except at Square Lake where values were highly significant ($P < 0.01$) for all months (Table 4). Flooded Tundra and small Shallow-*Carex* wetlands were avoided apparently because of the lengthy distance of open water required for takeoff and landing. Brood habitat included Classess II, III, and IV wetlands and Deep-open lakes (Table 5).

Table 4. *Seasonal habitat selection*[a] *by arctic loons at four sites on the Arctic Coastal Plain in 1978.*

Study site and month	Wetland class I	II	III	IV	V	VII
East Long Lake (X^2 = 638.83, n = 111)						
June	- 9.02	+ 2.11	+ 4.00	+15.08	- 1.70	+ 3.45
July	- 7.76	- 1.94	+ 9.45	+18.65	- 3.62	- 0.72
August	- 4.90	+ 0.39	+ 0.73	+14.90	- 2.30	- 0.46
Island Lake (X^2 = 858.50, n = 69)						
June	- 5.01	- 1.57	- 1.12	+24.61	+ 3.16	- 0.12
July	-11.73	- 3.68	- 2.62	+ 4.62	+21.29	- 0.28
August	- 6.97	- 2.19	- 1.55	+ 2.50	+12.71	- 0.17
Storkersen Point (X^2 = 1,211.90, n = 120)						
June	-10.15	- 5.68	+ 4.05	+35.47	+ 1.80	+ 3.24
July	- 8.85	- 5.18	- 1.88	+15.29	+16.61	+ 3.55
August	- 5.02	- 1.30	- 1.06	+10.83	+ 6.59	- 0.77
Square Lake (X^2 = 417.11, n = 174)						
June	- 5.50	+ 8.18	- 0.90	+ 0.42	—[b]	+16.44
July	- 7.48	+ 4.07	- 1.03	+ 5.25	--	+ 4.97
August	-10.45	+ 9.72	- 1.43	+ 5.72	-	- 0.38

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, - = avoidance. Critical values are 1.96 ($P < 0.005$), 2.58 ($P < 0.01$).

[b] No Class V wetlands present.

Table 5. *Number of broods on Arctic Coastal Plain wetlands at Meade River, East Long Lake, Island Lake, Singiluk, Square Lake, and Storkersen Point in 1977 and 1978.*

Species	Wetland class I	II	III	IV	V	VII	River	Totals
Yellow-billed loon	0	0	0	1	0	0	0	1
Arctic loon	0	13	6	20	5	0	0	44
Red-throated loon	0	3	5	2	0	0	1	11
Whistling swan	0	0	0	1	2	4	0	7
Snow goose	0	0	0	0	0	1	0	1
White-fronted goose	0	2	0	8	8	14	1	33
Black brant	0	4	0	0	16	5	0	25
Oldsquaw	0	7	2	16	9	2	0	36
Pintail	0	4	0	12	0	1	0	17
Spectacled eider	0	10	1	2	4	0	1	18
King eider	0	2	0	7	0	0	0	9
Greater scaup	0	0	0	9	1	0	0	10
White-winged scoter	0	0	0	6	0	0	0	6
Totals	0	45	14	84	45	27	3	218

Red-throated Loon

Red-throated loons occurred in much lower densities than arctic loons and were not recorded during surveys at the two sites near the Brooks Range foothills (Table 3). However, they were found in small numbers on lakes near the Square Lake study area. The highest mean seasonal red-throated loon densities were at East Long Lake in 1977 (1.3/km^2). Davis (1972) found that distance to the coast of Hudson Bay was an important factor influencing the distribution of red-throated loons because they fed their young with fish gathered from the sea. Bergman and Derksen (1977) noted similar behavior at Storkersen Point where red-throated loons flew from nest ponds to the Beaufort Sea to capture fish for their young. Further inland, in large lakes near East Long Lake, red-throated loons were observed capturing whitefish (*Coregonus* sp.), which they took to adjacent nest ponds. It is apparent that reliance on fish limits the distribution of red-throated loons to coastal areas and where freshwater fishes are available.

Red-throated loons used Class III (Shallow-*Arctophila*) wetlands during all months at East Long Lake ($P < 0.01$), and during June and July at Storkersen Point (Table 6). Loons also used Class IV (Deep-*Arctophila*) wetlands during June and August ($P<0.01$) at Storkersen Point. Red-throated loons fed in pools of Beaded Streams (Class VII) that contained stands of *Arctophila fulva* throughout the summer at East Long Lake. Much of the Beaded Stream at Storkersen Point was either too deep or swift to support *Arctophila fulva*, which may account for the relative lack of use by red-throated loons (Table 6).

Table 6. *Seasonal habitat selection*[a] *by red-throated loons at two sites on the Arctic Coastal Plain in 1979.*

Study site and month	Wetland class I	II	III	IV	V	VII
East Long Lake (X^2 = 485.59, n = 60)						
June	- 4.31	+ 2.08	+10.07	- 0.99	- 2.52	+ 2.95
July	- 5.88	0.52	+12.87	+ 1.15	- 2.82	+11.37
August	- 5.67	+ 1.04	+ 9.69	- 0.04	- 2.70	+14.51
Storkersen Point (X^2 = 539.73, n = 48)						
June	8.40	3.80	+27.88	+ 5.56	2.18	1.29
July	4.78	1.24	+15.51	0.81	- 1.24	+ 1.30
August	- 2.42	+ 1.39	- 0.51	+ 5.22	- 0.63	- 0.37

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, - = avoidance. Critical values are 1.96 ($P < 0.05$), 2.58 ($P < 0.01$).

Whistling Swan

King (1970) estimated 800 whistling swans (*Olor columbianus*) on Alaska's Arctic Slope. This population winters in Chesapeake Bay (Sladen 1973) and represents about 1.3% of a 14-year mean of 62,000 that breed in Alaska (King 1973).

Aerial surveys in NPR-A revealed highest whistling swan densities southeast of Teshekpuk Lake and east to the Colville River (R. King, personal communication). We observed swans at all of our Arctic Coastal Plain study sites (Table 3), but breeding pairs were recorded only at East Long Lake and Meade River. Broods of two, three, and four cygnets were observed at these two sites. King (1970) determined a mean brood size of 2.2 cygnets per pair for the Arctic Coastal Plain, which is lower than 3.57 cygnets per pair reported for Yukon River delta whistling swans. Lensink (1973) attributed high productivity in the delta to the more favorable climate there.

King and Hodges (1981) tested 10 independent variables for correlation with whistling swan density in the Yukon-Kuskokwim River Delta, Alaska. They found significant correlations between the number of swans counted in air surveys and linear miles of lake shoreline, number of lakes, and number of small islands, which they concluded were the most important features to breeding birds. Small sample sizes made it impossible to test our observations with chi-square analysis. Therefore, we evaluated habitat preference based on frequency of occurrence of sightings combined from four study areas (Table 7) in 1978. Swans used Deep-*Arctophila* wetlands almost exclusively in June and July. They were observed feeding on *Arctophila fulva*, which may be a key species in their summer diet. These larger wetlands also provide ample space to take flight. Swans also were seen on Deep-open lakes and on the Meade River during molt, and a family group of seven was observed on the Beaufort Sea near Prudhoe Bay. At Meade River groups of 2 to 37 nonbreeders fed and loafed on river bars and partially drained basins breached by the river. Small groups of swans completed the wing molt at several study sites.

Table 7. *Percent frequency of occurrence*[a] *of whistling swans by wetland class at Storkersen Point, Square Lake, East Long Lake, and Island Lake in 1978.*

Month	Wetland class I	II	III	IV	V	VII	VIII	N
June	0	0	0	90.6	4.7	4.7	0	43
July	0	0	0	54.9	35.3	0	9.8	51
August	0	0	0	79.3	20.7	0	0	29

[a] Includes observations from weekly surveys and sightings made during other fieldwork.

Canada Geese

Canada geese (*Branta canadensis*) were observed at all study sites except Meade River (Table 3). There was no evidence of breeding at any of the NPR-A sites and no broods were observed during extensive aerial surveys of a 2,000-km^2 area of large lakes northeast of Teshekpuk Lake from 1976 through 1979 (J. King, personal communication). No Canada goose broods were seen during July, August, and September 1977 and 1978 air surveys that covered 95,044-km^2 of NPR-A (R. King, personal communication).

Canada geese breed on the Arctic Coastal Plain and barrier islands near Prudhoe Bay (Gavin 1975, 1979). One nest was found on the Storkersen Point study area in 1978, which is the first record from that site in 8 years (Bergman et al. 1977; this study). Kessel and Cade (1958) found 200-300 pairs of breeding Canada geese in the Arctic Foothills province along bluffs and steep talus slopes of the Colville River above Umiat (Fig. 1).

King (1970) estimated 15,000 molting Canada geese along the Beaufort Sea coast from Smith Bay to the Canning River (Fig. 1) and suggested that most of these birds were nonbreeders from interior Alaska south of the Brooks Range. King and Hodges (1979) summarized air survey results from 1957-78 for a 2,000-km^2 area northeast of Teshekpuk Lake. They determined that this unique area supported up to 50,000 molting geese of four species. Derksen et al. (1979*b*) evaluated the distribution of Canada geese in this large lake area and found most to be inland west of Cape Halkett (Fig. 1) during the flightless period.

Nonbreeding Canada geese first arrived at East Long Lake and Island Lake on 10 and 11 June, respectively. Peak buildup of Canada geese at these two sites was in mid-July. Derksen et al. (1979*b*) showed that molting Canada geese preferred Deep-open (Class V) lakes at East Long Lake and Island Lake. Birds capable of flight fed in upland sites and occasionally in Classes I and II wetlands in early June, but as flight feathers were lost in July they shifted to large Class V lakes (Table 8) where open water afforded safety from predators and adjacent shorelines provided ample food (Derksen et al. 1979*b*).

Table 8. *Seasonal habitat selection*[a] *by Canada geese at two sites in NPR-A in 1978.*

Study site and month	Wetland class I	 II	 III	 IV	 V	 VII
East Long Lake (χ^2 = 545.24, n = 320)						
June	- 5.83	+13.95	- 3.35	- 2.92	- 2.19	+ 1.45
July	-15.22	- 7.48	- 5.04	- 4.39	+29.05	+ 0.75
August	- 1.27	- 2.62	- 1.52	- 1.32	+ 5.35	- 0.54
Island Lake (χ^2 = 686.18, n = 230)						
June	- 3.85	- 2.08	- 1.48	- 0.45	- 1.99	- 0.16
July	-20.13	-11.14	- 7.92	- 2.43	+46.99	- 0.86
August	- 6.03	- 2.51	- 1.79	- 0.55	+12.70	- 0.19

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, - = avoidance. Critical values are 1.96 ($P < 0.05$), 2.58 ($P < 0.01$).

Black Brant

Gabrielson and Lincoln (1959) considered black brant (*Branta bernicla nigricans*) common nesters on the Alaskan Arctic coast from Point Hope on the Chukchi Sea to Barter Island near the Canadian border (Fig. 1). Palmer (1976) identified the Beaufort Sea coastal fringe as the principal brant breeding area on Alaska's North Slope. In NPR-A, black brant were found breeding at Meade River, Island Lake, and East Long Lake, but not at the southern edge of the coastal plain at Singiluk or Square Lake (Table 3). The southern limit of this species on the Arctic Coastal Plain is not precisely known, but we suggest that brant do not regularly breed farther than 40 km inland from the Beaufort Sea coast. In early August adults with young were seen 23 and 28 km inland near Kogrua Bay and Teshekpuk Lake (Fig. 1), respectively, and pairs were observed 47 km inland south of Barrow (R. King, personal communication). There are records of brant farther inland in the Foothills Province (Kessel and Cade 1958) and even in mountain passes (Cade 1955; Irving 1960) during migration in May.

Breeding pairs of black brant arrived the first week of June at Meade River, Island Lake, East Long Lake, and Storkersen Point. Populations remained relatively stable through the summer at Meade River and Storkersen Point. Flocks of nonbreeders and failed breeders migrating from Canada, western Alaska, and Wrangel Island, U.S.S.R. (King and Hodges 1979) first arrived in late June and early July at Island Lake and East Long Lake. Peak populations of molting brant occurred on 24 July at East Long Lake (Fig. 10) where wing feather molt lasted about 3 weeks (Derksen et al. 1979*b*). There were few molting birds at Island Lake and East Long Lake after 5 August, although adults with young remained on the study area through September.

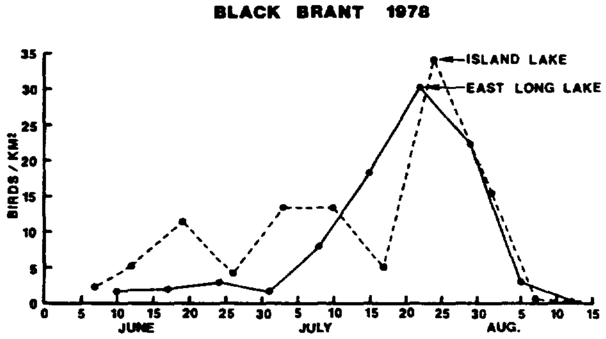

Fig. 10. Summer populations of black brant at two study sites in 1978.

Bergman et al. (1977) showed that brant used coastal wetlands (73% frequency) during migration, then shifted to Class IV wetlands (91% frequency) for nesting. Our observations from the large lake regime northeast of Teshekpuk Lake revealed that brant selected larger bodies of water with emergent vegetation (Class IV) for nesting in June (Table 9). The presence of small islands for nest sites also was important although nests were sometimes found along shorelines of larger vegetated wetlands. Most broods, however, were found on large Class V lakes (Table 5) that do not support emergent vegetation. We observed downy brant in small creches with several adults move from Class IV to

Table 9. *Seasonal habitat selection*[a] *by black brant at two sites in NPR-A in 1978.*

Study site and month	Wetland class					
	I	II	III	IV	V	VII
East Long Lake (X^2 = 10,167.59, n = 2,989)						
June	7.40	- 0.86	- 1.96	+14.58	- 3.71	+33.54
July	-224.29	-94.62	-59.38	-51.74	+375.58	+120.32
August	9.69	- 4.43	2.57	- 2.57	+14.50	+15.24
Island Lake (X^2 = 12,392.31, n = 1,226)						
June	8.45	- 3.33	2.37	+75.36	- 2.41	- 0.26
July	-172.75	-55.70	-39.61	+11.64	+330.72	- 4.28
August	- 5.12	- 1.60	- 1.14	- 0.35	+ 9.91	- 0.12

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference. - = avoidance. Critical values are 1.96 ($P < 0.05$) 2.58 ($P < 0.01$).

Deep-open (Class V) lakes where they grazed with adults. At Storkersen Point brant moved broods from wetlands near the coast to Beaufort Sea lagoons. Mickelson (1975) reported similar brant brood movement from lakes to tidal sloughs and a river on the Yukon-Kuskokwim Delta, Alaska. Sedges and grasses preferred by brant were most abundant in wet meadows adjacent to Deep-open lakes (Derksen et al. 1979*b*), which very likely induced brood movements and distribution. As is true among duck broods (Bengtson 1971), food availability may be an important factor influencing brant brood movements between wetland habitats.

White-fronted Geese

King (1970) stated that white-fronted geese (*Anser albifrons*) were fairly evenly distributed throughout the lake areas of the Arctic Slope. Our data from the Arctic Coastal Plain province supports King's aerial observations. Mean seasonal densities of breeding white-fronted geese were from 0.7/km² at Meade River near the Beaufort Sea to 2.7/km² inland 138 km at Singiluk (Table 3). Although densities are low north of the Brooks Range, King (1970) estimated 50,000 white-fronted geese on the Arctic Slope, which represents about 67% of the mid-continent winter population (Bellrose 1976).

White-fronted geese migrate to the large regime northeast of Teshekpuk Lake to molt (King and Hodges 1979). We found white-fronted geese molting in small groups of 5 to 20 at Meade River, Singiluk, Square Lake, Island Lake, and Storkersen Point and in larger flocks of up to 600 near East Long Lake. Although molting flocks of white-fronted geese are found over most of their Arctic Coastal Plain breeding range, they are apparently most concentrated on a few lakes near Teshekpuk Lake. Derksen et al. (1979*b*) showed that this population was largely separated from other geese molting in this area. Furthermore, white-fronted geese do not shift to coastal wetlands like brant and Canada geese, perhaps because of their food preferences and their interior migration route through Canada to south central United States wintering areas (Bellrose 1976).

White-fronted geese nested on upland sites or polygonal ridges near Shallow-*Carex* and *Arctophila* wetlands. Family groups and pairs grazed in upland sites during June and July. Postbreeding birds including failed breeders, selected Deep-open lakes for the annual molt in July and August (Table 10), where they fed on grasses and sedges in wet meadows (Derksen et al. 1979*b*). Bergman et al. (1977) showed that Deep-open lakes were used at a frequency of 94% by white-fronted geese during the postbreeding period in August at Storkersen Point. At East Long Lake, Beaded Streams were preferred ($P<0.01$) throughout the summer by white-fronted goose pairs and pairs with broods (Table 10). Streams that connect lakes may be important corridors of travel which allow adults with broods to use several lakes without leaving the protection of the water. Forty-two percent of white-fronted goose broods were found on Beaded Streams (Table 5).

Table 10. *Seasonal habitat selection*[a] *by white-fronted geese at East Long Lake in 1978.*

Study site and month	Wetland class					
	I	II	III	IV	V	VII
East Long Lake (X^2 = 6,904.36, n = 181)						
June	- 1.49	- 1.27	- 1.40	+ 0.78	- 2.61	+28.05
July	- 4.11	- 4.06	- 2.35	- 2.05	+ 0.01	+51.02
August	-13.92	- 6.36	- 3.68	- 3.21	+ 5.10	+97.41

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, - = avoidance. Critical values are 1.96 ($P< 0.05$), 2.58 ($P< 0.01$).

Lesser Snow Geese

Migrating lesser snow geese (*Anser caerulescens caerulescens*) were seen in June at all study sites except Square Lake (Table 3), but regular sightings during July and August were made only at East Long Lake where a few molted on Deep-open lakes (Derksen et al. 1979*b*). Apparently, lesser snow geese nested over much of the Arctic Coastal Plain (Gabrielson and Lincoln 1959) before 1900, but there have been few records in recent years. A pair nested on the East Long Lake study area in 1978 and fledged one young. Aerial surveys conducted in 1979 from Cape Halkett to Drew Point (Fig. 1) and south to Teshekpuk Lake revealed 86 adults and two broods of two and four (J. King, personal communication). A small colony of lesser snow geese nest on Howe Island in the Sagavanirktok River delta near Prudhoe Bay. Fewer birds have been seen in recent years, possibly due to disturbance from intensive helicopter traffic.

Farther east there is a major fall staging area near the Canning River delta (Fig. 1) within the boundary of William O. Douglas Arctic National Wildlife Range. Michael Spindler (personal communication) recorded 80,000 lesser snow geese while traveling from the outer delta to Barter

Island in September 1979. These birds migrate west from breeding grounds in the MacKenzie and Anderson river delta and other Canadian nesting areas (Barry 1967).

Pintail

The pintail *(Anas acuta)* is probably the most numerous duck on the Arctic Coastal Plain, especially in the western half (Gabrielson and Lincoln 1959). Densities were equal to or greater than those of other duck species at all sites near the coast, but ranked second to oldsquaws (*Clangula hyemalis)* near the foothills (Table 3). Maher (1959) recorded only one bird during two field seasons on the Kaolak River in the northern foothills, but Irving (1960) considered them the most numerous resident duck at Anaktuvuk Pass in the Brooks Range (Fig. 1).

The most dynamic facet of pintail populations is the periodic drought displacement of birds to the arctic from the southern prairies where the species is highly mobile and adapted to temporary wetlands (Derrickson 1978). Such an occurrence was documented from this study in 1977 by Derksen and Eldridge (1980). The greatest density recorded was 45.6/km² at East Long Lake on 20 June 1977. In 1978 populations declined as much as 62% but remained above average. Superimposed on the annual variations are low densities during molt in the latter half of July and subsequent premigration increases in August (Fig. 11).

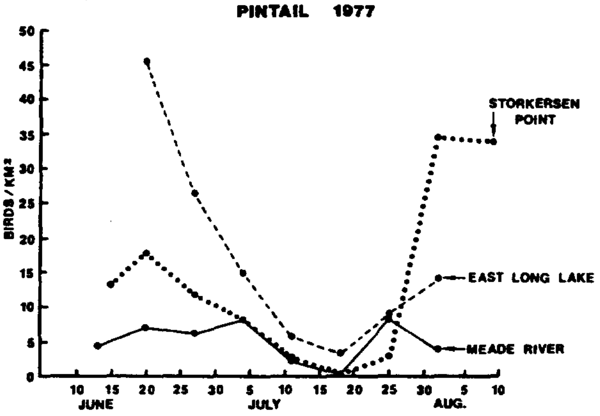

Fig. 11. Summer populations of pintail at three study sites in 1977.

Although pintails are abundant on the coastal plain, sex ratios are heavily skewed toward males, and most are probably nonbreeders (Bergman et al. 1977; Derksen and Eldridge 1980). Nesting is more regular on the western coastal plain (Pitelka 1974), encompassed by NPR-A, and the easternmost Alaskan records are from near Prudhoe Bay (Gavin 1975; Bergman et al. 1977). We found no more than one nest at each study site and none during the single season at Island Lake. Broods were observed at Singiluk (eight), Square Lake (two), and Meade River (one).

Table 11. *Seasonal habitat selection*[a] *by pintails at three sites on the Arctic Coastal Plain in 1978.*

Study site and month	Wetland class					
	I	II	III	IV	V	VII
East Long Lake (χ^2 = 6,116.28, n = 681)						
June	-12.43	- 9.13	+57.48	+ 0.96	-11.70	+ 6.96
July	-13.98	- 6.38	+50.94	+ 1.04	- 8.18	+ 4.77
August	-19.50	- 4.18	+24.26	+49.71	-11.41	- 1.82
Storkersen Point (χ^2 = 8,036.59, n = 652)						
June	-20.03	-13.19	+79.51	+ 5.32	- 4.54	- 0.42
July	- 9.00	- 6.08	+40.47	- 1.52	- 2.34	- 1.38
August	-27.47	- 7.17	+56.22	+43.97	- 5.23	- 4.21
Square Lake (χ^2 = 12,365.71, n = 172)						
June	- 1.60	+ 2.72	+ 1.77	- 2.20	—[b]	+31.07
July	- 6.94	- 1.13	+ 0.36	+ 0.12	—	+114.67
August	- 8.99	+ 5.08	- 1.23	+ 2.53	—	+64.16

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, - = avoidance. Critical values are 1.96 ($P < 0.05$), 2.58 ($P < 0.01$).

[b] No Class V wetlands present.

Pintails preferred *Arctophila* wetlands, including Beaded Streams, throughout the summer (Table 11). When pintails first arrived in spring they fed in the only water areas available, Flooded Tundra meadows, but soon moved to Shallow-*Arctophila* ponds (Bergman et al. 1977). At Square Lake Shallow-*Arctophila* ponds were uncommon (Table 2) and pintails used Beaded Stream *Arctophila* beds and Shallow-*Carex* ponds. The Beaded Stream at Storkersen Point was underutilized, probably because *Arctophila* was not abundant there.

The dense cover of Shallow-*Arctophila* ponds was preferred in July at the onset of molt but some of these ponds later became dry, causing a shift in use to Deep-*Arctophila* ponds and, at Square Lake, to Beaded Streams. Observations at all sites on Deep-*Arctophila* ponds accounted for 70% of brood sightings (Table 5) and there is a strong preference for this class during the August staging period (Table 11). At Island Lake the unique shallow Class V lakes provided accessible feeding for postmolt flocks. Basin-complexes with *Arctophila* pools supported high densities of pintails for the entire season at Meade River, East Long Lake, and Storkersen Point (Bergman et al. 1977).

Pintails may be attracted to *Arctophila* wetlands because of their feeding habits. With their long necks they can use deeper ponds than other dabbling ducks. *Arctophila* beds seed profusely in shallow ponds and stream floodplains that are dry by August. When reflooded in spring these beds are used intensively by pintails that often consume high proportions of plant material (Bellrose 1976) and select seed-rich areas (Krapu 1974*a*). *Arctophila* wetlands also produce more diverse communities of invertebrates (Bergman et al. 1977) that are important to breeding birds (Krapu 1974*b*).

Oldsquaw

Among north slope duck species the oldsquaw is the most ubiquitous and abundant regular breeder (Bailey 1948; Gabrielson and Lincoln 1959). It is recorded as a common breeder near Barrow (Pitelka 1974), at all NPR-A study sites (Table 3), and eastward along the Canadian arctic coast (Barry 1960). Sage (1974) noted that oldsquaws were common and bred on numerous ponds and lakes south into the Sagavanirktok and Atigun valleys, but Maher (1959) considered them rare on the upper Kaolak River in the foothills of southwestern NPR-A.

The highest mean densities of oldsquaws were recorded at Singiluk and Square Lake near the foothills (Table 3), but they were numerous at all sites. Local populations were moderately stable during June when breeders established territories. Paired males remained with their hens longer than most sea ducks, but began leaving nesting areas during late July (Fig. 12; Alison 1975) to molt in the nearshore waters of the Beaufort Sea (Vermeer and Anweiler 1975; Schamel 1978; Johnson 1979). From late July through August females and broods gathered to molt on large inland lakes or coastal lagoons (Alison 1975; Bergman et al. 1977), which resulted in lower densities of birds at Meade River where they left the study area, and at Storkersen Point where they moved to the Beaufort Coast (Fig. 12). All other sites had higher densities because of the concentrations on large lakes.

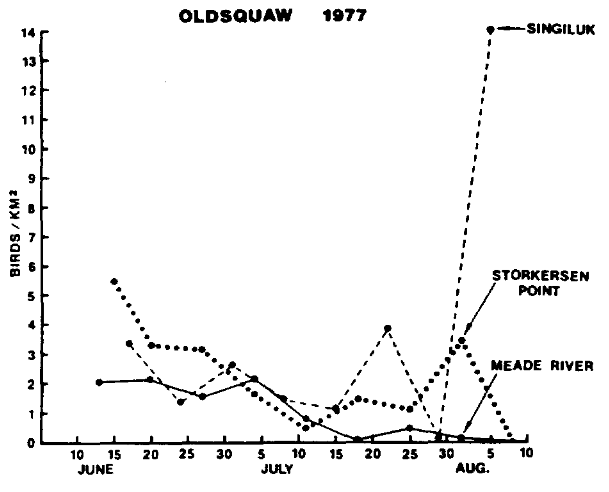

Fig. 12. Summer populations of oldsquaw at three study sites in 1977.

Habitat selection by oldsquaws (Table 12) was generally similar to that reported at Storkersen Point (Bergman et al. 1977). Birds congregated in spring on open-water moats of large lakes and used Deep-*Arctophila* wetlands as they became ice-free. Breeding pairs dispersed to smaller Shallow-*Carex* ponds at East Long Lake and Square Lake, Shallow-*Arctophila* ponds at Storkersen Point, and Deep-*Arctophila* wetlands at all sites into July. During July postbreeding and nonbreeding birds preferred Deep-*Arctophila* and Deep-open lakes. Beaded Streams were used significantly ($P < 0.01$) more than expected throughout the summer at Square Lake, through July at East Long Lake and Storkersen Point, but only during July at Island Lake.

Table 12. *Seasonal habitat selection*[a] *by oldsquaws at four sites on the Arctic Coastal Plain in 1978.*

Study site and month	Wetland class I	II	III	IV	V	VII
East Long Lake (X^2 = 9,907.12, n = 375)						
June	7.40	+ 1.94	0.07	+ 6.12	+ 3.77	+24.10
July	7.31	+ 0.37	1.30	+24.15	4.28	+96.42
August	-30.71	-13.08	7.64	- 7.08	+55.51	- 2.86
Island Lake (X^2 = 1,119.45, n = 192)						
June	- 9.19	+ 0.69	- 0.72	+ 7.43	+10.94	- 0.22
July	-22.73	- 7.13	- 4.52	- 1.55	+43.13	+ 4.13
August	- 8.74	- 2.74	- 1.95	- 0.60	+16.92	- 0.21
Storkersen Point (X^2 = 630.99, n = 143)						
June	-13.05	+ 1.21	+ 6.13	+12.78	+ 0.66	+15.52
July	- 7.50	+ 1.35	+ 3.84	+ 7.69	+ 7.13	+ 2.53
August	- 6.04	- 4.09	- 1.28	+ 6.52	+17.10	- 0.93
Square Lake (X^2 = 182.71, n = 179)						
June	- 3.00	- 0.72	- 0.90	+ 3.22	—[b]	+ 5.30
July	- 9.42	+ 7.71	- 1.29	+ 5.39	—	+ 4.49
August	- 8.77	+ 0.23	- 1.20	+ 8.57	—	+ 4.60

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, - = avoidance. Critical values are 1.96 ($P < 0.05$), 2.58 ($P < 0.01$).

[b] No Class V wetlands present.

Nearly all oldsquaw broods were seen on Deep-*Arctophila* (44%), Deep-open (25%), and Shallow-*Carex* (19%) wetlands (Table 5), all characteristically with central zones of open water. Our observations generally support those of Alison (1976) that older broods use larger wetlands. During the August molt and staging period oldsquaws strongly preferred Deep-open lakes at all sites except Square Lake (Table 12) where Deep-open lakes did not occur (Table 2). Flocks of birds also selected Deep-*Arctophila* wetlands at Square Lake and Storkersen Point.

Habitat selection by oldsquaws reflects preferences of strongly territorial breeding birds (Alison 1975) for small discrete wetlands, the combination of cover and water permanence for broods in Deep-*Arctophila* ponds, and open-water areas important to all diving species, especially during molt.

Spectacled Eider

The summer breeding range of the spectacled eider (*Somateria fischeri*) is centered on the Yukon-Kuskokwim Delta, but extends in a coastal band along the Bering and Beaufort Seas east to the Colville River delta (Gabrielson and Lincoln 1959: Dau and Kistchinski 1977). Spectacled eiders are listed as occasional breeders at Barrow (Pitelka 1974), but were more common at our Meade River, East Long Lake, and Island Lake sites (Table 3), within a breeding area surmised by Bailey (1948). Occasional breeding has been recorded at Storkersen Point (Bergman et al. 1977; Table 3) and Prudhoe Bay (Gavin 1975). An affinity for coastal areas is apparent, and spectacled eiders have only been seen near the foothills as casual visitors at Singiluk; thus, the most important North Slope breeding range lies within NPR-A boundaries.

Spectacled eiders were most numerous at East Long Lake but densities were relatively low at all four sites near the coast (Table 3). Nests or broods were found on each of these study areas. Seasonal changes in populations could not be detected from weekly census data but males had left the study areas by 8 July in both years. During July and August females with broods were seen, occasionally accompanied by groups of hens ("aunts"), similar to common eiders, *Somateria mollissima* (Guignion 1967).

There were insufficient observations of spectacled eiders to test habitat preferences, but sightings at East Long Lake indicate that they are similar to those of oldsquaws. Shallow-*Arctophila* ponds and Deep-open lakes were used only during June, but Shallow-*Carex* ponds were used increasingly throughout the summer. Deep-*Arctophila* ponds were used extensively during July and less so during August (Bergman et al. 1977). Broods were most often seen on Shallow-*Carex* ponds (56%) and Deep-open lakes (22%) (Table 5). Like oldsquaws, spectacled eiders dive for invertebrates and generally prefer open-centered wetlands.

King Eider

Gabrielson and Lincoln (1959) indicated that Alaskan king eiders *(Somateria spectabilis)* were most abundant near Barrow; however, Pitelka (1974) considered them only irregular breeders there. Furthermore, we found no evidence of breeding at Meade River delta, within 55 km of Barrow, or at the other NPR-A sites near the coast (Table 3). The most productive breeding areas of king eiders are east of the Colville River. They are considered regular breeders at Storkersen Point (Bergman et al. 1977; Table 3) and are relatively numerous near Oliktok (Divoky 1979), Prudhoe Bay (Gavin 1975; Schamel 1978), Barter Island (Spindler 1978), Humphrey Point (Dixon 1943), and in the Canadian arctic (Barry 1968). Breeding was recorded at both near-foothills sites, but there is no evidence that it occurs south of the coastal plain.

At Storkersen Point, king eider population densities were second only to pintails, but they were low at all sites in NPR-A (Table 3). Males abandoned nesting hens in late June and early July (Fig. 13) and were observed on molt migrations to coastal waters where they move westward (Barry 1968; Flock 1973) around Point Barrow (Thompson and Person 1963; Johnson 1971). Unlike oldsquaws, eiders spend relatively little time staging in nearshore waters during late summer (Schamel 1978) but are found along their migration paths 13-16 km from shore (Bartels 1973).

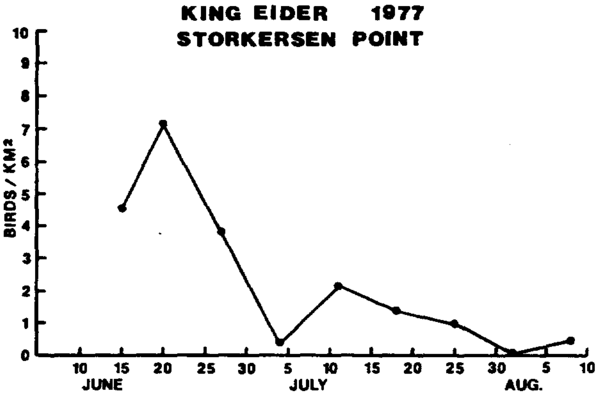

Fig. 13. Summer population of king eider at Storkersen Point in 1977.

Sufficient wetland use data on king eiders was collected in 1978 only at Storkersen Point (Table 13). Wetland preferences were the same as those reported by Bergman et al. (1977) at this site. Shallow- and Deep-*Arctophila* wetlands were differentially selected during nesting in June. Deep-open lakes were preferred only in July, probably by postbreeding groups. Frequent use of Deep-*Arctophila* ponds through July and August resulted from strong selection by hens and broods (78% of observations). All other broods were seen on Shallow-*Carex* ponds (Table 5).

Table 13. *Seasonal habitat selection*[a] *by king eiders at Storkersen Point, 1978.*

Study site and month	Wetland class I	II	III	IV	V	VII
Storkersen Point (X^2 = 1,564.79, n = 177)						
June	-11.96	- 2.25	+23.79	+11.54	- 3.10	+ 6.09
July	-11.42	+ 0.11	2.42	+16.27	+ 7.49	+10.22
August	- 5.78	- 3.91	1.23	+31.42	- 0.66	- 0.89

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, = avoidance. Critical values are 1.96 ($P_1 < 0.05$), 2.58 ($P < 0.01$).

Greater Scaup

Gabrielson and Lincoln (1959) considered the west coast of Alaska as the major breeding range of greater scaup *(Aythya marila)*. Greater scaup were listed as casual visitors at Barrow (Pitelka 1974), East Long Lake, and Meade River delta in NPR-A (Table 3), Okpilak River delta (Spindler 1978), and for several years at Storkersen Point (Bergman et al. 1977). A brood was seen in the Colville River delta but most North Slope breeding records are from the foothills region (Kessel and Cade 1958; Maher 1959). Notable breeding populations were reported near Anaktuvuk Pass

(Irving 1960), in the Atigun-Sagavanirktok River valleys (Sage 1974), and Square Lake. One brood was seen at Singiluk.

Densities of scaup were moderately high in June at both near-foothills sites, and the highest recorded was 2.4/km^2 at Square Lake on 8 July. Irving's (1960) records indicate that scaup nest from early to mid-June in the mountains. Five nests were found at Square Lake, the earliest backdated to initiation on 24 June. Drakes left the area to molt around mid-July and the first flightless male was seen on 18 July. Broods were first observed the last week in July and densities increased as mixed-sex flocks gathered through August.

Greater scaup used all wetland classes in early June but moved to Deep-*Arctophila* lakes when they had open water. The latter wetland class provided 77% of all observations in June, 92% in July, and 100% in August. Molting males also used similar Beaded Stream habitat during July. Nine of 10 brood sightings were on Deep-*Arctophila* lakes (Table 5).

White-winged Scoter

During the breeding season white-winged scoters *(Melanitta deglandi)* have been seen from Barrow to Demarcation Point on the Canada border (Gabrielson and Lincoln 1959) but they are more abundant in interior Alaska and Canada (Bellrose 1976). Most observations were of stragglers and migrants, but Irving (1960) reported white-winged scoters as common breeders near Anaktuvuk Pass and collected a brood on the Killik River. Our Square Lake site had a moderate resident population and was the only NPR-A site where the species was seen. The single nest found there is the northernmost Alaska record.

Densities of white-winged scoters increased at Square Lake to a high of 1.8 km^2 on 1 July (Fig. 14). The largest flock seen was 44 males. From 19-30 July males were not observed on the study area and probably were beginning postnuptial molt (Dement'ev and Gladkov 1967). In behavior similar to greater scaup, white-winged scoters used Deep-*Arctophila* lakes almost exclusively, amounting to 94% of all observations in June and 100% from July through August. All brood sightings also occurred on this wetland class (Table 5).

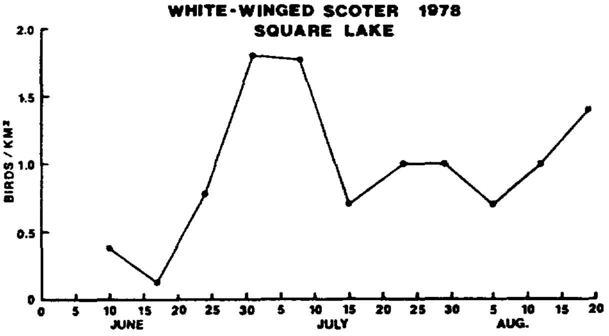

Fig. 14. Summer populations of white-winged scoter at Square Lake in 1978.

The single nest found was well hidden in a dense upland thicket of dwarf birch *(Betula nana)*, approximately 6 m from a large Deep-*Arctophila* lake. The nest site was similar to those described by Brown (1977) in Alberta. Nest initiation was backdated from hatching (8 August) to 4 July. Seven of nine eggs hatched and the ducklings were led to water within 30 h of the start of hatch.

Other Ducks

Small numbers of eight other duck species were seen at one or more of our NPR-A sites (Table 3), mostly in early June. Although there is no record of mallards *(Anas platyrhynchos)* at Barrow (Pitelka 1974), they were seen nearby in the Meade River delta and at East Long Lake. They may occur more frequently to the east near Prudhoe Bay where Gavin (1975) has reported irregular breeding (Bergman et al. 1977). Green-winged teal *(Anas crecca carolinensis)* are occasionally seen near the coast, but nesting was recorded only at Square Lake near their known breeding range in the foothills (Kessel and Cade 1958; Irving 1960; Sage 1974). American wigeon *(Anas americana)* have been seen in many locations on the North Slope and were recorded at all NPR-A sites. Broods have been seen in the Brooks Range (Irving 1960) and at Umiat (West and White 1966). All of these dabbling duck species are probably more common in years of drought on the southern prairies.

Common eiders occur along the entire Arctic coast (Gabrielson and Lincoln 1959) especially during migrations. Breeding is widespread coastally but is more concentrated on the barrier islands east of the Colville River (Schamel 1974; Gavin 1979) and near Icy Cape on the Chukchi Sea (Divoky 1978). The Steller's eider *(Polysticta stelleri)* is relatively uncommon and was seen only at Singiluk, but breeding has been recorded along the entire north coast of Alaska (Gabrielson and Lincoln 1959). Surf scoters *(Melanitta perspicillata)* have been seen at many locations but breeding records are not clear (Gabrielson and Lincoln 1959). Reed (1956) observed a hen and brood on the Kikiakrorak River in eastern NPR-A. Red-breasted mergansers (*Mergus serrator)* are regular stragglers, mostly on rivers (Gabrielson and Lincoln 1959). Nests or broods have been found on the Kaolak (Maher 1959), Atigun (Sage 1974), and Firth rivers (Dixon 1943), and near Anaktuvuk Pass (Irving 1960).

Six species of ducks may occur only rarely in NPR-A and were not seen during our investigations: gadwall, *Anas strepera* (Child 1972); redhead, *Aythya americana* (Kessel and Cade 1958); lesser scaup, *Aythya affinis* (Irving 1960; Hall 1975); common goldeneye, *Bucephala clangula* (Kessel and Cade 1958); harlequin duck, *Histrionicus histrionicus* (Kessel and Cade 1958; Irving 1960); and black scoter, *Melanitta nigra* (Gabrielson and Lincoln 1959; Watson and Divoky 1972). The authors also saw black scoters in the Colville River delta on 27 June and off Point McIntyre near Storkersen Point on 30 June 1976. The latter record was during westward migration at their western landfall in crossing Prudhoe Bay. Four flocks, the largest with 59, totaled 127 birds.

Red Phalarope

Red phalaropes *(Phalaropus fulicarius)* ranked either first or second in abundance among shorebirds at study sites near the coast, but were much less common at Square Lake and Singiluk (Table 3). At our sites, red phalaropes were most numerous in June; numbers gradually declined in July, then dropped off sharply in late July and early August (Fig. 15). At Storkersen Point and Island Lake an influx in early August occurred as birds staged for migration. Red phalarope migration occurs in stages based on sex and age with females departing for the Beaufort Sea coast in late June and early July, males in mid- to late July, and juveniles in August (Connors et al. 1979).

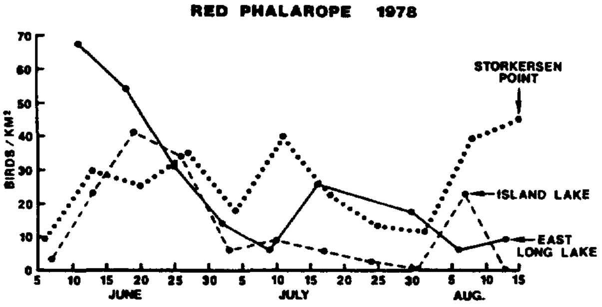

Fig. 15. Summer populations of red phalarope at three study sites in 1978.

Connors et al. (1979) suggested that red phalaropes shift from almost exclusive use of tundra for breeding activities to heavy dependence on littoral areas by postfledging juveniles and adult males. They reported that the differences in migration schedules of adult males and females and juveniles coincided with differences in habitat use. Females rarely appeared in littoral sites, male use of littoral habitats depended on annual variations in the timing of sea-ice, and juveniles extensively used the littoral zone, particularly along the Beaufort Sea shorelines as they accumulated fat for migration. Our data indicate that red phalaropes utilize Flooded Tundra in early June, although use was less than expected at all sites because of the extensiveness of this habitat type (Table 14). Various other wetland types also were important at particular sites in June. Beaded Streams were used significantly ($P < 0.05$) more than expected at all sites in June and appear to be an important source of food early in the season. Shallow-*Carex* and Shallow-*Arctophila* wetlands were used more than expected at Island Lake and Storkersen Point in June (Table 14). In July and August most use was concentrated on Shallow-*Carex* and Shallow-*Arctophila* wetlands although Beaded Streams and Flooded Tundra were still used. The importance of Deep-*Arctophila* wetlands differed in varying degrees between periods and sites. Use in July and August was generally higher than expected although these wetlands were also important in June at Storkersen Point. Use of Deep-open lakes was less than expected at all sites except East Long Lake in July.

Table 14. *Seasonal habitat selection*[a] *by red phalaropes at three sites on the Arctic Coastal Plain in 1978.*

Study site and month	Wetland class					
	I	II	III	IV	V	VII
Island Lake (X^2 = 27,839.97, n = 383)						
June	- 7.27	+10.82	+ 2.77	+ 1.06	- 5.81	+26.43
July	- 1.40	+ 3.90	- 1.48	- 0.45	- 0.75	- 0.16
August	-29.86	- 9.36	6.66	+253.18	8.94	- 0.72
East Long Lake (X^2 = 4,643.61, n = 1,147)						
June	- 5.09	- 4.30	- 4.83	- 3.33	- 2.04	+76.97
July	-31.83	+16.97	+ 3.09	+19.32	+10.40	+ 4.22
August	- 6.28	+ 8.96	+ 0.80	0.80	2.08	+ 7.92
Storkersen Point (X^2 = 1,875.88, n = 686)						
June	- 5.14	0.95	+11.24	+ 7.27	- 3.27	+ 2.23
July	-11.79	3.31	+ 6.00	+38.84	+ 1.53	+ 0.90
August	-35.21	+42.37	+ 0.18	0.28	- 5.95	4.87

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, = avoidance. Critical values are 1.96 ($P < 0.05$), 2.58 ($P < 0.01$).

Northern Phalarope

Northern phalaropes *(Phalaropus lobatus)* were less common than red phalaropes at all sites except Singiluk and Square Lake (Table 3). Although they were common at the East Long Lake site in 1977 and 1978, numbers were low at Storkersen Point, Meade River, and Island Lake. Numbers of northern phalaropes were highest in early June and decreased in late June and early July (Fig. 16). A premigration increase to 20.4 and 8.8 birds/km² occurred at East Long Lake and Storkersen Point, respectively, in mid-July as northern phalaropes staged in large flocks up to 1,500 birds. By early August there were few northern phalaropes at our study sites.

Trends in habitat use by northern phalaropes were similar to red phalaropes (Table 15). Flooded Tundra and Beaded Streams were important wetlands in June. Use of Shallow-*Carex* and Shallow-*Arctophila* wetlands varied among study areas, but generally they were more important in July and August as Flooded Tundra dried. Deep-*Arctophila* wetlands were important throughout the summer at Storkerson Point, but were used less than expected at the other sites. Deep-open wetlands were used less than expected or as expected at East Long Lake in summer 1978. This wetland type did not occur at Square Lake so no comparisons can be made.

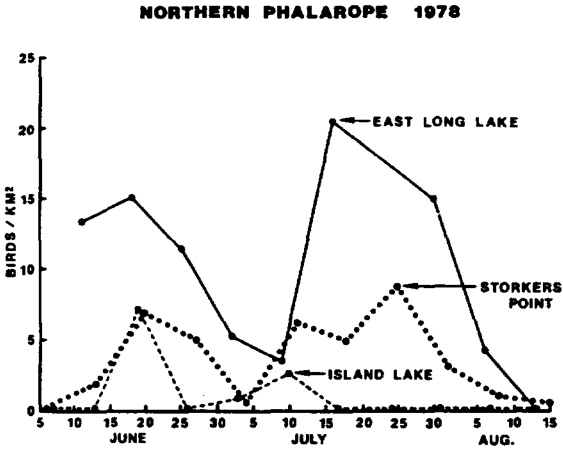

Fig. 16. Summer populations of northern phalarope at three study sites in 1978.

Table 15. *Seasonal habitat selection*[a] *by northern phalaropes at three sites on the Arctic Coastal Plain in 1978.*

Study site and month	Wetland class I	II	III	IV	V	VII
East Long Lake (χ^2 = 4,029.20, n = 270)						
June	- 8.25	- 5.13	+ 6.37	+ 1.42	- 7.54	+83.23
July	-10.88	+10.68	+ 5.06	+13.64	- 8.10	+ 9.74
August	3.15	- 1.69	+ 2.46	+ 4.33	- 2.17	+18.14
Storkersen Point (χ^2 = 967.80, n = 108)						
June	3.90	- 1.78	+10.46	+ 7.43	- 1.87	- 1.10
July	12.36	2.12	+ 0.20	+43.14	3.21	+ 4.47
August	3.76	+ 3.34	0.80	+ 4.84	0.98	0.58
Square Lake (χ^2 = 4,002.74, n = 74)						
June	2.45	+ 9.23	1.11	2.97	—[b]	+14.47
July	2.62	+ 3.52	0.65	3.70	—	+73.25
August	3.45	+ 1.28	0.47	+ 2.88	—	- 0.13

[a] The tabular adjusted residuals are measures of deviation from expected values. + = preference, = avoidance. Critical values are 1.96 ($P < 0.05$), 2.58 ($P < 0.01$).

[b] No Class V wetlands present.

Pectoral Sandpiper

Pitelka (1959) considered pectoral sandpipers the most numerous and widespread shorebird on the Alaskan tundra. Pectoral sandpipers were the most abundant shorebird at all study sites in 1977 but were second or third in 1978 when mean seasonal densities declined by as much as half (Table 3). Variation in populations of pectoral sandpipers between years seems to be related to differences in spring melt and availability of food resources (Pitelka 1959; Holmes and Pitelka 1968). Pectoral sandpipers have a flexible territorial system and are capable of compressing territories and increasing densities when and where food is abundant (Pitelka 1959; Holmes and Pitelka 1968). There is a progressive movement of postbreeding males, postbreeding females, and fledged juveniles to the coast from mid- to late July (Pitelka 1959; Connors et al. 1979). Premigration population increases in late July and early August were recorded at several but not all of our study sites.

Connors et al. (1979) include pectoral sandpipers in a shorebird group more restricted to tundra than coastal habitats. These sandpipers preferred drier sites on all study areas. At East Long Lake in 1978 99% of all June and July observations of pectoral sandpipers were on Flooded Tundra. However, pectoral sandpipers use littoral habitats of Shallow-*Carex*, Shallow-*Arctophila*, and Deep-open wetlands, particularly in late July and August.

Dunlin

Dunlins *(Calidris alpina)* were third or fourth in abundance at sites closest to the coast in 1977 and 1978, but were uncommon in the southern coastal plain (Table 3). Holmes (1970) reported that in Alaska dunlins are widespread with little population variation from year to year. However, Baker and Baker (1973) found large year-to-year shifts in foraging behavior and habitat use by dunlins in the eastern arctic. Differences in population densities and feeding behavior could be due to successive occupation by morphologically different subspecies (Holmes 1970). Dunlins establish 12- to 15-acre territories in early June which are utilized for all life functions until young hatch in early to mid-July (Holmes 1966). Dunlins remain on the tundra longer than other shorebirds due to the strong territorial system but shift to littoral wetland areas in mid-summer when young hatch. We recorded a gradual decline in dunlin populations from mid-June to mid-August.

Dunlins utilize a wide range of habitat types and appear to be a broad-niched species (Holmes 1966; Baker and Baker 1973; Baker 1979). Habitat selection varies with moisture conditions and food availability (Holmes 1966). Feeding activities are concentrated on Tipulid larvae and a high overlap with the diet of pectoral sandpipers occurs throughout the year (Holmes 1966; Holmes and Pitelka 1968). After leaving fledged young on wetter sites, adults return to upland areas for flocking and departure to the coast (Holmes 1966).

Other Shorebirds

We recorded 17 other species of shorebirds at six study sites in 1977 and 1978. Densities varied considerably between sites and years (Table 3). Semipalmated sandpipers *(Calidris pusilla)* were considered a common breeding species at all sites each year, with highest densities recorded at Storkersen Point. Holmes and Pitelka (1968) described their distribution as coastal and along river corridors. Semipalmated sandpipers are one of the earliest shorebirds to migrate to winter areas, flocking in early July and departing by the end of July (Holmes and Pitelka 1968). Semipalmated sandpipers are considered a broad-niched species (Baker and Baker 1973) and utilize both inland tundra and coastal habitats throughout the season (Connors et al. 1979; this study). Shorelines of ephemeral Class II wetlands were important feeding sites in late June and early July. Breeding cycles and behavior of semipalmated sandpipers are discussed by Ashkenazie and Safriel (1979).

Bar-tailed godwits *(Limosa lapponica)* were second in abundance at Singiluk in 1977, and were regularly sighted at Square Lake in 1978, but were uncommon at coastal sites. American golden plovers *(Pluvialis dominica)* and black-bellied plovers *(P. squatarola)* were present in low numbers at all sites. Activities of these species are restricted almost entirely to drier areas throughout the summer with some movement to littoral habitats later (Connors et al. 1979; this study). The buff-breasted sandpiper *(Tryngites subruficollis)*, observed in small numbers at all sites except Meade River and Singiluk, also utilized drier habitats. This sandpiper was a common breeder at Storkersen Point and one of the latest nesting of all shorebirds (Bergman et al. 1977). Long-billed dowitchers *(Limnodromus scolopaceus)* and ruddy turnstones *(Arenaria interpres)* were observed in low numbers at all sites.

Observations of other species were sporadic during each season (Table 3) and data are insufficient for comments on habitat use.

Discussion

Species Composition

Although there are notable differences in avifauna between Storkersen Point and the western coastal plain sites, the greatest dissimilarity is between coastal and near-foothills areas. The Singiluk and Square Lake sites were located at the interface of northern foothills tussock tundra-tall shrub habitats with the morphologically unique wetlands of the southern coastal plain.

Species richness was greatest at Storkersen Point, where marine and tundra species were present. However, of 62 species recorded in 1977 and 1978 only 25 (40.3%) nested (Table 3). The greater percentage of visitors at this site, when compared to inland sites located in NPR-A, may be due to the effects of the Beaufort Sea coast in channeling movements of birds, as in the Barrow region (Pitelka 1974). Storkersen Point is also located between two major rivers that may be followed north to the coast by redpolls *(Carduelis* sp.), horned larks *(Eremophila alpestris)*, and other casual visitors from shrub and mountain valley habitats (Bergman et al. 1977). Barn swallows *(Hirundo rustica)* and Say's phoebes *(Sayornis saya)* may be attracted to buildings (Kessel 1979) in the Prudhoe Bay oil development area where snow buntings *(Plectrophenax nivalis)* were found nesting in structures, discarded barrels, and other debris that provided crevices.

Species richness was next highest at Square Lake near the southern margin of the Arctic Coastal Plain. Twenty-seven of 53 species seen (50.9%) (Table 3) were known breeders. Shrub height, especially *Salix* spp., was significantly greater at the southern Arctic Coastal Plain sites of Singiluk and Square Lake, which attracted four breeding passerines. Closer to the Beaufort Sea coast where shrubs were prostrate as a result of more severe climate, lapland longspurs *(Calcarius lapponicus)* were the only breeding passerines on tundra habitats. Falconiformes breed on the Arctic Coastal Plain along rivers where steep bluffs provide nest sites. Gyrfalcons *(Falco rusticolus)*, peregrine falcons *(Falco peregrinus)*, and rough-legged hawks *(Buteo lagopus)* nest along the Colville River bluffs (Kessel and Cade 1958; White and Cade 1971) about 40 km south of the Square Lake study site where gyrfalcons and peregrine falcons were seen hunting. Although habitats were similar to those at Square Lake, no falconiformes were seen at Singiluk, perhaps because of Singiluk's greater distance from known breeding sites (Ritchie 1979).

East Long Lake and Island Lake had 25 and 16 breeding birds, respectively (Table 3), although the study sites were only about 25 km apart. More varied and interspersed wetland habitats and greater area of dry upland sites at East Long Lake attracted more species than the more homogeneous wetland habitat at Island Lake (Table 2). East Long Lake had a greater percentage of Classes IV and VII wetlands which were important to water birds. Upland species such as the buff-breasted sandpiper and willow ptarmigan *(Lagopus lagopus)* were seen rarely because of the large percentage of wetland (85.8%) in the Island Lake study area.

Species composition of breeding birds at Meade River was most like the East Long Lake study site (Table 3). Only lesser snow geese, buff-breasted sandpiper, northern phalarope, and long-tailed jaeger *(Stercorarius longicaudus)* were not found breeding at one or the other site (Table 3). There were no breeding birds characteristically associated with fluviatile waters at Meade River. Yellow-billed, arctic and red-throated loons, whistling swans, and greater scaup actively fed and loafed on river channels and oxbows. Kessel and Cade (1958) provided a list of birds found in fluviatile habitats along the Colville River and its tributaries.

Density

Alaska's Arctic Coastal Plain supports relatively low breeding densities of most water birds (King 1970; Bergman et al. 1977; this study) compared to more productive wetlands farther south and west. King and Lensink (1971) summarized aerial survey data and reported breeding densities of 257.4 ducks/km^2 for the Yukon River flats in interior Alaska and 124.1 ducks/km^2 in the Yukon-Kuskokwim Delta on the west coast. Breeding duck densities on the Arctic Coastal Plain of NPR-A were estimated to be 2.8/km^2 in both 1977 and 1978 (King 1979). Our ground surveys in NPR-A revealed breeding duck densities of 8.9 to 19.2/km^2 in 1977 and 9.8 to 11.7/km^2 in 1978. Comparative density data for other water bird groups in wetland habitats other than the Arctic Coastal Plain are not available, but shorebirds dependent on wetland habitats may be as dense on the Arctic Coastal Plain as elsewhere.

Despite low breeding densities of some groups, large numbers of water birds annually use the Arctic Coastal Plain. King (1979) estimated 5.4 and 4.9 million water birds on the Arctic Coastal Plain of NPR-A in July 1977 and July 1978, respectively. Shorebirds represented 91% of the total in 1977 and 93% in 1978. Aerial surveys indicate that habitats up to 50 km inland from the Beaufort Sea have the highest concentrations of breeding water birds (King 1979; U.S. Fish and Wildife Service unpublished maps). Coastal areas in NPR-A from Cape Halkett to Barrow (Fig. 1) are especially important for breeding water birds, and for some it is the primary breeding range. Some river deltas also have higher densities of certain species than adjacent tundra habitats.

Postbreeding congregations of water birds have been recorded in nearshore waters of the Beaufort and Chukchi seas, and in freshwater lakes on the Arctic Coastal Plain. Shallow coastal lagoons protected by barrier islands are important to oldsquaws during molt in August and September. Johnson (1979) counted 106,000 birds in Simpson Lagoon 25 km west of Prudhoe Bay in September 1977. Ongoing studies by our group indicate that tidal flats of barrier island lagoons rich in *Carex subspathacea* and *Puccinellia phryganodes* attract up to 15,000 migrating black brant at Icy Cape (Fig. 1) in late August and September.

Wetland Use

Classes III (Shallow-*Arctophila*) and IV (Deep-*Arctophila*) wetlands were the principal breeding habitat for loons, black brant, oldsquaws, white-winged scoters, and king eiders. These wetlands were characterized by dense stands of *Arctophila fulva*. This grass is a key habitat stimulus because it is used as food by grazing waterfowl, affords protective cover and nest material for loons, provides substrate for aquatic invertebrates, and perhaps is important in cycling of nitrogen, phosphorus, and other nutrients (Kadlec 1979). Brood observations were most frequent in Class IV wetlands which may be related to the greatest populations of aquatic invertebrates and the most dense escape cover available among all types. Patterson (1976) determined that habitat requirements of duck broods included both escape cover and food availability. Krapu and Swanson (1975) noted that aquatic invertebrates were a prime source of highly digestible protein which was especially important in the diet during early growth of pintails (Krapu and Swanson 1977).

The attractiveness of Deep-open (Class V) lakes, northeast of Teshekpuk Lake, to molting geese seems to be related to abundant nutrient-rich sedges and grasses along shorelines and safety from predators provided by large expanses of open water. However, Deep-open lakes elsewhere in NPR-A were not intensively used by molting geese. Diving species such as red-throated loons, oldsquaws, and greater scaup were attracted to Deep-open lakes because of the availability of invertebrates and anadromous whitefish (*Coregonus* spp.). Resident ninespine stickleback (*Pungitius pungitius*), blackfish (*Dallia pectoralis*), and large populations of Chironomidae larvae and Sphaeriidae mussels also were important to diving birds.

Beaded Streams (Class VII) were least abundant compared to other wetland types, but because pools often contained stands of *Arctophila fulva* and submergent vegetation they were attractive to loons, white-fronted geese, oldsquaws, king eiders, and phalaropes. Breeding red-throated loons, whistling swans, and white-fronted geese tended to use these systems throughout the summer while pintails, oldsquaws, and king eiders exploited them only during June and July. Beaded Streams were important transportation corridors for larger water birds that had broods and were flightless. Movement over considerable distances, without travel across tundra where fox predation would occur, was possible between lakes connected by Beaded Streams. These streams also contribute to replacement of water lost through evaporation in larger basins.

Class II (Shallow-*Carex*) wetlands are probably the second most abundant type on the Arctic Coastal Plain of NPR-A. Because of the considerable variation in depth, size, and shape (Bergman et al. 1977) they received use by most water birds but seemed especially important to arctic loons and spectacled eiders with broods, oldsquaws, and phalaropes. The most diverse taxa of aquatic invertebrates was found in Shallow-*Carex* wetlands, where Cladocera made up 35% of all organisms collected (Derksen et al. 1979*a*). Although individual types vary in value to birds, most species obtain breeding requirements by seasonally utilizing several different types. Decrease in Class II wetland depth, as a result of evaporation, exposed sediments (Bergman et al. 1977) which we found to be favored feeding sites in late July and August for pectoral sandpipers, semipalmated sandpipers, black-bellied and American golden plovers, and ruddy turnstones.

The most dominant and widely distributed wetland type in NPR-A was Flooded Tundra (Class I). This type may make up as much as 50% of the total surface area of all wetlands on the Arctic Coastal Plain in NPR-A. Class I wetlands seemed to be the least important to all water birds despite their tremendous surface area. The duration of Flooded Tundra habitat is short because of the rapid loss of standing water to evaporation and runoff. Loons, swans, and diving ducks were never observed on Flooded Tundra. Geese grazed on water-tolerant sedges and grasses in June but moved to Deep-open lakes during the wing molt. Bergman et al. (1977) suggested that this type seemed most important to phalaropes, and although we noted both red and northern phalaropes feeding in Flooded Tundra in early spring, our data revealed little use of this habitat by all species. Flooded Tundra is important in the stability and dynamics of larger basins and is a major source of water for recharge of Classes II, III, IV, and V wetlands that are fed by surface runoff, sheet flow, or Beaded Streams.

Management Recommendations

Exploration for petroleum is expected to continue in NPR-A either under the direction of the Federal Government or through lease sales to petroleum companies. If marketable quantities of petroleum are discovered it will be important to consider wetland habitats that could be adversely affected during development and production. Impacts on wildlife resources in NPR-A, on about 58% of the Alaskan Arctic Coastal Plain, would be cumulative with those on current production and exploratory leases covering more than 4,000 km² between the Canning and Colville Rivers (Fig. 1). Based on our quantitative assessment of the relative value of Arctic Coastal Plain wetlands to water birds, we offer the following recommendations for habitat protection and consequently the stability of populations.

Weller (1978) suggested that the best management for freshwater marshes may be through preservation to maintain high productivity of characteristic flora and fauna. We support the recommendation of Bergman et al. (1977) to preserve large blocks of water bird habitats from petroleum development because of the Coastal Plain's homogeneous mosaic of wetland types and relatively uniform distribution of water birds. The only arctic preserve established, the William O. Douglas Arctic Wildlife Range (Fig. 1), contains less than 13% of the Arctic Coastal Plain province with only a narrow zone of wetland habitat along the Beaufort Sea. If leasing, exploration, and production plans are also evaluated in moderately large blocks, the subtle cumulative impacts associated with piecemeal development may be avoided.

Deep-open lakes and adjacent wet sedge-grass meadows used by molting geese in the Cape Halkett area should be protected from all exploration and development activities (Derksen et al. 1979*b*). Criteria for selecting other conservation units should include high-density or unique breeding, molting, and staging areas; sites representative of different Coastal Plain physiographic sections; and areas that have additional wildlife and natural resource values (i.e. caribou range, fisheries, recreation potential). Primary consideration should be given to areas within a few kilometers of the coast, especially those with contingent barrier island lagoon systems and river deltas.

Wetlands that support emergent *Arctophila fulva* are important and vulnerable because of their relatively low abundance in NPR-A and their high use by water birds. Filling of wetlands, water extraction, or other developmental activities is likely to cause severe damage to Classes III, IV, and VI wetlands and Beaded Streams (Class VII).

Beaded Streams should not be diverted, channelized, or have constricting culverts emplaced because of their importance in maintaining water levels in contiguous ponds, lakes, and meadows (Craig and McCart 1975). If culvert crossings cannot be properly designed, use of bridges that do not alter stream hydrology would ensure greater protection of important habitat. Rolligon trails, gravel roadways, drill pads, facility pads, and airstrips should be carefully sited to avoid wetlands, preferably on dry upland tundra. Roads and pipeline pads should have structures to provide adequate cross-drainage of spring melt water and sheetflow, especially through wet meadows and in crossing drained lake basins.

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Contents

WATER BIRDS AND THEIR WETLAND RESOURCES IN RELATION TO OIL DEVELOPMENT AT STORKERSEN POINT, ALASKA

by

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Abstract

During a 5-year study of the bird populations at Storkersen Point on the Alaska Coastal Plain, 25 of the 72 species observed were recorded as breeding. There are few resident species in an avifauna dominated by swimming and wading birds. To provide insight into habitat use and to devise systems for protecting key habitats, wetlands were classified on the basis of size, depth, vegetation, and water chemistry. The resulting eight classes then were related to bird use.

To determine factors influencing differential use of classes of wetlands, and to provide a basis for understanding the food relationships and problems of pollution of wetlands, invertebrate populations were examined in major freshwater wetlands. There is a strong relationship between the presence of emergent *Arctophila* and *Carex* and high invertebrate populations. Peak populations coincide with peak hatching of shorebirds and ducks. It is concluded from limited sampling of bird food habits that invertebrates constitute the major food source for many bird species on the Coastal Plain.

Retention of large breeding populations of tundra birds is uncertain with the disturbance and change that comes with oil development. Foremost problems will be pollution of these wetlands with oil and wetland modification by impoundment or drainage due to road and pipeline systems.

Based on the characteristics of the birds and their wetland resources, it is recommended that preservation of tundra wetlands is vital to most breeding birds of the moist tundra. Preservation should include: (1) large tracts where no oil development occurs, (2) small and well-distributed units of about 42 km² which should be left undisturbed but which should not prevent oil removal, and (3) protection of key production units from pollutants even in areas of intensive development for oil.

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Introduction and Objectives

Discovery and proposed removal of large oil and gas reserves on Alaska's Arctic Coastal Plain have prompted national concern over potential environmental damage (Bartonek et al. 1971). Current industrial development is limited primarily to the vicinity of Prudhoe Bay, but activities are expanding rapidly as construction of the pipeline for transporting oil nears completion. Moreover, development of potential resources of National Petroleum Reserve No. 4 to the west of Prudhoe Bay was approved by Congress in 1975.

The effects of petroleum exploitation on arctic faunas or habitats could be severe in this relatively simple ecosystem. Serious damage to tundra vegetation results from mechanical disturbance of the surface layer which is subject to seasonal freezing and thawing. Although direct killing of wildlife may be controlled in the area, the indirect and direct effect of human activity may be harmful to animal populations (Bartonek et al. 1971). The tundra ecosystem characteristically has few species but their populations oscillate widely. As a result, this system seems to be one that can exist only in large units (Dunbar 1973).

The most conspicuous habitat feature of the moist coastal tundra is the presence of extensive wetlands that cover 50 to 75% of the coastal plain (Black and Barksdale 1949). Although the ice-free season is short, these wetlands provide the principal attraction for many water-related birds such as sea ducks, geese, swans, loons, and shorebirds. Small lakes and ponds probably are the most vulnerable part of the landscape because they represent discrete units that may collect pollutants, and both fauna and flora may be eliminated without conspicuous signs.

The influence of oil spills on the invertebrate fauna and the flora of such areas could be extremely serious. Aquatic invertebrates seem to be a major food resource for breeding waterfowl (except geese), but information on either invertebrates or water-bird food habits from tundra areas is limited. Evidence from other habitats suggests that invertebrates provide a significant portion of the diet of young waterfowl of various species (Chura 1961; Bartonek and Hickey 1969; Sugden 1969; Bartonek 1972), as well as an essential nutrient source for laying female ducks (Krull 1968; Bengtson 1971*a*; Krapu 1974). Aquatic invertebrates are also a major source of food for shorebirds (Holmes and Pitelka 1968).

The present study was established to assess populations of water birds in relation to their aquatic habitats in the Prudhoe Bay oil fields (Fig. 1). Specific objectives were to: (1) determine the importance of this region to water birds, (2) derive a wetland

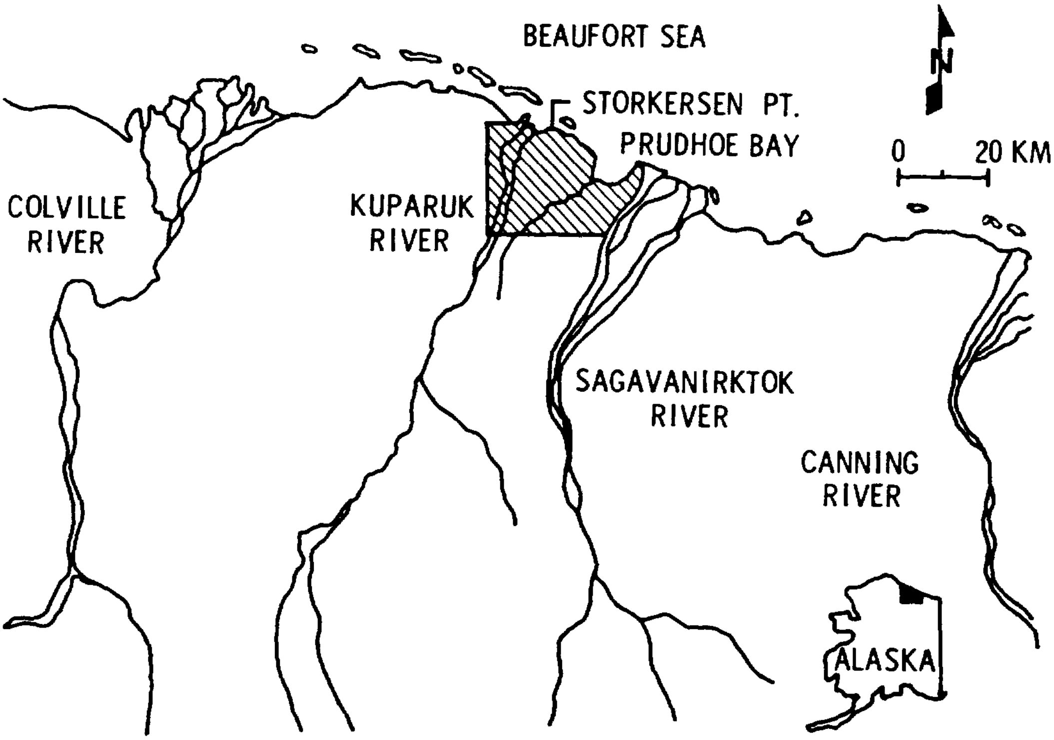

Fig. 1. Location of Storkersen Point study area (black insert) and zone of current intensive oil development (shaded).

classification system that identifies important relationships between birds and wetlands, (3) relate the seasonal abundance and availability of aquatic macroinvertebrates to use by water birds, and (4) provide recommendations for minimizing negative effects of petroleum development on water birds.

This project was part of the Trans-Alaska Pipeline Investigations conducted by River Basins Studies (now Ecological Services) of the U.S. Fish and Wildlife Service. Field seasons extended from about 1 June to mid-August each year except 1975 when field work ended in late July. Bergman was on the site from 1971-1973 and part of 1974, Howard during 1972 and 1973, and Abraham during 1974 and 1975. Assistants included R. F. Bartels (1971 and 1972), D. Janke (1974), and D. V. Derksen (1975). This manuscript constitutes major parts of a Ph.D. dissertation by Bergman (1974), and M.S. theses by Howard (1974) and Abraham (1975) at Iowa State University. Weller supervised this work from 1971 to 1974 while employed at Iowa State University and during 1975 while at the University of Minnesota.

Key individuals involved in the initiation and facilitation of the program were: L. W. Sowl, C. D. Evans, M. A. Monson, J. L. Haddock, and J. C. Bartonek. Many other persons aided the program and their help is sincerely appreciated.

We are indebted to numerous individuals who took time from busy schedules to comment on an earlier draft of this manuscript: J. C. Bartonek, D. V. Derksen, T. Dwyer, C. D. Evans, R. T. Holmes, K. Hussey, B. Kessel, C. Lensink, P. Meyers, H. Nelson, F. Pitelka, and L. W. Sowl. However, we assume total responsibility for the final statements.

Robert D. Bergman, Larry Haddock, and Leonard Boughton of the U.S. Fish and Wildlife Service and their pilot, Robert Johnson, were lost when their plane went down during aerial surveys in south-central Alaska in the fall of 1974. It is sincerely hoped that the results and recommendations presented here will help reduce the potential damage that concerned these dedicated men.

Study Area

The study site is near Storkersen Point (Lat. 70°24'N, Long. 148°43'W) on the Arctic Coastal Plain adjacent to the Beaufort Sea (Fig. 1). Field quarters and landing strip were afforded by an abandoned DEW-line site at the eastern edge of the study area known as Point McIntyre. The climatic regime of the summer months is reflected in data on snow cover and physical characteristics (Table 1).

Efforts were confined mainly to an 18-km^2 area bordering the Beaufort Sea coast on the north and extending inland 7 km. A capped well is present at Storkersen Point, but, as of 1975, major oil operations were 20 km southeast near Prudhoe Bay. The Kuparuk and Sagavanirktok Rivers form large deltas about 8 km west-northwest and 25 km east-southeast, respectively, of Storkersen Point (Fig. 1). The region is part of what Pitelka (1974) termed the Central River Sector of the North Slope. Elevations in the study area range from sea level at coastal lagoons to 10 m on surface residuals a few kilometers inland. The Return Islands form a barrier that affords some protection to the shoreline from wind and sea ice.

The coastal plain is an unglaciated, emergent region of the continental shelf and has low relief and poor drainage. Total area exceeds 65,000 km^2, and the east-west length is about 800 km. Typical relief features are numerous lake basins, polygonal ground, ice-cored mounds (pingos), and relief characteristics of streams and gentle slopes (Hussey and Michelson 1966). Surficial materials on the study area and most of the coastal plain are marine silts, sands, and gravels of the Pleistocene Gubik Formation (Payne et al. 1951).

The Arctic Slope is underlain with permafrost to depths of 508 m (Wahrhaftig 1965; Brooks et al. 1971), portions of which may be products of earlier climates (Pewe 1967). North of the Brooks Range, precipitation is as low as 10.2 cm annually, but arid surface conditions are prevented by low evaporation and transpiration rates and by the lack of subterranean drainage because of permafrost (Johnson and Hartman 1969). The Arctic Slope is further characterized by poor soils (Everett 1975) and tundra vegetation of low growth form (Spetzman 1959; Wiggins and Thomas 1962; Nieland and Hok 1975; Webber and Walker 1975). In spring, water from rapidly melting snow flows over frozen surfaces and fills the numerous shallow thaw lakes and ponds, streams, and rivers (Irving 1972). As summer progresses, the active layer thaws to a depth ranging from 15 cm to 3.66 m, depending on soil type, exposure, drainage, and climate. Standing water disappears from some depressions late in July, but the percentage of the surface area covered by wetlands remains high.

Thaw basins on the Arctic Coastal Plain may form wherever water accumulates on the surface due to restricted drainage (Carson and Hussey 1962). Basins originate in low-center polygons and at junctions of ice wedges. Water impounded in these depressions is heated by insolation in summer and thaws the ground ice below. Alternating processes of freezing, thawing, and water movement enlarge and deepen the basins. As the basins enlarge, breaching

Table 1. *Weather data and phenological events at the Storkersen Point study area from about 1 June to 15 August each year except 1975 when field work ended in late July.*

	1971	1972	1973	1974	1975
Mean temperature (C) (1 June–14 Aug.)					
Daily average	5.0	2.8	3.3	2.8	—
Daily minimum	1.1	0.6	0.6	0.6	-1.1
Daily maximum	7.8	5.0	5.6	5.6	4.4
Extreme temperature (C)					
High	23.3	15.6	24.4	26.1	21.1
Low	-3.3	-4.4	-2.8	-8.3	-6.7
Wind					
Prevailing direction	ENE	ENE	NE	NE	NE
Mean velocity (km/h)	17.7	19.3	16.1	—	—
Highest steady velocity (km/h)	56.3	64.4	56.3	—	—
Sky condition (Percent)					
Clear-partly cloudy	50	40	40	47	—
Overcast	35	35	45	37	—
Fog	15	25	15	17	—
Snow cover (Date)					
50 percent	3 June	10 June	3 June	10 June	10 June
Small wetland ice-free	8 June	15 June	10 June	18 June	11 June
Largest lake (60 ha) Ice-free	22 June	2 July	1 July	8 July	2 July

of shorelines by thawing results in fusion or in drainage. Much of the coastal plain land surface is marked by numerous such drained basins in which second generation wetlands have formed in the bottom of the drained lake (Livingstone et al. 1958).

Based on size and shape differences of thaw lakes, Carson and Hussey (1962) divided the coastal plain into eastern and western sections, separated by a boundary paralleling the Colville River at approximately longitude 152°W. In the eastern section, which included the study area, wetlands generally range from about 3 m to rarely more than 1.6 km in length. In the western section, wetlands frequently xceed 1.6 km and several are more than 13 km long. Thaw lakes commonly are elongate with the long axis oriented 10 to 15 degrees west of true north. According to Carson and Hussey (1962), regularity in asin orientation is caused by a system of circulating currents set up in the lakes by prevailing northeasterly winds.

Part I—Bird Populations

Procedures

Numbers of waterfowl (Anatidae), loons (Gaviidae), phalaropes (Phalaropodidae), sandpipers (Scolopacidae), plovers (Charadriidae), and jaegers (Stercorariidae) were appraised by weekly or biweekly censuses conducted by two or three men. Birds were counted on two 2.6-km² plots in 1971, and a third plot was added during the period 1972 to 1975. The three areas were sections 13, 24, and 25 of R 13 E, T 12 N, Umiat meridian, as shown on the 1970 U.S. Geological Survey maps 2561 1 NW and 2561 SW (Fig. 2). Because home ranges of whistling swans *(Olor columbianus)* were larger than the census plots, swan densities were estimated from observations on an 18-km² area frequently traversed by the investigators. Other birds were counted on a strip 8 km long and 100 m wide in 1971 and on nine widely spaced

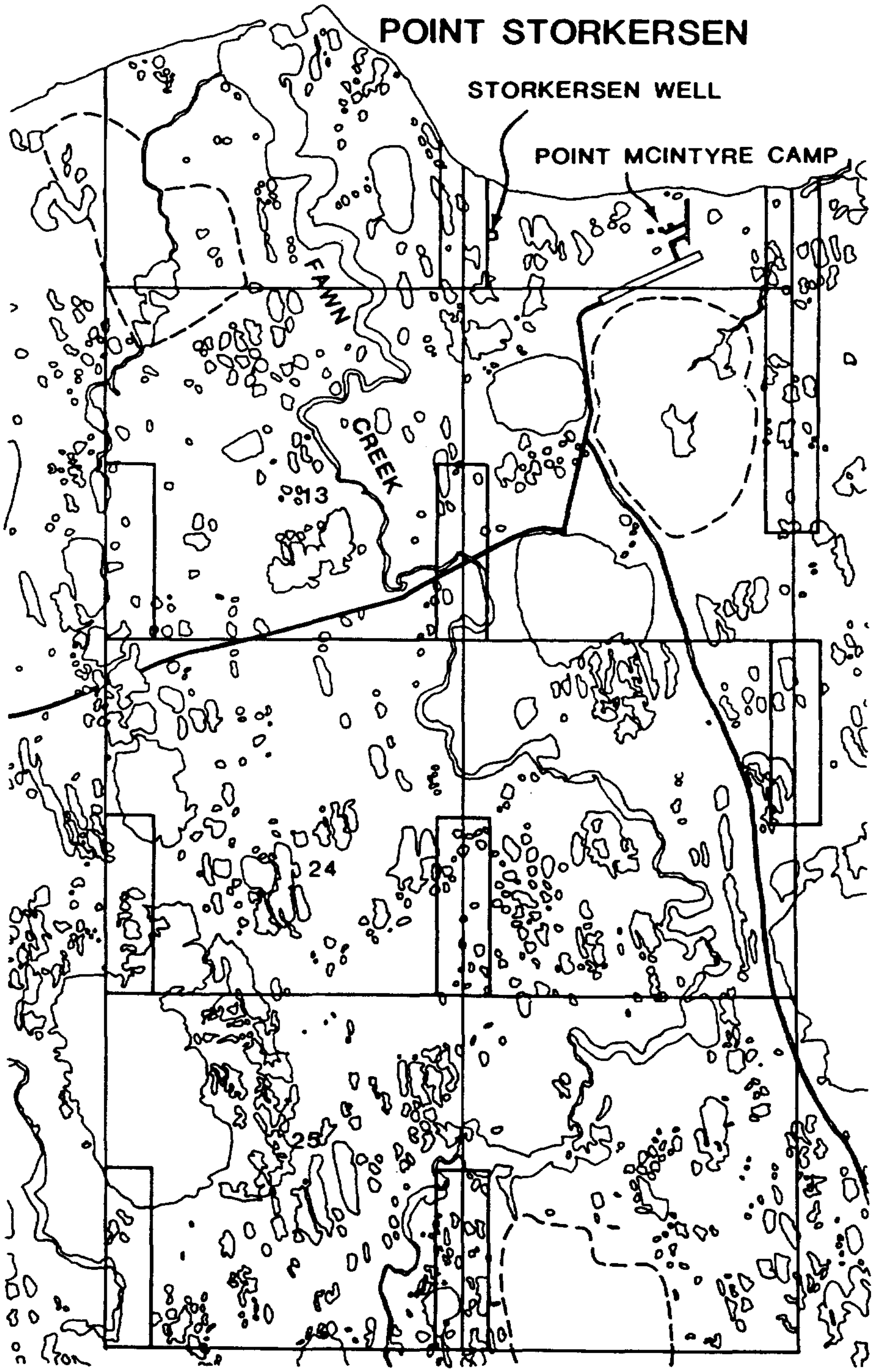

Fig. 2. Map of the Storkersen Point study area showing the Pt. McIntyre Distant Early Warning (DEW-line) site, Storkersen Well, the sections (1.6 km intervals) used for large-bird surveys, and the strips (0.2 km wide) used for small-bird surveys.

quadrats of the same length but 200 m wide totaling 1.6 km^2 in 1972 through 1975 (Fig. 2).

Although no attempt was made to find all nests, those found in the study area were marked with a garden wand and the location was recorded on a map. During 1971-73, nests were rechecked approximately weekly to determine clutch size and nest success. Any nest in which one egg or more hatched was considered successful.

Nesting Species

Water-related birds dominated the bird fauna near Storkersen Point. Of the 25 species that nested in the study area, 11 were swimming birds (waterfowl, loons, and phalaropes), and 4 were wading birds (sandpipers). In addition, black-bellied plovers *(Pluvialis squatarola)*, jaegers *(Stercorarius)*, and glaucous gulls *(Larus hyperboreus)* occasionally used water areas. Lapland longspurs *(Calcarius lapponicus)* and snow buntings *(Plectrophenax nivalis)* were the only breeding passerines, primarily because brush and shrub habitats used by other species on the Arctic Slope (Kessel and Cade 1958; Pitelka 1974) do not exist on this portion of the coastal plain.

Eighteen of the 25 species of nesting birds arrived when snow covered more than 75% of the tundra (Table 2). Water used by black brant *(Branta nigricans)*, ducks, and red phalaropes *(Phalaropus fulicarius)* at this time was in tundra depressions or partially thawed ponds. Terrestrial or grazing birds occupied snow-free patches of tundra. The arctic loon *(Gavia arctica)* and red-throated loon *(Gavia stellata)* were among the last birds to arrive.

Before the ice had melted at Storkersen Point, water birds gathered in nearby staging areas where water was available. Each year, arctic loons, red-throated loons, and king eiders *(Somateria spectabilis)* concentrated in deltas of the Sagavanirktok and Kuparuk Rivers and adjacent zones of the Beaufort Sea where rivers carried melt water to the coast from the phenologically advanced Arctic Foothills and interior coastal plain. An extensive zone partially free of snow and ice also surrounded oil facilities a few

Table 2. *First sighting of 25 species of breeding birds in relation to spring thaw, based on observations from 30 or 31 May each year, 1971-75, at Storkersen Point.*

Species	Range of arrival dates	Maximum snow cover (Percent)
Whistling swan *(Olor columbianus)*	[a]	> 90
Glaucous gull *(Larus hyperboreus)*	[a] to 1 June	> 90
Lapland longspur *(Calcarius lapponicus)*	[a] to 1 June	> 90
White-fronted goose *(Anser albifrons)*	[a] to 3 June	> 90
Dunlin *(Calidris alpina)*	[a] to 3 June	> 90
Baird's sandpiper *(C. bairdii)*	[a] to 3 June	> 90
Semipalmated sandpiper *(C. pusilla)*	[a] to 4 June	> 90
Ruddy turnstone *(Arenaria interpres)*	[a] to 4 June	> 90
Snow bunting *(Plectrophenax nivalis)*	[a]	> 90
American golden plover *(Pluvialis dominica)*	[a] to 5 June	> 75
Oldsquaw *(Clangula hyemalis)*	[a] to 5 June	> 75
Pectoral sandpiper *(Calidris melanotos)*	[a] to 5 June	> 75
Pintail *(Anas acuta)*	[a] to 7 June	> 75
Black-bellied plover *(Pluvialis squatarola)*	[a] to 7 June	> 75
Parasitic jaeger *(Stercorarius parasiticus)*	[a] to 3 June	> 75
King eider *(Somateria spectabilis)*	1 to 5 June	> 75
Red phalarope *(Phalaropus fulicarius)*	1 to 8 June	> 75
Black brant *(Branta nigricans)*	2 to 3 June	> 75
Long-tailed jaeger *(Stercorarius longicaudus)*	2 to 11 June	> 75
Northern phalarope *(Lobipes lobatus)*	2 to 11 June	50–75
Red-throated loon *(Gavia stellata)*	5 to 11 June	25–50
Arctic loon *(Gavia arctica)*	7 to 12 June	25–50
Spectacled eider *(Somateria fischeri)*	7 to 16 June	25–50
Buff-breasted sandpiper *(Tryngites subruficollis)*	7 to 16 June	0–25
Long-billed dowitcher *(Limnodromus scolopaceus)*	16 to 29 June	0–10

[a] Birds on study area when investigators arrived on 30 or 31 May.

kilometers south at Prudhoe Bay, but this early melting was probably caused by road dust covering the snow (Benson et al. 1975).

Of the total number of birds in the study area each spring (Table 3), shorebirds (plovers, sandpipers, and phalaropes) made up 60 to 70%, and waterfowl represented about 15%. Red phalaropes were most abundant, ranging from 15 to 37 birds per km^2 in June. Among waterfowl, densities of pintails *(Anas acuta)*, oldsquaws *(Clangula hyemalis)*, and king eiders were highest, but about 80% of the pintails were males, suggesting that most were nonbreeders. Only two pintail nests were found, both in 1973 when the Prairie Pothole Region was dry, and no broods were seen. Pitelka (personal communication) indicates that breeding of pintails is more regular in the Point Barrow area. Nonbreeders formed approximately 50 to 75% of the black brant and white-fronted goose *(Anser albifrons)* populations in June. Lapland longspurs varied from 10 to 49 birds per km^2 and constituted the dominant upland bird.

Nest initiation by summer residents closely followed their arrival (Table 4). Whistling swans, semipalmated sandpipers *(Calidris pusilla)*, and Lapland longspurs began nesting first, and loons and buff-breasted sandpipers *(Tryngites subruficollis)* started last. Laying was late in 1972 (Table 3), especially for early nesters, due to a delay of approximately 1 week in thawing of snow and ice in nesting habitats. Nesting occurred mainly during periods shown in Fig. 3. Because no attempt was made to find all nests in the study area, numbers shown in Table 4 give only a relative index of nest densities for the majority of species. Red phalaropes and semipalmated sandpipers nested in the highest densities. Pectoral sandpipers *(Calidris melanotos)* and dunlins *(Calidris alpina)* undoubtedly nested in larger numbers than indicated in Table 3, but females usually flushed so far from investigators that they could not locate the nest. All nests of loons and whistling swans and most nests of eiders and white-fronted geese probably were found during the study,

Table 3. *Range of densities of 24 species of breeding birds as shown by lowest and highest values recorded in June, July, and August 1971-75.*

	No. per km^2					
	June		July		1-15 August	
Species	Low	High	Low	High	Low	High
Arctic loon	0.0	1.6	1.0	2.9	1.6	2.2
Red-throated loon	0.0	1.6	0.1	1.6	0.1	1.6
Whistling swan	0.0	0.1	0.0	0.5	0.0	0.4
Black brant[a]	0.0	5.1	0.0	2.0	0.0	0.0
White-fronted goose[a]	0.3	1.6	0.0	2.0	0.4	8.6
Pintail[b]	0.3	7.8	0.0	6.6	8.6	21.1
King eider	0.3	8.9	0.1	3.5	0.4	1.2
Spectacled eider	0.0	1.8	0.0	0.4	0.0	0.6
Oldsquaw	0.3	5.1	1.2	4.3	0.1	9.0
American golden plover	0.1	3.8	0.0	3.5	0.0	5.9
Black-bellied plover	0.0	0.6	0.1	1.6	0.4	2.3
Ruddy turnstone	0.0	3.2	0.0	0.4	0.0	0.4
Buff-breasted sandpiper	0.0	10.0	0.0	3.0	0.0	3.2
Pectoral sandpiper	3.8	22.0	2.5	19.0	8.0	40.4
Dunlin	9.0	21.2	0.0	20.0	5.0	16.0
Baird's sandpiper	0.0	4.0	0.0	6.0	0.4	5.0
Semipalmated sandpiper	11.0	20.0	8.0	47.0	2.0	17.3
Red phalarope	15.6	37.0	3.2	32.0	8.0	83.9
Northern phalarope	0.0	5.0	0.0	3.0	0.0	53.2
Parasitic jaeger	0.4	0.5	0.1	1.2	0.0	0.8
Long-tailed jaeger	0.0	0.4	0.0	0.4	0.0	0.4
Glaucous gull	0.1	0.2	0.3	0.3	0.3	0.3
Lapland longspur	10.0	48.8	6.0	10.0	2.0	5.1
Snow bunting	0.0	3.0	0.0	4.0	0.0	5.0

[a] Nonbreeders made up 50 to 75% of the population in June.

[b] Nonbreeders made up more than 90% of the population in June.

Table 4. *Estimated date of first egg laying and clutch size of birds at Storkersen Point, 1971-73.*

Species	No. of nests	Est. date first egg laid in June			Clutch size			
		1971	1972	1973	Mean	Mode	Range	No.
Arctic loon	42	20	23	21	2.0	2	-2-	23
Red-throated loon	28	18	25	21	1.8	2	1-2	21
Whistling swan	4	1	12	—	3.0	3	-3-	3
Black brant	11	5	18	12	5.0	5	-5-	4
White-fronted goose	8	5	15	9	4.7	4	3-8	7
Pintail	2	—	—	8	6.0	6	6	1
King eider	32	8	19	10	4.5	4	2-7	17
Spectacled eider	3	—	21	—	4.5	4-5	4-5	2
Oldsquaw	16	9	19	23	6.7	7	6-7	3
Golden plover	13	7	22	9	3.8	4	3-4	10
Black-bellied plover	1	—	20	—	4.0	4	4	1
Ruddy turnstone	1	—	20	—	4.0	4	4	1
Buff-breasted sandpiper	4	17	24	22	3.8	4	3-4	4
Pectoral sandpiper	2	23	26	—	4.0	4	-4-	2
Dunlin	9	20	7	10	4.0	4	-4-	7
Baird's sandpiper	5	—	10	—	3.6	4	3-4	5
Semipalmated sandpiper	34	4	8	6	3.9	4	3-4	29
Red phalarope	46	14	15	15	3.8	4	3-4	30
Northern phalarope	2	14	20	—	4.0	4	-4-	2
Parasitic jaeger	7	14	16	10	2.0	2	-2-	7
Long-tailed jaeger	4	18	18	12	2.0	2	-2-	4
Glaucous gull	3	—	—	10	3.0	3	-3-	2
Lapland longspur	15	2	7	1	5.6	6	3-7	9
Snow bunting	8	9	12	10	6.0	6	-6-	2

because incubating birds were conspicuous and considerable time was devoted to this effort. Data on clutch size shown in Table 4 represent those nests in which egg numbers did not change on subsequent nest checks made about 1 week apart. A red phalarope nest containing eight eggs is not included in Table 4, because two females probably laid in the nest.

The number of avian predators such as jaegers, glaucous gulls, and common ravens *(Corvus corax)* did not appear to vary over the 5 years. Most predation seemed to be by arctic foxes *(Alopex lagopus)* which were present each year but could not be counted. Losses of eggs of loons, eiders, shorebirds, and jaegers were lowest in 1972 when there were fewer sightings of foxes (Table 5). One gray wolf *(Canis lupus)* was observed in 1974, and one barren ground grizzly bear *(Ursus horribilis)* was seen in 1975.

In addition to recruitment of young, emigration and immigration of birds influenced composition and densities (Table 3) of populations in the postnesting period. Changes were most noticeable for sexually dichromatic species. Male king eiders and spectacled eiders *(Somateria fischeri)* abandoned their mates in late June or early July and migrated to sea; females unsuccessful at nesting left by August. Male oldsquaws moved to the coastal waters of the Beaufort Sea in mid-July to pass their flightless stage. However, numbers of oldsquaw increased on the study area in August, because females without young grouped on a large lake during their annual wing molt. Female red phalaropes gathered in large flocks and emigrated in late June or early July, and most adult males were gone by August. Large flocks, presumed to be mainly juveniles, reappeared in August in some years. Increased densities of white-fronted geese and pintails in August (Table 3) resulted from an influx of postmolting birds.

The latest observations were made on 1 and 2 September 1973 when loons, swans, and female oldsquaws occupied the same wetlands they used in August, and flocks of pectoral sandpipers and snow buntings *(Plectrophenax nivalis)* were common. Numbers of other species, however, were considerably reduced from summer levels. Species not seen in September included ruddy turnstone *(Arenaria interpres)*, buff-breasted sandpiper *(Tryngites subruficollis)*, Baird's sandpiper *(Calidris bairdii)*, semipalmated sandpiper, and long-tailed jaeger *(Stercorarius longicaudus)*. Few red phalaropes were on the study area, but several groups of immatures occupied coastal waters of the Beaufort Sea.

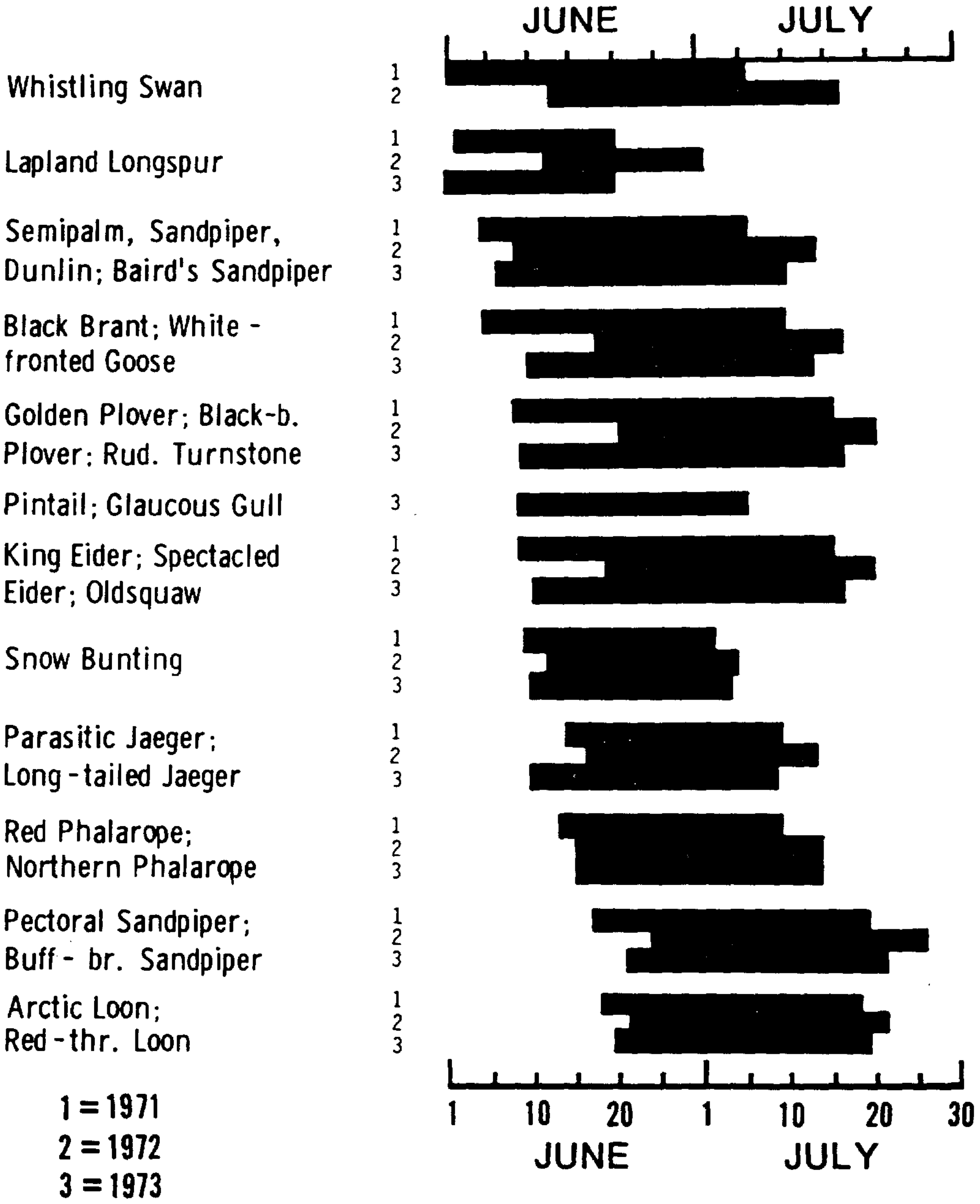

Fig. 3. Chronology and duration of nesting at Storkersen Point, 1971-73.

Table 5. *Estimates of nest success and production for birds in the Storkersen Point area, 1971-73.*

	1971		1972		1973	
Species	Percent nest success (No.)	Average young per km²	Percent nest success (No.)	Average young per km²	Percent nest success (No.)	Average young per km²
Arctic loon	28(14)	0.4	92(12)	0.7	53(15)	0.6
Red-throated loon	33(6)	0.3	78(9)	0.6	45(9)	0.4
Whistling swan	100(1)	0.2	100(1)	0.2	100(1)	0.2
Black brant	0(4)	—	0(2)	—	0(2)	—
White-fronted goose	100(1)	0.6	100(4)	1.4	50(2)	0.5
Pintail	—	—	—	—	0(2)	—
King eider	0(3)	0.4	15(13)	1.6	0(16)	0.4
Spectacled eider	—	—	50(2)	0.2	0(1)	—
Oldsquaw	0(4)	—	0(6)	0.3	0(6)	—
Golden plover	25(4)	0.4	60(5)	1.0	33(3)	0.6
Black-bellied plover	—	0.2	100(1)	0.2	—	0.2
Ruddy turnstone	—	—	0(1)	0.2	—	—
Buff-breasted sandpiper	0(1)	—	50(2)	0.4	0(1)	—
Pectoral sandpiper	0(1)	0.4	—	2.7	—	3.9
Dunlin	0(2)	1.6	100(4)	13.3	33(3)	9.8
Baird's sandpiper	—	0.4	67(3)	2.0	0(1)	1.2
Semipalmated sandpiper	18(13)	2.3	88(8)	3.9	75(4)	6.6
Red phalarope	17(23)	2.3	80(10)	11.7	25(8)	6.6
Northern phalarope	0(1)	0.4	—	0.4	—	0.4
Parasitic jaeger	0(2)	—	100(2)	0.6	50(2)	0.2
Long-tailed jaeger	0(1)	—	100(1)	0.2	0(1)	—
Glaucous gull	100(1)	0.2	100(1)	0.2	—	—
Lapland longspur	0(4)	1.2	80(5)	3.1	67(6)	5.9
Snow bunting	67(3)	0.8	100(3)	0.8	100(2)	0.8
Total		12.1		45.7		38.3

Visitors

In addition to the 25 species of birds known to breed at Storkersen Point, 47 species of birds were observed but not found nesting (Table 6). Some obviously visited from nearby nesting or roosting areas: Canada goose *(Branta canadensis)*, lesser snow goose *(Chen caerulescens)*, common eider *(Somateria mollissima)*, glaucous gull, arctic tern, and common raven. Based on brood sightings, a few Canada geese nested on the mainland about 10 to 15 km south of Storkersen Point and in the Kuparuk River delta. In 1973, nests of 40 lesser snow geese were found on Howe Island in the Sagavanirktok River delta. The colony seemingly was first established in 1971 (Gavin 1975) and is the only known nesting colony of lesser snow geese on the North Slope of Alaska although single pairs were known to nest (King 1970). Common eiders, king eiders, glaucous gulls, and arctic terns nested on gravel islands a few kilometers off the mainland coast (Schamel 1974). Although snowy owls *(Nyctea scandiaca)* were observed in all months of the study, their occurrence was irregular during weekly censuses.

Discussion

The bird fauna near Storkersen Point reflects the preponderance of aquatic habitats as opposed to the scarcity of other avian habitats. Only 25 of 72 species nested on or near the study area. Of these, 20 species were water-related birds (loons, waterfowl, shorebirds, and gulls). The only terrestrial birds observed nesting on the study area were lapland longspurs and snow buntings, probably because tall brush and dwarf shrub habitats used by other species (Kessel and Cade 1958) did not exist on this portion of the coastal plain. Neither snowy nor short-eared owls nested on the area during this study but snowy owls hunted in the area and may nest in high lemming years.

The number and composition of breeding birds near Storkersen Point is comparable to information published about other arctic coastal tundra areas. Kessel and Cade (1958) listed 51 species in the coastal region, but at least 15 were considered rare and sporadically distributed. Andersson (1973) reported 30 species possibly nesting at Nuvagapak Point, 270 km east on the Beaufort Sea coast, and status and densities of birds were similar to birds found in this study. Gavin (1975) observed 67 species on the entire plain and suggested some breeding by at least 23 species. A thorough analysis of published data through 1974 by Pitelka (1974) indicates that, of 97 species known to breed on the entire North Slope, 44 species breed regularly on the coastal zone. However, only 22 breed regularly at Point Barrow and 13 breed occasionally.

The apparent geological and vegetational homogeneity of the coastal plain in the Prudhoe Bay tundra indicates that numbers and status of birds at Storkersen Point is fairly representative of the region. Studies just a few kilometers inland (Norton et al. 1975) reflect similar dominant breeding birds but also some casual migrants that we did not observe on the coastal areas. Number of species probably is even higher along inland river valleys where habitat diversity is greater, but coastal areas, of which the Arctic Coastal Plain habitat at Storkersen Point is an important segment, are exceptionally valuable to breeding birds such as black brant, king eiders, oldsquaws, and many shorebirds.

Part II—Wetland Types in Relation to Water Birds

Procedures

Physical and vegetational characteristics of aquatic habitats were appraised during late June and early August of 1972 and 1973. Wetlands (defined here as clearly-defined basins holding water part of the summer) sampled were those encountered while walking along seven east-west lines spaced approximately 1 km apart; four of these transects were 3.2 km long and three were 1.6 km long. In August 1972, measurements of water depth and plant distribution were made in all wetlands within the 7.8 km^2 areas used to census loons and waterfowl. Sampling procedure in 1972 involved determining water depths, hydrogen ion concentration (pH), and free carbon dioxide. Water depths, recorded as the distance from water surface to the surface of basin sediments, were measured 1 m from the eastern and western shores and in the center of the basin. The two shoreward measurements and two measurements in the center of the basin were used to calculate mean water depth of each wetland. Hydrogen-ion concentration was determined with a Hach pH Kit (Model 17-N)[1]. In 1973, specific conductance of surface water was measured in 18 ponds with a Hach Conductivity Meter (Model 2510) that recorded in micromhos per centimeter. Temperature was recorded in ponds of different sizes with Marshalltown Model 1000 continuous-recording thermographs.

In June 1972, two lines were established across each wetland in east-west and north-south directions, and the presence or absence of various plants was recorded at 10-cm intervals along each line. During August of 1972, visual estimates were made of the percentage of each wetland supporting vegetation.

Use of wetlands by loons and waterfowl was appraised by weekly or biweekly ground surveys via the same techniques used for assessment of populations of small birds. Base maps prepared from the U.S. Geological Survey 1:24,000 series Orthophotomap (Topographic) were used to record locations of water birds.

Characteristics of Wetlands

Characteristics of wetlands useful in deriving a classification system were size, depth, species, and abundance of vascular aquatic plants and water chemistry. Data on thermal regimes also were collected.

Size and depth.—Wetlands near Storkersen Point varied from small, flooded tundra depressions a few meters long to open lakes or marshy, partially-drained lake basins over 1 km long. Still larger lakes were prominent further inland and in the western part of the plain. Depths ranged from a few centimeters in flooded tundra to a maximum of 1.1 m in the larger lakes. Flooded depressions and small, shallow ponds rimmed with sedge *(Carex aquatilis)* were the most numerous wetlands, representing nearly one-half of the total wetland area during the period of available aquatic habitat. Their small size lessened their use by large water birds. Large lakes and marshy areas in partially-drained basins provided the largest units of permanent aquatic habitat.

The relationship between surface area and water depth of wetlands (Fig. 4) revealed that mean depth of the smaller classes of first generation basins increased directly with increasing surface area. The relationship was less predictable in the large size classes because of partial drainage of these wetlands or union with adjacent basins lying at a lower level.

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[1] Reference to trade names does not imply Government endorsement of commercial products.

Table 6. *Birds observed at Storkersen Point that did not nest in the study area.*

Species	Date of first observation 1971	1972	1973	1974	1975	Status[a]	Maximum number seen
Common loon *(Gavia immer)*	—	2 July	—	—	6 June	E	6
Yellow-billed loon *(G. adamsii)*	—	4 June	—	11 June	—	C	4
Canada goose *(Branta canadensis)*	19 June	4 June	4 June	12 June	16 June	A	110
Lesser snow goose *(Chen caerulescens)*	4 June	4 June	8 June	8 June	29 June	A	105
Mallard *(Anas platyrhynchos)*	4 June	2 Aug.	20 June	13 June	—	C	5
American wigeon *(A. americana)*	2 June	9 June	2 June	31 May	—	C	145
Northern shoveler *(A. clypeata)*	—	—	9 June	—	—	C	10
Green-winged teal *(A. crecca carolinensis)*	4 June	8 Aug.	6 June	—	—	C	65
Greater scaup *(Aythya marila)*	4 June	—	14 June	—	18 June	C	7
Common eider *(Somateria mollissima)*	7 June	—	9 June	30 May	3 June	A	3
Steller's eider *(Polysticta stelleri)*	8 June	12 June	7 June	—	—	C	36
Surf scoter *(Melanitta perspicillata)*	7 June	1 July	25 June	7 July	—	C	66
Red-breasted merganser *(Mergus serrator)*	—	28 June	—	7 July	—	C	2
Rough-legged hawk *(Buteo lagopus)*	5 Aug.	29 June	8 June	—	—	C	5
Golden eagle *(Aquila chrysaetus)*	—	9 July	—	—	28 July	C	1
Peregrine falcon *(Falco peregrinus)*	27 June	27 July	11 July	—	—	C	5
Rock ptarmigan *(Lagopus mutus)*	—	b	b	—	—	D	17
Semipalmated plover *(Charadrius semipalmatus)*	—	—	8 June	—	—	C	1
Common snipe *(Capella gallinago)*	4 June	—	—	—	—	C	1
Lesser yellowlegs *(Tringa flavipes)*	—	—	6 June	—	—	C	1
Stilt sandpiper *(Micropalama himantopus)*	30 July	1 Aug.	24 July	2 Aug.	—	B	180
Whimbrel *(Numenius phaeopus)*	—	—	—	—	17 July	C	1
White-rumped sandpiper *(Calidris fuscicollis)*	2 June	—	—	—	—	C	20
Bar-tailed godwit *(Limosa lapponica)*	—	4 June	—	—	—	C	2
Pomarine jaeger *(Stercorarius pomarinus)*	b	2 June	1 June	31 May	3 June	B	180
Thayer's gull *(Larus thayeri)*	—	15 June	9 Aug.	—	—	C	2
Sabines's gull *(Xema sabini)*	6 June	6 June	4 June	9 Aug.	—	C	50
Arctic tern *(Sterna paradisaea)*	4 June	9 June	5 June	5 June	7 June	A	250
Murre *(Uria sp.)*	20 July	—	—	—	—	E	30
Tufted puffin *(Lunda cirrhata)*	—	12 Aug.	—	—	—	E	1
Snowy owl *(Nyctea scandiaca)*	b	b	b	b	b	B	40
Short-eared owl *(Asio flammeus)*	b	3 June	4 June	11 June	4 June	C	21
Horned lark *(Eremophila alpestris)*	—	—	6 June	—	—	C	2
Cliff swallow *(Petrochelidon pyrrhonota)*	7 June	—	—	—	7 June	C	1
Bank swallow *(Riparia riparia)*	—	9 June	—	—	5 June	C	1
Common raven *(Corvus corax)*	b	16 June	5 June	30 May	5 June	B	150
American robin *(Turdus migratorius)*	—	—	b	—	—	C	1
Wheatear *(Oenanthe oenanthe)*	—	8 June	—	—	1 July	C	1
Yellow wagtail *(Motacilla flava)*	—	5 July	—	—	—	C	1
Water pipit *(Anthus spinoletta)*	—	—	—	—	7 June	C	1

Continued

Table 6. *Birds observed at Storkersen Point that did not nest in the study area.—Continued*

Species	Date of first observation 1971	1972	1973	1974	1975	Status[a]	Maximum number seen
Wilson's warbler *(Wilsonia pusilla)*	—	—	1 Sept.	—	—	C	1
Redpoll *(Acanthis* sp.*)*	—	2 June	6 June	8 June	8 June	C	100
Savannah sparrow *(Passerculus sandwichensis)*	2 June	—	11 June	—	9 June	C	4
Dark-eyed junco *(Junco hyemalis)*	—	—	—	5 June	—	C	1
Tree sparrow *(Spizella arborea)*	—	4 June	5 June	2 June	—	C	2
White-crowned sparrow *(Zonotrichia leucophrys)*	—	2 June	—	—	—	C	2
Fox sparrow *(Passerella iliaca)*	—	9 June	—	—	—	C	1

[a] Status: A = Visitor from nearby nesting or roosting sites.
B = Regular summer visitor.
C = Casual or accidental visitor.
D = Winter visitor.
E = Individuals observed over coastal water of the Beaufort Sea.
— = Not seen.

[b] Birds on study area when investigators arrived on 30 or 31 May.

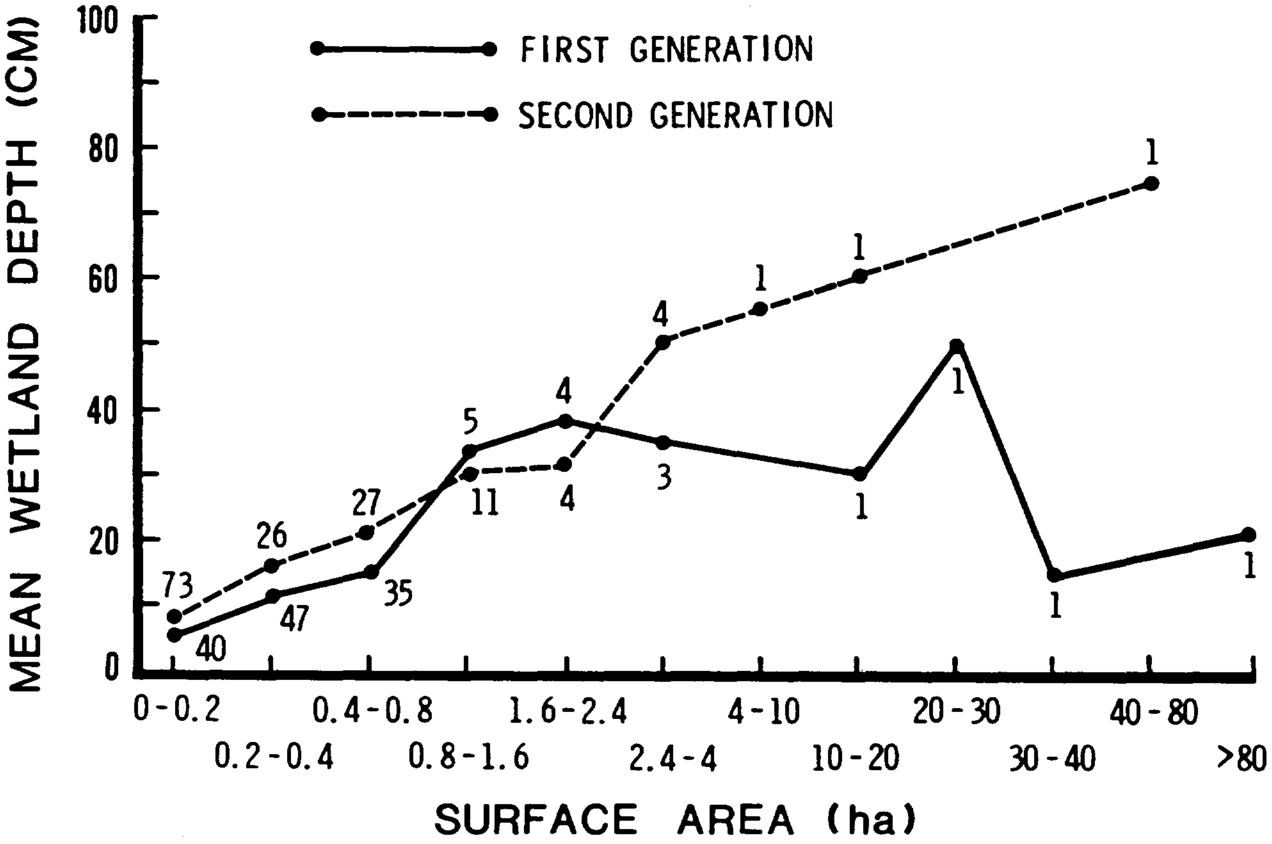

Fig. 4. Relationship between mean water depth and surface area of first and second generation wetlands, 2-8 August 1973. Sample size shown by points.

In contrast, second generation wetlands formed in drained basins showed a uniform increase in mean depth as basin area increased. Presumably, drainage of these newer basins was rare because of their low elevation.

First generation wetlands can attain considerable size before drainage occurs. Several lakes of more than 150 ha and more than 1.5 m deep occurred within 10 km of the study site. Consequently, the depth-area curve for that region would differ markedly from Fig. 4.

Factors other than drainage also contributed to variations in the direct relationship between basin area and water depth. Carson and Hussey (1962) ascribed differences in depth of similar size thaw lakes near Barrow, Alaska (Lat. 71°20'N, Long. 156°50'W), to irregularities in ground ice distribution, particle size of sediments, and individual basin histories. In the Storkersen Point area, a noticeable cause was recent coalescence of two or more basins which, in effect, increased surface area relative to water depth.

Vascular aquatic plants.—Distribution of vascular plants in wetlands on the coastal plain is influenced by water depth (Britton 1957). Fig. 5 illustrates the occurrence of *Carex aquatilis* (water sedge) and *Arctophila fulva* (pendant grass) in relation to water depth of wetlands near Storkersen Point; depth measurements were taken at the shallow and deep water margins of stands. Of 69 stands examined, *C. aquatilis* was prevalent on moist soils and progressively less so at increasing water depth; plants were not found at water depths greater than 30 cm. Optimal depths for *A. fulva* (52 stands) occurred between 20 and 45 cm, and plants were absent in depths exceeding 80 cm. Few stands were encountered that contained large numbers of both species, and an obvious belted pattern in wetlands resulted where *C. aquatilis* formed shoreward stands abutting deeper water stands of *A. fulva*. The intersection of depth-frequency lines in Fig. 4 indicates that 15 cm is the most frequent depth interface between the two species. Because *C. aquatilis* and *A. fulva* are dominant vascular plants

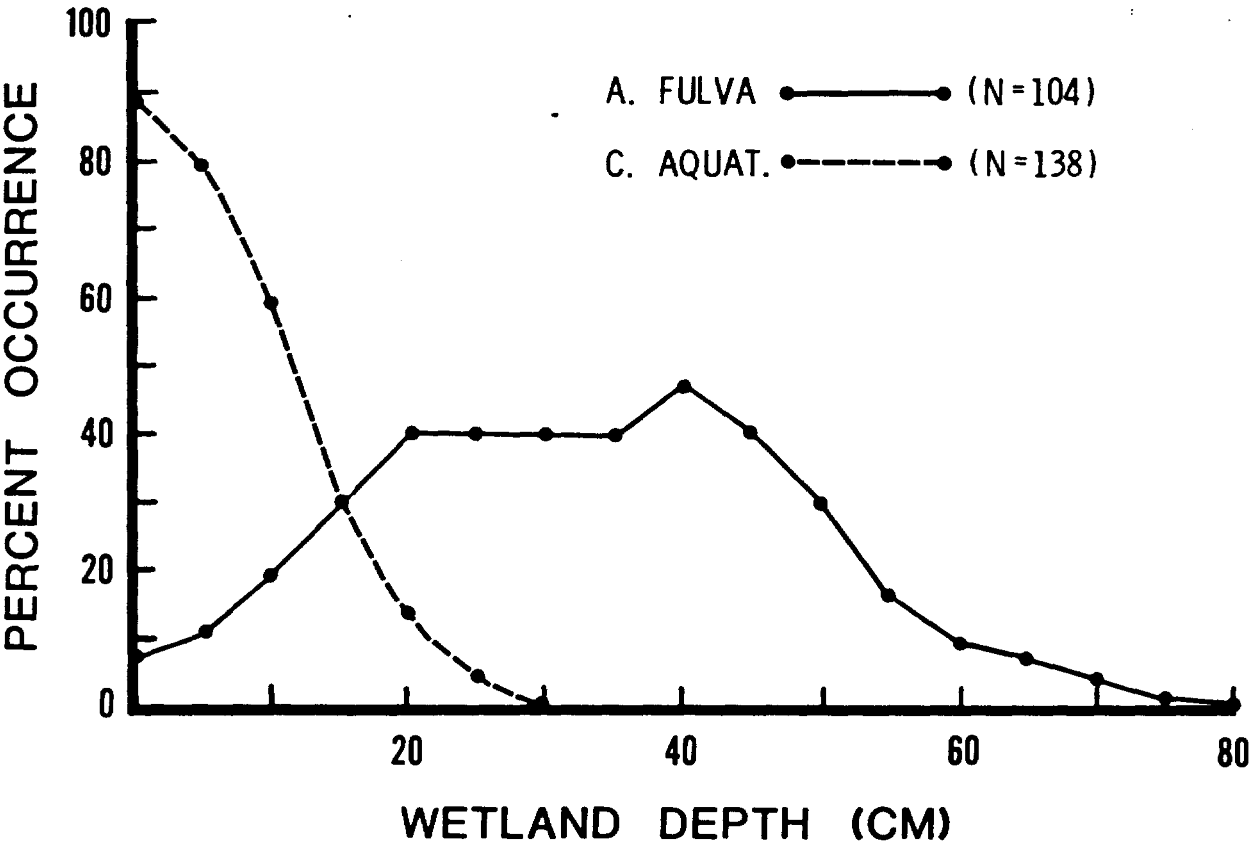

Fig. 5. Occurrence of *Carex aquatilis* and *Arctophila fulva* in relation to water depths. Measurements are an average of minimum and maximum depths in stands found in 80 wetlands, 2–3 August 1973.

in freshwater habitats near Storkersen Point and throughout the coastal plain (Spetzman 1959), the distribution of these emergents is a good indicator of changes in wetland basins resulting from thawing of the permafrost.

Other vascular plants found in freshwater wetlands near Storkersen Point were less widely distributed than *Carex aquatilis* and *Arctophila fulva: Eriophorum angustifolium, E. russeolum* and *E. scheuchzeri* often formed mixed stands with *C. aquatilis* but were less tolerant of standing water; few such plants grew in depths greater than 10 cm. *E. angustifolium* frequently formed nearly pure stands on moist soils and on low-center polygon basins covered by a few centimeters of water. *Hippuris vulgaris, Caltha palustris, Cardamine pratensis, Ranunculus pallasii, R. gmelini,* and *R. hyperboreus* usually were found submerged and growing from a peat substrate. An aquatic moss, *Drepandocladus* sp., also was common in such situations.

The influence of water chemistry on the distribution and composition of aquatic plants was apparent in coastal wetlands containing brackish or subsaline water. These basins lacked *Carex aquatilis* and *Arctophila fulva.* Moreover, the only plants found in these wetlands were a sedge *(Carex subspathacea)* and a grass *(Puccinellia phryganodes)*, two relatively prostrate and diminutive species that inhabit shallow water and adjacent uplands. At Storkersen Point, neither was found outside zones occasionally flooded by sea water, a pattern in agreement with Wiggins and Thomas (1962).

Water chemistry.—Wetlands were ranked by salinity groupings used by Stewart and Kantrud (1972) for classification of prairie ponds. Basins connected to the sea or periodically flooded by sea water during tides or storms (coastal lowlands in Table 7) contained brackish or subsaline water (3,800 to 20,000 micromhos/cm; n = 10, 2 to 9 August 1973). Specific conductivity of coastal sea water in

Table 7. *Specific conductance and hydrogen ion concentration of wetlands near Storkersen Point in early August 1972.*

Location of wetlands	Specific conductance (micromhos/cm)			pH		
	Mean	Range	No.	Mean	Range	No.
Coastal lowlands	>14,440[a]	3,800 - >20,000[a]	11	8.9	8.9	3
Coastal uplands	730	405 - 1,370	17	8.7	8.5–8.9	11
Inland (>1.609 km)	365	220–550	50	8.5	6.2-9.0	43

[a] Maximum meter reading was 20,000 micromhos/cm.

August varied from 16,000 to more than 20,000 micromhos/cm (the scale limit of the conductivity meter, n - 3), values which are within the normal subsaline range (14,000 to 45,000 micromhos/cm). Wetlands lying within a few meters of the coast, but situated above sea level, were slightly brackish, and measurements were never higher than 1,370 micromhos/cm in August. As distance from the sea increased, conductivity of waters decreased, and a level of 500 micromhos/cm between slightly brackish and freshwater wetlands occurred approximately 1.5 km inland from the coast.

The pH of surface water (Table 7) in aquatic habitats ranged from slightly acid (6.2) to very basic (9.0). Waters of coastal lowlands had pH values of 8.9 ($n = 3$), measurements identical to coastal Beaufort Sea water. Seasonal increases in specific conductance of wetlands were evident from measurements taken in late June and early August 1972. Presumably, this seasonal change results from dilution by relatively pure melt water during spring breakup, followed by declining water levels during summer. Seasonal variation in water chemistry (Table 8) shows the effects of seasonal drying.

Thermal regimes.—Because ice forms to depths of about 2 m in coastal plain lakes (Brewer 1958), wetlands near Storkersen Point were completely frozen until late May or early June. Open water first occurred where snow melt filled tundra depressions and where snow and surface ice thawed on shallow ponds. Once thaw began, ice in these shallow wetlands melted from top to bottom within a few days. Mean daily temperature of shallow waters often exceeded the mean for surrounding air due to differential warming and cooling rates (Danks 1971). Large, deep lakes thawed last and were completely open by late June 1971 and early July in other years. In contrast to smaller wetlands, ice on lakes floated after it had melted sufficiently to become free from the bottom. This resulted in a moat of open water surrounding a central cake of ice which persisted as long as 2 weeks.

Most arctic lakes and probably all coastal plain wetlands are essentially isothermal in summer. Livingstone et al. (1958) found no thermal stratification even in arctic mountain lakes 18 m deep. Near Point Barrow, constant mixing of waters by wind maintains an isothermal condition in all wetlands (Brewer 1958), although Carson and Hussey (1962) did find some stratification in shallow, marshy portions of lakes where water was free from intense wave agitation.

The magnitude of diurnal temperature fluctuations in wetlands was inversely related to basin volume

Table 8. *Seasonal changes in some chemical variables of aquatic habitats at Storkersen Point, 1972.*

	1 June - 14 June	15 June - 14 July	15 July - 8 August
pH	6.9 (6.2- 7.9)[a]	7.6 (6.2- 8.5)	8.0 (6.7- 8.7)
Total hardness (ppm $CaCO_3$)	66.5 (17.1-138.8)	95.4 (51.3–153.9)	207.1 (102.6–973.5)
Alkalinity (ppm $CaCO_3$)	43.7 (17.1-102.6)	68.4 (34.2-102.6)	108.6 (68.4-136.8)
Dissolved oxygen (ppm)	14.1 (13 - 15)	13.9 (10 - 15)	13.8 (13 - 15)
Free CO_2 (ppm)	7.8 (5 - 15)	6.6 (5 - 15)	8.5 (5 - 20)

[a] Mean (range).

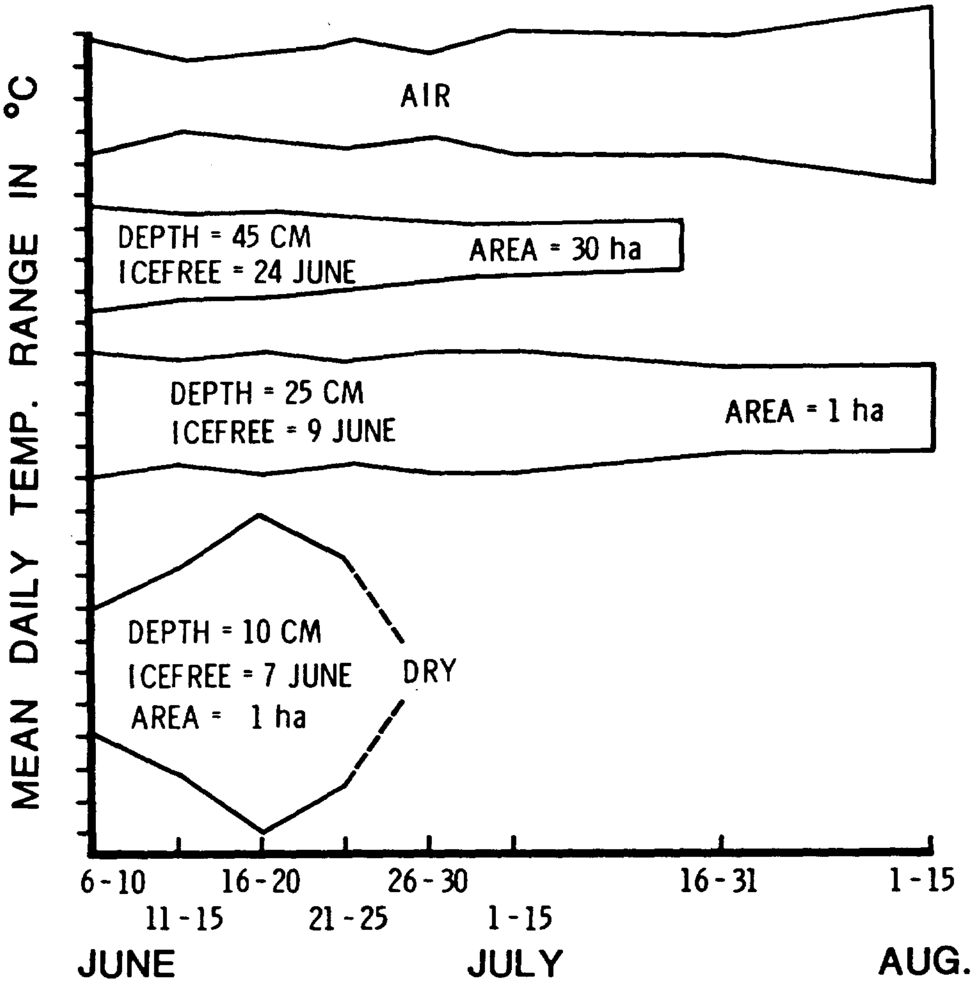

Fig. 6. Mean daily range of temperatures (C) in 1972, measured in three wetlands of different areas and depths compared with data from a weather station 2 m above ground.

(Fig. 6). Temperatures in shallow, flooded depressions underwent daily variations greater than those recorded for temperature of ambient air 2 m above ground, while the largest and deepest wetland exhibited the smallest diurnal temperature change.

Classification of Wetlands

Following the general guidelines established by Martin et al. (1953) for temperature areas, the wetland classification system outlined in Table 9 is designed to: (1) delineate aquatic habitats preferred by conspicuous swimming birds, such as loons and waterfowl, and (2) provide classes of wetlands useful for wetland inventories. Loons and waterfowl were used as indicator species, because they are conspicuous, widely distributed, and feed on a variety of aquatic invertebrates and, therefore, are more easily used to demonstrate change in habitat conditions. This system does not consider large riverbeds and their complex oxbow systems. It considers mainly wetlands that are nonfluvial and those fluvial waters identified as beaded streams by Hussey and Reckendorf (1963). Basin size is used in the system only to distinguish two size categories, ponds and lakes, following the definition by Stewart and Kantrud (1971) that ponds are less than 20 ha and lakes exceed 20 ha. Some classes possess wetlands of only pond or lake size.

Because of the large size range of wetlands, a sliding scale was used to delineate the shoreward and central zones of individual water basins. The shore zone extended approximately 10 m from shore in lakes, 6 m in large ponds, and 2 m in small wetlands.

Table 9. *Criteria used to delineate classes of wetlands near Storkersen Point.*

Wetland designation	Dominant emergents: Shore zone	Dominant emergents: Central zone	Conductivity	Common size
Flooded Tundra (Class I)	*Eriophorum angustifolium* or *Carex aquatilis*	*E. angustifolium* or *C. aquatilis*	Fresh or slightly brackish	Pond
Shallow-*Carex* (Class II)	*C. aquatilis*	Semi open to open	Fresh or slightly brackish	Pond
Shallow-*Arctophila* (Class III)	*C. aquatilis* or *Arctophila fulva*	*A. fulva*	Fresh or slightly brackish	Pond
Deep-*Arctophila* (Class IV)	*A. fulva*	Open	Fresh or slightly brackish	Pond or lake
Deep-open (Class V)	Open	Open	Fresh or slightly brackish	Lake
Basin-complex (Class VI)	Basin interspersed with *C. aquatilis, A. fulva,* and open water		Fresh or slightly brackish	Lake
Beaded Streams (Class VII)	*C. aquatilis, A. fulva,* or Open	Open or *A. fulva*	Fresh or slightly brackish	Pond= Bead
Coastal Wetlands (Class VIII)	*Puccinellia phryganodes, C. subspathacea,* or Open	Open	Brackish or subsaline	Pond or lagoon

The shoreward zone in large lakes is an obvious sublittoral shelf that abruptly fell to the deeper central zone. Depth zones were not distinct in ponds, except that the shoreward zone usually was most shallow and, consequently, vegetation often was found only near shore. Zones of wetlands were considered open if vegetation occurred in less than 5% of the area. The eight classes of wetlands are described as follows:

Class I: Flooded Tundra.—Shallow waters formed during spring thaw when melt water overflows stream basins (Plate I) or is trapped in vegetated tundra depressions (Plate II). Such pools formed in low centers of polygonal ground often produce a mosaic pattern of ridges and flooded sedge (Plate III). Water depths in June rarely exceed 10 cm, and surface water is absent or only a few centimeters deep by August. Unlike other classes, basins of these wetlands are poorly defined because *Carex aquatilis* and other plants tolerant of periodic flooding cover all or most of the basin. It is sometimes convenient to separate flooded tundra as flooded creek flats (Class Ia) or seasonally flooded basins in upland tundra (Class Ib).

*Class II: Shallow-*Carex.—Shallow ponds with a gently sloping shore zone surrounded by and usually containing emergent *Carex aquatilis* with a central open water zone. At Storkersen Point, maximum water depths in June vary between 10 cm and 30 cm. By August, water levels decline due to evaporation or drainage and sediments may be exposed over a large portion of the basin. Such basins also may be very small and may occur in a block mosaic pattern resulting from low center polygons (Plate III). Others are large and lack vegetation in the basin. This class can be subdivided as IIa, vegetated shore zone, and IIb, unvegetated shore zones.

*Class III: Shallow-*Arctophila.—Ponds or pools in beaded streams containing *Arctophila fulva* in the central zone and shoreward stands of *A. fulva* or *Carex aquatilis*. Shores are more abrupt than those of Class II ponds, and maximum water depths typically range from 20 to 50 cm. Pond margins occasionally are exposed during August.

Plate I. Type I flooded tundra in the low-lying areas along Fawn Creek, Storkersen Point study area. Rollagon tracks lead to the highest pingo on the area, which is about 10 m above the level of the surrounding plain.

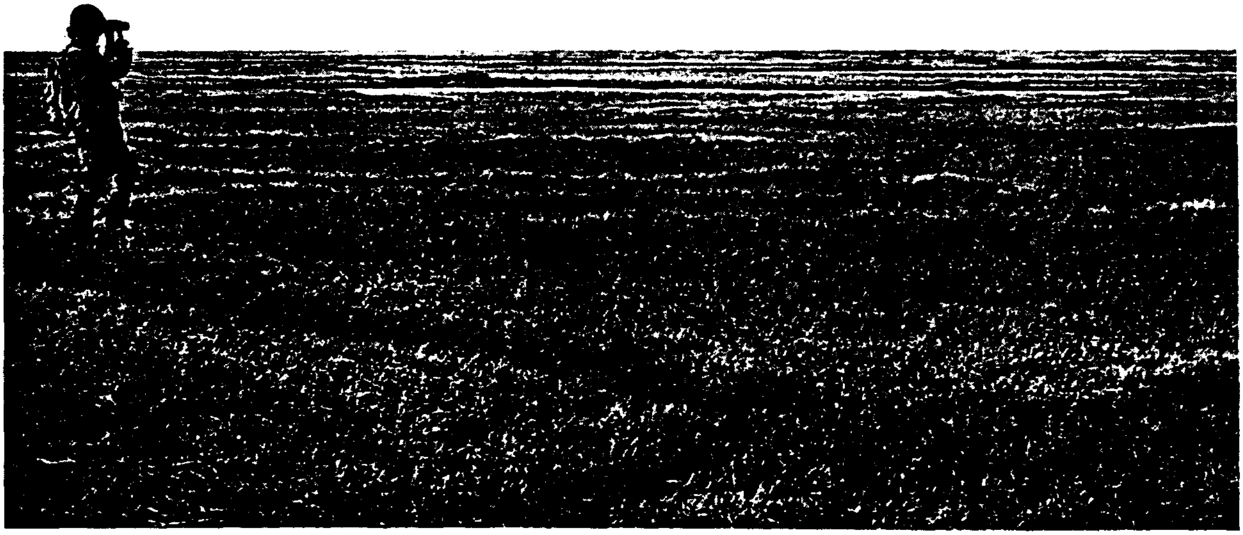

Plate II. Ground view of low center polygons on Storkersen Point study area, some of which are dry and some still flooded in early July. Open Shallow-*Carex* ponds in the background.

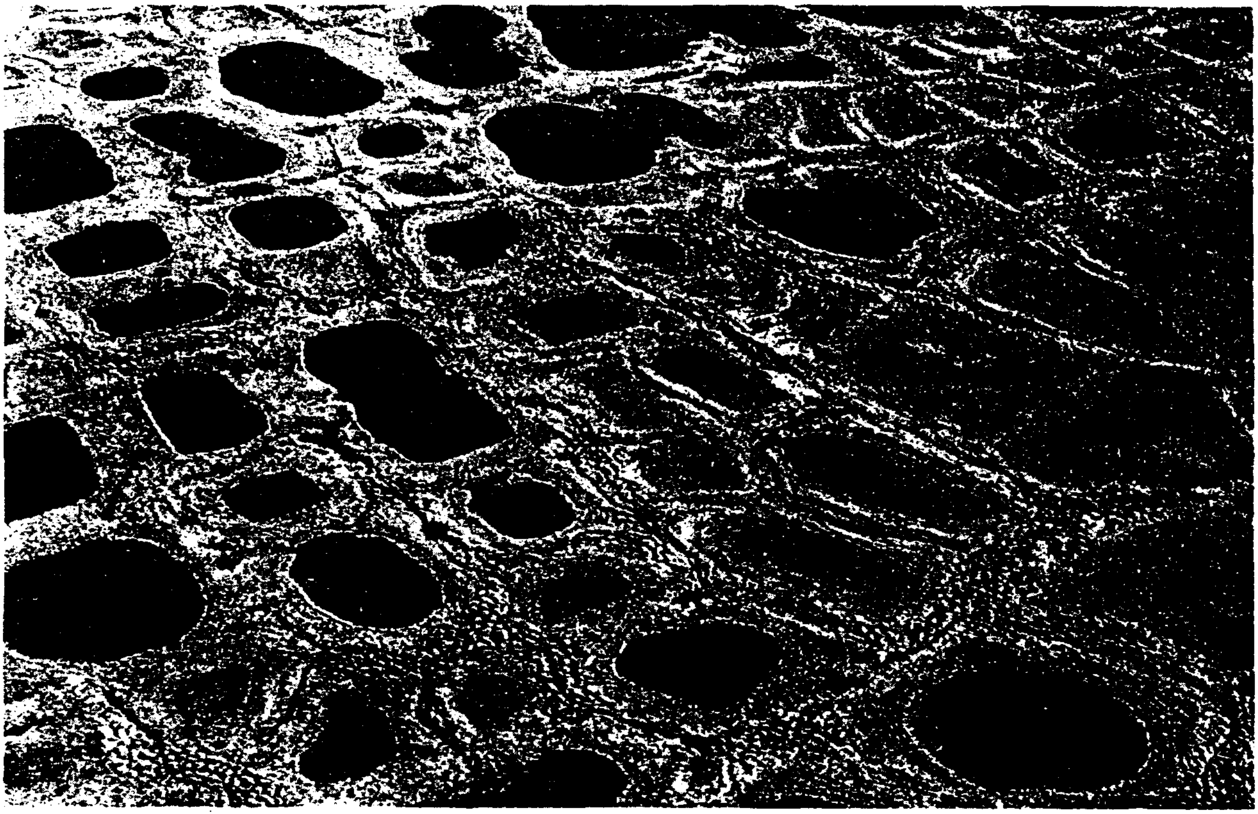

Plate III. Aerial view of Type I flooded tundra in low center polygons at right, and deeper more open Shallow-*Carex* (Type II) ponds at left. Note breakdown of ridges resulting in larger ponds made up of two to six or more polygons. These mosaic type areas are prominent in deltas and are less common at Storkersen Point.

Class IV: Deep-Arctophila.—Wetlands of either large pond or lake size that lack emergents in the central zone and contain stands of *Arctophila fulva* near the shore (Plate IV). These basins have abrupt shore and flat or gently sloping bottoms. Maximum water depths exceed 40 cm. Class IV wetlands are common as second generation basins resulting from melting of ice-rich zones in drained basins.

Class V: Deep-open.—Large, deep lakes that have abrupt shores, sublittoral shelves, and a deep central zone. Water depths are greater than in Deep-*Arctophila* wetlands, and *A. fulva* is absent or present in less than 5% of the shoreline. Maximum water depth found in the largest lake was 1.1 m.

Class VI: Basin-complex.—Large, partially drained basins that may contain nearly continuous water in spring due to flooding of the bottom by melt water. By mid-July, water levels recede leaving a pattern of green *Carex aquatilis* and open water where *Arctophila fulva* may grow along the margin of deeper pools or throughout shallow pools (Plate V). In late summer, relatively upland-like areas are present in some basins, and they are characterized by stands of *Alopecurus alpinus* and *Dupontia fischeri* growing on a moss substrate. Plant communities are most diverse and prolific in this class where the greatest variety of water conditions occur.

Class VII: Beaded Stream.—Small, often intermittent, streams consisting of a series of channels formed in ice-wedges and linked to pools that develop at ice-wedge intersections (Hussey and Reckendorf 1963). Intersection pools often become greatly enlarged as contiguous ice-rich soils thaw and subside (Plate VI). Relationships between water depths and aquatic plants appear to be similar to those in ponds and lakes. Stream pools usually are deeper than nonfluvial wetlands of equivalent size, and vegetation distribution and composition corresponds to Shallow-*Arctophila* and Deep-*Arctophila* wetlands. During the spring thaw, Beaded Streams may flood surrounding lowlands, creating extensive wetlands of the Class I Flooded Tundra. By mid-July, water

Plate IV. Deep-*Arctophila* pond at Storkersen Point.

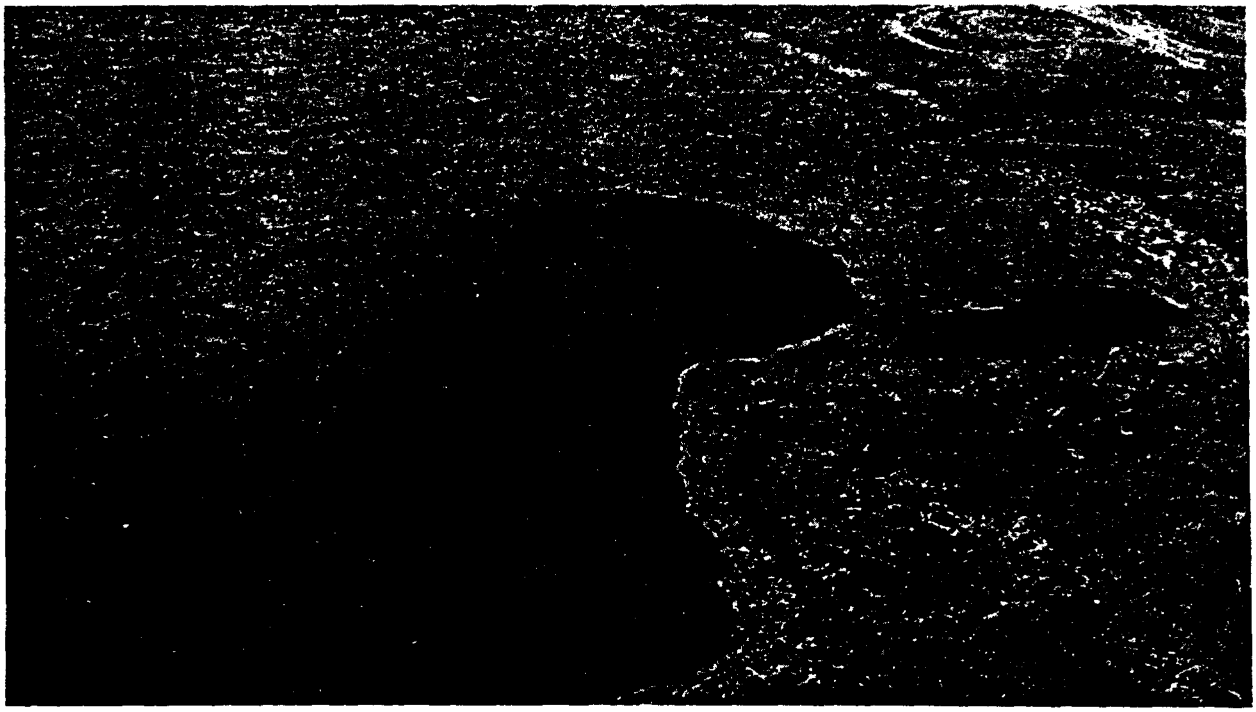

Plate V. Basin-complex showing drained basin, drainage channel, and Deep-*Arctophila* ponds of two sizes. High center polygons and interstitial pools at right.

Plate VI. Beaded stream showing very Deep-*Arctophila* pools connected by short lengths of stream between high center polygons. Storkersen Point.

usually is confined to stream channels and beads, and flow may be intermittent. Beaded Streams are common throughout the coastal plain, and they are often the only class of wetlands in large areas of well-drained regions of the interior coastal plain.

Class VIII: Coastal.—Aquatic habitats that occupy low areas bordering the Beaufort Sea and within a zone directly influenced by sea water (Plate VII). Wetlands vary from lagoons confluent with the sea to ponds periodically inundated by high wind tides. Unlike all other classes, Coastal wetlands are brackish or subsaline in specific-conductance, and have a characteristic vegetation dominated by *Carex subspathacea* and *Puccinellia phryganodes* at basin margins and on adjacent flats. Two general modes of origin probably account for most Coastal wetlands: (1) thaw basins breached by outward thawing through the dam between the basin and the sea beach or from inward erosion by sea ice or water, and (2) lagoons and ponds resulting from the formation of sand or gravel spits or barrier beaches by currents.

Abundance and Development of Wetlands

A summary of the areal and numerical importance of wetland classes appears in Table 10 with mean values of basin size, water depth, and occurrence of plants. The small, shallow Class I and II wetlands were by far most numerous, constituting one-half of the total area of all wetlands on the Storkersen Point study area. Class V and VI lakes were few but their large size contributed 26% of the total wetland area. The number of Coastal wetlands (Class VIII) averaged 2 per km^2 over the entire study area; however, all 29 basins sampled were in one 50-ha area bordering the sea.

The following sequential description places wetlands of Classes I through VI into the perspective of basin development (Fig. 7). Water impounded in low center polygons or other tundra depressions (Class I-Flooded Tundra) initiates the insolation-thawing process that deepens the basin. As water depth increases, tundra plants (dominantly *Carex aquatilis* and *Eriophorum angustifolium*) are reduced in the deeper central zone and restricted to shallow shoreward zones; wetlands of this stage are Shallow-*Carex* (Class II) ponds. As shoreward subsidence continues, *Arctophila fulva* becomes established throughout the basin, forming Shallow-*Arctophila* (Class III) ponds. Further thawing of the central zone causes depths not tolerated by *A. fulva*; consequently, distribution of *A. fulva* is confined to shore, and these basins are Deep-*Arctophila* wetlands (Class IV). Deep-open (Class V) lakes result when shoreward zones become too deep to support extensive stands of

Plate VII. Coastal wetlands along Bering Sea at Storkersen Point showing drift line.

Table 10. *Characteristics of classes of wetlands in the Storkersen Point study area, August 1972.*

				Wetland volume		Percent occurrence in wetland	
	Percent of total wetland area	Basins per km²	Basins in sample	Area (ha)	August depth (cm)	Sedges	Arct.
				$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)
Flooded Tundra (I)	29	>100	47	0.1 (0.2)	3 (3)	84 (18)	1 (4)
Shallow-*Carex* (II)	21	35	263	0.3 (0.3)	12 (7)	7 (7)	0 (0)
Shallow-*Arctophila* (III)	4	6	19	0.6 (0.7)	22 (10)	7 (6)	52 (23)
Deep-*Arctophila* (IV)	11	5	39	1.8 (2.3)	35 (13)	2 (4)	14 (11)
Deep-open (V)	9	<1	2	46.0 (25.4)	60 (28)	0 (0)	1 (0)
Basin-complex (VI)	17	<1	3	46.4 (39.1)	22 (8)	32 (10)	18 (10)
Beaded Stream (VII)	5	2	3	3.8 (3.9)	47 (20)	4 (2)	32 (43)
Coastal Wetland (VIII)	3	2	3	0.6 (0.6)	22 (11)	0 (0)	0 (0)

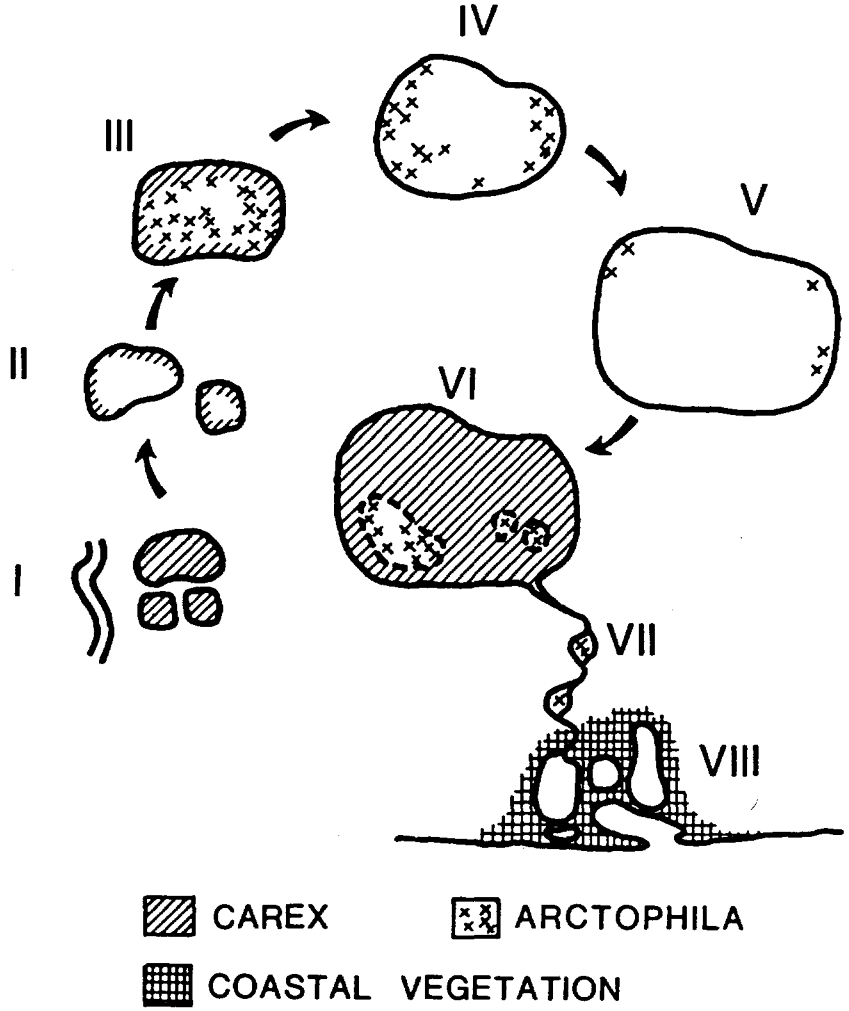

Fig. 7. Evolution of tundra wetlands showing relationships between size and vegetation. (Classes are in Roman numerals.)

A. fulva. The final stage of first generation basins occurs when shores erode and partial drainage lowers water levels to depths conducive for growth of aquatics (Basin-complex) (Class VI). Further drainage exposes areas where thawing processes create second generation wetlands.

Functional use of the classification system requires wetland indicators that are readily identifiable from either air or ground. Distribution of *Carex aquatilis* and *Arctophila fulva* provides the best determination of the stage of basin development in the classes of nonfluvial, freshwater thaw basins (Class I-VI). The two species are readily distinguished by late June because *A. fulva* becomes distinctly red while *C. aquatilis* is bright green. Coastal wetlands are easily identified because of their occurrence in low areas connected to the sea beach, their deep reddish-brown vegetation, and a characteristic line of driftwood and other debris windrowed by storm tides (Plate VII).

Occasionally, wetlands have two or more regions that are morphologically and vegetationally distinct. This occurs where two wetlands originally of different classes coalesce, or where embayments of Deep-open lakes are more shallow than the lake itself. Because differences were apparent in use of such portions of wetlands by birds, these regions were classified as separate units.

Other wetlands not considered in this system are incised and braided streams, their deltas, and associated nonfluvial wetlands. Such waters significantly influence bird species on coastal plain wetlands (Kessel and Cade 1958).

Water-bird Use of Various Wetland Classes

Frequencies of wetland use by water birds during 1971 to 1973 (Table 11) were evaluated using a Chi-square 1 × 2 contingency table test. Differential utilization of a wetland class by a species was indicated if the number of birds recorded on surveys as using wetlands in that class was significantly greater than the number of birds expected on those wetlands. The expected value was calculated by multiplying the total number of birds using wetlands in the class by the percentage of the total wetland area covered by wetlands in the class. For example, of 31 arctic loons in the sample, 16 (52%) were observed in Deep-*Arctophila* wetlands (Table 11). This class constitutes 11% of the wetlands of the study area (Table 10), so 31 × 0.11 = 3.4 loons expected on such wetlands. Because observations of whistling swans using wetlands were few, they were not tested statistically.

Class I: Flooded Tundra.—Pintails fed and loafed on Flooded Tundra before and after their wing molt in July (Table 11), but they made most intensive use of this class during spring thaw when other wetlands were frozen. Primary use of Flooded Tundra seemed to be by red phalaropes. Birds frequently were seen feeding or swimming in Class I basins throughout spring and summer.

*Class II: Shallow-*Carex.—Although most species of waterfowl occurred on Shallow-*Carex* ponds, only adult oldsquaws and king eider hens with broods used the ponds in significant frequencies (Table 11). Use by oldsquaws, primarily pairs, was significant before nesting ($p < 0.01$) and during nesting ($p < 0.05$). Feeding was a common activity of oldsquaws on Class II ponds. Twelve of the 19 (69%) observations of king eider broods were on Shallow-*Carex* ponds. Birds were seen feeding in water or loafing on or near shore. Although their frequencies of use were not significant, adult king eiders often were seen feeding in waters of Class II ponds.

Six of the eight white-fronted goose nests were less than 4 m from the edge of Shallow-*Carex* ponds. Other species constructed nests close to ponds or on islets, but frequencies of use were low: 2 of 42 arctic loon nests; 5 of 28 red-throated loon nests; 1 of 11 black brant nests; and 6 of 32 king eider nests.

*Class III: Shallow-*Arctophila.—Use of Shallow-*Arctophila* ponds by pintails was significant ($p < 0.01$) before and after their wing molt in July (Table 11). Shallow water and extensive stands of *A. fulva* provided feeding habitat and cover for birds. Most other species were on Class III wetlands, but less frequently than pintails; use by king eiders was significant ($p < 0.05$), both before and during nesting. One arctic loon nest and three red-throated loon *(Gavia stellata)* nests were on detritus platforms in Class III ponds.

*Class IV: Deep-*Arctophila.—Deep-*Arctophila* ponds and lakes were principal aquatic habitats for all waterfowl except white-fronted geese and pintails (Table 11). In 1971 and 1972, a pair of whistling swans nested adjacent to a large complex of Class IV ponds, and used Deep-*Arctophila* wetlands for escape cover. King eiders and spectacled eiders favored Class IV wetlands in all phases of their reproductive cycle at Storkersen Point (Table 11). Frequencies of use by king eiders were significant, ranging from 26% for hens with broods to 52% for postnesting females without young. Birds usually were seen loafing on shore. Of the 36 observations of adult spectacled eiders throughout their summer residence, 33 (92%) were on Class IV wetlands. Birds were swimming or loafing but were not observed feeding.

Oldsquaws preferred ($p < 0.01$) Deep-*Arctophila* wetlands before and during nesting (Table 11). Densities of pairs were highest on portions of drained lakes possessing a network of second generation Class IV ponds. A 50-ha complex of basins was used each year by 4 pairs; that density extrapolates to 16 birds per km^2 compared to mean peak densities of 4.3 to 5.1 birds per km^2 for the entire study area. Because oldsquaws are highly territorial (Alison 1975), the ridges that commonly separate ponds probably provide visual isolation from neighbors. Oldsquaws often were seen diving in Class IV wetlands.

Ten of the 11 black brant nests and 2 of the 3 spectacled eider nests found in 1971-73 were at Deep-*Arctophila* wetlands. Nests were placed on tundra or islets next to an abrupt shore. All nest-ponds were second generation wetlands in drained basins.

Preferential use of Class IV wetlands by arctic loons and red-throated loons was obvious throughout summer (Table 11); however, red-throated loons showed an even greater preference for Basin-complex ponds (Class VI). The proportion of observations of arctic loons on Class IV wetlands ranged from 52% before and after nesting to 59% during the nesting period. Sightings of red-throated loons were less frequent: prenesting (22%); nesting (33%); and postnesting (24%). Adult arctic loons fed or captured food for young in freshwater wetlands, whereas red-throated loons captured food at sea and returned to brood-ponds with fish for their young. Because of relatively deep water in Class IV wetlands, nests of arctic and red-throated loons were placed on islands or shores rather than on detritus platforms such as those used in more shallow wetlands.

Class V: Deep-open.—Deep-open lakes were used most frequently by water birds in July and August when they were ice-free. Principal use in June was by oldsquaws loafing on banks or ice and diving in the moat of water near shore.

Table 11. *Percentage frequency of occurrence that loons and waterfowl used various classes of wetlands in broods are in parentheses.*

	Arctic loon			Red-throated loon			Black brant			White-fronted goose
Classes	Pre-nest (31)	Nest (79)	Post-nest[a] (57)	Pre-nest (55)	Nest (115)	Post-nest[a] (65)	Pre-nest (55)	Nest (22)	Post-nest[a] (12)	Post-nest (189)
Flooded Tundra (I)	—	—	—	—	—	—	—	—	—	—
Shallow-*Carex* (II)	—	5	9	2	6	2	—	9	—	—
Shallow-*Arctophila* (III)	—	3	—	3	8	3	—	—	—	3
Deep-*Arctophila* (IV)	52**	59**	52**	22**	33**	24**	9	91**	—	—
Deep-open (V)	—	5	16*	—	—	3	—	—	—	94**
Basin-complex (VI)	36**	18	16	73**	51**	65**	18	—	—	3
Beaded Stream (VII)	6	5	2	—	2	3	—	—	—	—
Coastal Wetland (VIII)	6	5	5	—	—	—	73**	—	100**	—

[a] Adults and young.

[b] Adults only.

* Chi-square value significant ($P<0.05$).

** Chi-square value highly significant ($P<0.01$).

Use of Class V lakes by arctic loons was significant ($p<0.05$) following nesting. Birds observed were adults, usually in small flocks, that presumably were unsuccessful at nesting or brood-rearing.

Deep-open lakes and adjacent tundra were used by Canada geese and white-fronted geese during their wing molt in the last half of July and during August. In 1973, a flock of Canada geese, numbering about 100 flightless adults and 20 goslings, resided in the vicinity of two large lakes (175 ha and 200 ha) located 10-15 km southeast of Storkersen Point. Groups of white-fronted geese, containing mostly parents and broods, were counted in the study area on 21 occasions, and, of these, 19 involved groups on or near a 60-ha Class V lake. Similar-sized flocks of white-fronted geese were seen on other Deep-open lakes in the Prudhoe Bay area. While undisturbed, Canada geese and white-fronted geese rested or grazed in upland tundra near lake shores. Flightless geese responded to disturbance from men on the ground or low-flying aircraft by moving offshore to open water or by moving overland to another lake.

Oldsquaws, predominantly females, gathered on Deep-open lakes in the last week of July or the first week of August to pass their flightless stage. The oldsquaw population at this time was composed of about 95% females. Of the birds counted after the nesting period (Table 11), 85% were on the largest lake (60 ha) in the study area. Moreover, all flightless oldsquaws in the study area used two lakes of the class. Peak use of the lake occurred in mid-August when numbers varied from 45 to 70.

Class VI: Basin-complex.—Nonbreeding pintails preferred ($p<0.1$) Basin-complex ponds throughout their residence (Table 11). Use by pintails was greatest during the wing molt in July; 92% of the flightless pintails counted were in the largest (85 ha) Class VI lake near Storkersen Point. Pintails usually were well hidden in the cover created by stands of *Arctophila fulva* and *Carex aquatilis*. Based on birds

1971-73. Numbers of birds observed during phases of summer residence and the number of king eider

Pintail			King eider				Spectacled eider			Oldsquaw			
Pre-molt (544)	Molt (270)	Post-molt^b (871)	Pre-nest (23)	Nest (188)	Post-nest^b (87)	Brood (19)	Pre-nest (20)	Nest (9)	Post-nest^b (7)	Pre-nest (223)	Nest (261)	Post-nest^b (345)	Total (3,763)
8	—	9	—	—	—	—	—	—	—	—	1	—	3
7	—	14	14	22	26	64**	—	—	—	31**	28**	5	12
26**	6	12**	7*	8*	8	5	—	—	—	5	3	—	10**
14	2	13	30**	42**	52**	26**	90**	89**	100**	40**	36**	9	22**
1	—	—	—	8	6	—	—	11	—	2	10	85**	14**
37**	92**	46**	39**	9	5	5	—	—	—	10	9	—	32**
5	—	3	3	3	—	—	10	0	0	8*	10**	1	3
2	—	3	7**	8**	3	—	—	—	—	4	3	—	4

observed during June (Fig. 6), feeding is a major activity of pintails on Basin-complex lakes.

King eiders, usually paired, gathered in large numbers on Class VI lakes during the first half of June. As a result, frequency of use by king eiders was significant ($p < 0.05$) before nesting (Table 11). Shallow areas of Class VI lakes frequently were used for feeding by king eiders (Fig. 6). As the thaw progressed, king eider pairs dispersed to other wetlands, especially the Deep-*Arctophila* class.

In 1973, a pair of whistling swans nested and raised young in a Class VI basin. The nest was placed on a detritus platform surrounded by shallow water and emergents. Adults and cygnets were able to conceal themselves in stands of *Arctophila fulva*.

Other waterfowl, especially visitors (Table 6), often were seen in Basin-complex wetlands during June.

Frequencies for arctic and red-throated loons using Basin-complex lakes were most significant before nesting (Table 11). Presumably, the higher frequencies in early summer resulted because loons were able to use the extensive areas of shallow water before deeper wetlands thawed. Both species used Class VI lakes for nesting and brood-rearing, but only use by red-throated loons was significant ($p < 0.01$). Pairs occupied isolated pools within basins and constructed nest platforms of dead vegetation. Feeding activities of loons corresponded with activities at Class IV wetlands.

Class VII: Beaded Streams.—All species of loons and ducks that resided in the study area occasionally used on larger Beaded Streams (Table 11), especially those vegetated by *Arctophila*. Pintails and eiders used portions of the flood plain temporarily inundated by water during spring breakup. Oldsquaw pairs established territories on segments of the stream during the prenesting and nesting periods.

Class VIII: Coastal.—Coastal wetlands were predominantly used by migrating black brant. During the first half of June, flocks of as many as 100 brant migrated east along the coast and often used open water and snow-free shores of Class VIII wetlands. During mid-summer, brant often visited wetlands on the study area. Fall migration of brant did not pass Storkersen Point until after field seasons terminated in mid-August. However, during a visit to the study area on 2 September 1973, a flock of more than 350 black brant stopped to rest and feed along

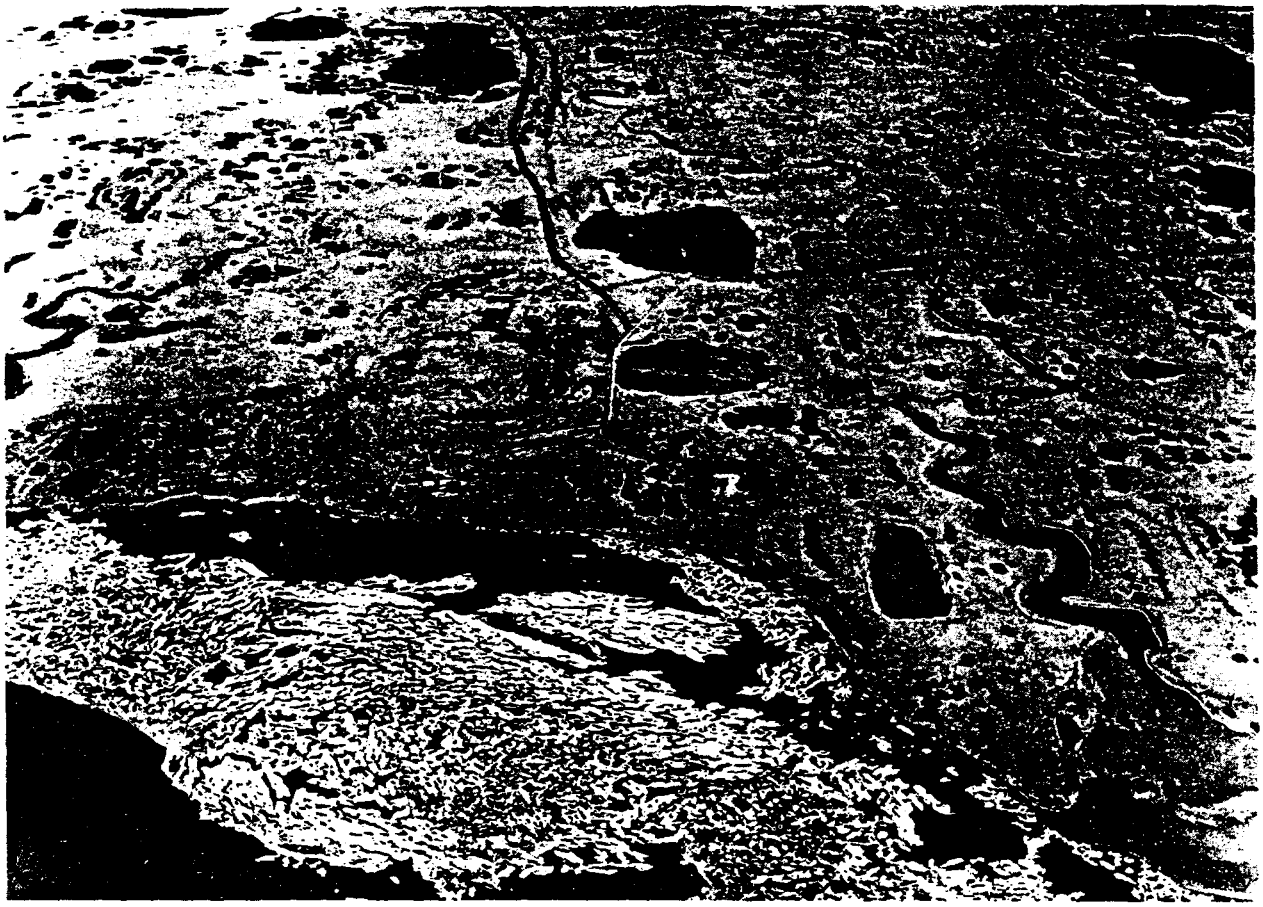

Plate VIII. Aerial view (south) of the Storkersen Point study area showing various wetland classes, the DEW-line site along the shore at left center, and Storkersen Point Well at right. Ice at the Beaufort Sea is at bottom. Photo by C. D. Evans.

shores of the Coastal wetlands. Presumably, *Carex subspathacea* or *Puccinellia phryganodes* form principal foods of black brant.

Black brant families moved to coastal habitats within a few days after their young had hatched. Two families were observed from 11 July to 17 July 1973 in a complex of Coastal wetlands. The birds fed and rested on flats between ponds and on a point jutting into the sea.

Part III—Macroinvertebrates of Tundra Wetlands and Their Use By Water Birds

Procedures

Aquatic macroinvertebrates were sampled weekly in selected wetlands from about 5 June to 8 August in 1972 and 1973. Chronology of thawing, drying of temporary wetlands, and logistical problems prevented sampling of all stations weekly. Nevertheless, a composite representation of seasonal changes in availability of various organisms was provided by the overlap of sampling schedules from the two field seasons.

In 1972, 10 sampling stations were established in ponds of differing morphometry and use by water birds. In 1973, the number of stations was expanded to 18 to insure coverage of all major wetland types. Sampling points at each station were random within either the open water areas or stands of emergent vegetation (usually *Carex aquatilis* and *Arctophila fulva*). Additional samples were taken from areas that were free of ice earliest in the season, from feeding sites where water birds were collected, and from waters disturbed by industrial activity.

Aquatic invertebrates were collected from open water with an Ekman dredge (15.2 cm × 15.2 cm) and in emergent vegetation with an aquatic sweep net described by Weller (1972). The sweep net measured 7.6 cm × 30.5 cm and had 7.9 meshes/cm. Sweeps were 3 m in length and were possible in water as shallow as 10 cm. Benthic samples were washed through the aquatic net to standardize the size of organisms taken by the two methods. Occasional "grab" samples were taken to facilitate identification of casually observed organisms. With few exceptions, living organisms were separated from vegetation and debris soon after collection. Invertebrates were preserved in a formaldehyde solution for later analysis.

Various physical and chemical variables were recorded as described in Part II in wetlands sampled for invertebrates. Depth of water, thickness of bottom sediments, and water temperature were taken at each sampling.

Activity and distribution of birds were noted during invertebrate sampling and on weekly bird surveys. Specific efforts were made to study feeding behavior of resident waterfowl, to record brood activities, and to quantitate wetland use for feeding. Seventeen birds of four species were collected for food analysis from areas outside the bird survey plots. All but two of the birds collected had fed at least 20 min. Birds were opened shortly after collection and contents of esophagi, proventriculi, and gizzards were separately preserved in a formaldehyde solution for later examination.

Aquatic Invertebrate Samples

Most aquatic macroinvertebrate specimens from Storkersen Point belong to 18 taxonomic groups. Individuals representing other taxa were collected (Table 12), but were considered of little value as food for water birds and were placed into a single group for analyses. One aquatic vertebrate, the fourhorn sculpin *(Myoxocephalus quadricornis)*, was found in brackish ponds connected to the sea, and other unidentified fish were seen in stream channels or wetlands connected to streams. Large and deep lakes south of the coastal tundra zone contained the nine-spined stickleback *(Pungitius pungitius)*. Taxonomic diversity and total volume of invertebrates available within taxa generally increased with seasonal warming of waters until late July. Mean total numbers and mean total volume of potential food organisms taken by the Ekman dredge and by net under 1 m^2 of water surface indicated a greater relative abundance of bottom-dwelling organisms than free-swimming forms (Fig. 8).

The weekly mean numbers/m^2 of the most numerous and frequently occurring taxa for each sample type generally increased from June to August (Figs. 9 and 10). Relatively high numbers of midge larvae of family Chironomidae in early sweep samples were caused by extensive sampling of shallow melt pools. The activity threshold of midge larvae is near 0 C, so they became active in flooded depressions and pond margins immediately after thawing (Danks 1971). Other organisms of potential importance as food items, either because of their high local populations or their large size, included snails (Gastropoda), tadpole shrimp (Notostraca), cranefly larvae (Tipulidae), stonefly larvae (Plecoptera), and caddisfly larvae (Trichoptera).

Relative occurrences of the major groups of invertebrates differed significantly ($p < 0.005$) among stands of *Carex aquatilis*, *Arctophila fulva*, mixed stands, and open water ($x^2 = 251.97$, d f = 60). Numbers and volume of invertebrates were greatest in stands of *Arctophila fulva* or in the edge between stands of *A. fulva* and *Carex aquatilis* stands (Table 13). Variations in wetland depth and vegetation density of wetlands accounted for much of the difference in invertebrate abundance among vegetation stands of like species. Fairy shrimp (Anostraca) and water fleas (Cladocera) were characteristic of open portions of wetlands and were of greatest potential as water-bird food during late summer, when these invertebrates were concentrated as a result of falling water levels in shallow, open ponds.

Limited samples by R. Howard (unpublished data) in other regions of the coastal plain indicated the same general composition of bottom organisms with midge larvae, earthworms (Oligochaeta), cranefly larvae, and caddisfly larvae contributing most in numbers and volume. Other large invertebrates found farther inland included large scuds (Amphipoda), additional species of snails, and clams (Pelecypoda).

Samples from a Class II pond near the Storkersen well that had been severely contaminated by crude oil and drilling wastes contained no macroinvertebrates. All vegetation below the high-water limit of the basin was dead. Sediments appeared heavily contaminated by oil residues, and oil slicks were produced when sediments were disturbed. A small amount of oil spread from this pond into other basins during snow melt.

Feeding Behavior of Resident Birds

The first water birds to arrive at Storkersen Point concentrated on or near the first available open water of flooded depressions and shallow ponds near the Beaufort Sea. Birds rapidly dispersed to other areas as open water became available and used all wetland types for feeding. Partially-drained Basin-complexes were favored throughout the season. Deep-open lakes were especially important as molting areas for female oldsquaws, white-fronted geese, and Canada geese.

Table 12. *Macroinvertebrates from Storkersen Point ponds, 1972 and 1973*[a].

- Class—Hydrozoa
  - Order—Hydroida
    - Family—Hydridae
- Phylum—Nematoda

- Class—Oligochaeta

- Class—Crustacea
  - Subclass—Branchiopoda
    - Order—Anostraca
      - Family—Branchinectidae
        - *Branchinecta paludosa* (O. F. Muller)
      - Family—Polyartemiidae
        - *Polyartemiella hazeni* (Murdock)
    - Order—Notostraca
      - *Lepidurus arcticus* (Pallas)
    - Order—Cladocera
      - Family—Daphinidae
        - *Daphnia pulex* (de Geer)
      - Family—Chydoridae
        - *Eurycerus lamellatus* (O. F. Muller)
    - Order—Copepoda
      - Suborder—Calanoida
      - Suborder—Cyclopoida
    - Order—Ostracoda

- Class—Arachnida
  - Order—Acari (Hydracarina)
  - Order—Araneae

- Class—Insecta
  - Order—Collembola
    - Family-Hypogastruridae
  - Order—Ephemeroptera
  - Order—Plecoptera
    - Family—Nemouridae
      - *Nemoura* sp.
  - Order—Trichoptera
    - Family—Limnephilidae
  - Order—Coleoptera
    - Family—Dytiscidae
  - Order—Diptera
    - Family—Tipulidae
      - *Tipula* sp.
      - *Prionocera* sp.
    - Family—Culicidae
      - *Culiseta* sp.
    - Family—Chironomidae
    - Family—Muscidae
      - *Mydaeina obscura*

- Class—Gastropoda
  - Order—Pulmonata
    - Family—Lymnaeidae
      - *Lymnaea* sp.
    - Family—Physidae
      - *Physa* sp.

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[a] Nomenclature based on Pennak (1953) and Usinger (1971).

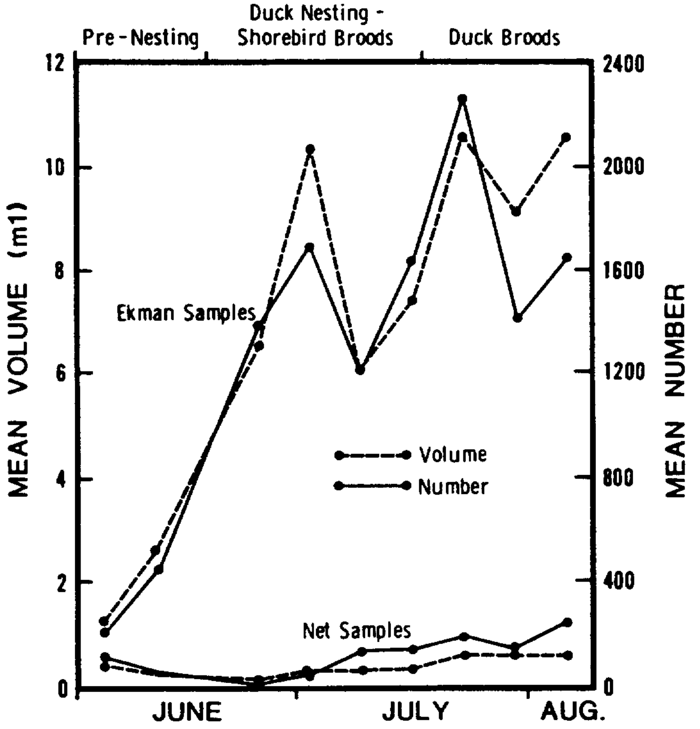

Fig. 8. Relationship of total invertebrates per m² to reproductive activity of dominant water birds.

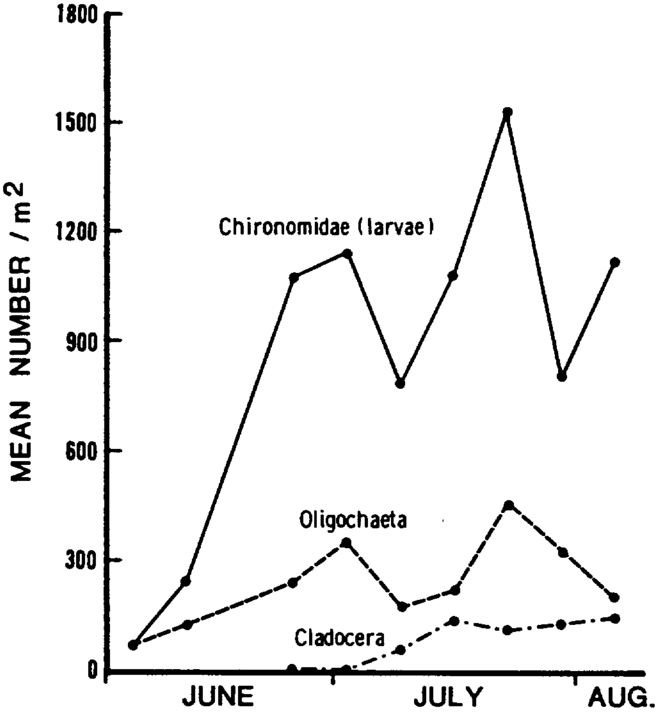

Fig. 9. Seasonal changes in abundance of important invertebrate groups, derived from Ekman dredge samples, 1973.

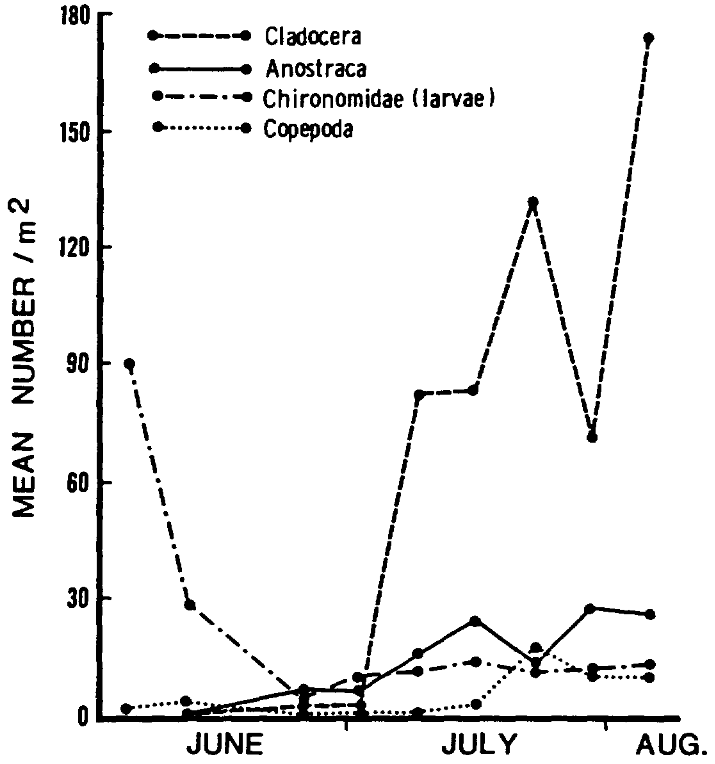

Fig. 10. Seasonal changes in abundance of some important invertebrates, taken in sweep-net samples, 1973.

Table 13. *Summary of invertebrates per m² for different vegetation stands, 1972-73.*

	Sweep samples					Ekman samples				
Vegetation	N	Total mean volume (ml)		Total mean number		N	Total mean volume (ml)		Total mean number	
		M.	S.D.	M.	S.D.		M.	S.D.	M.	S.D.
None	124	0.24	0.47	111.1	269.7	115	6.96	6.96	1371.3	1908.3
Arctophila fulva	67	0.54	0.71	182.1	293.0	33	13.04	11.30	2034.3	1498.3
Carex aquatilis	76	0.45	0.38	85.5	89.7	36	6.96	6.09	1431.3	1772.2
Mixed edge	11	0.59	0.39	206.4	244.0	1	10.86	0.0	3000.0	0.0

Late in the season, shallow ponds became increasingly important as feeding sites, when decreasing water levels concentrated free-swimming organisms and increased the total area of bottom surface that could be easily reached by swimming and wading birds.

Chironomidae and Trichoptera were the most important invertebrate foods for oldsquaw and king eider (Table 14). Earthworms did not occur in food samples as frequently as in bottom samples, while caddisfly larvae occurred at a higher frequency—suggesting feeding selectivity. The frequency of occurrence of water fleas in food materials was inflated by the presence of overwintering ephippia, which probably were picked up along with bottom detritus. Seven of the 17 birds collected had gravel in esophageal contents.

Oldsquaw.—Feeding was observed on all types of wetlands, including Flooded Tundra depressions. Edges of Deep-open lakes were used by small flocks of nonbreeding yearlings as well as adults. Nonbreeding yearlings left the study area near the end of June. By mid-July, most males had departed, and molting flocks were forming offshore in the Beaufort Sea. Single females were observed feeding in Shallow-*Carex* ponds throughout the nesting season. One nesting female under observation left her nest daily to forage in nearby ponds.

Feeding by diving accounted for 83% of 248 oldsquaw feeding observations. Early in June, oldsquaws commonly dived under floating ice and explored the newly exposed bottom. Diving seemed the preferred method of feeding in all but the most shallow wetlands where birds were able to reach the bottom by swimming with the head and neck submerged. One pair exhibited a third type of feeding by picking stonefly larvae from the surface of flooded ice at the edge of a Shallow-*Carex* pond.

Information on food habits of oldsquaws at Storkersen Point (Table 14) is in basic agreement with that from other breeding areas (Bengtson 1971*a*, 1971*b*). Midge larvae were dominant in the diet of adult birds, and the only brood observed was feeding by diving in a Class II pond with high populations of water fleas and fairy shrimp. Bengtson (1971*a*) reported that young oldsquaws fed almost exclusively on water fleas until half grown. During the first half of the field season, oldsquaws at Storkersen Point frequented areas where caddisfly larvae were abundant. One male and one female collected after feeding on such areas had consumed noticeable volumes of these insects.

King eider.—King eiders reached the study area during the first week of June and concentrated their feeding activity in Basin-complex ponds until they dispersed to nesting sites. Males left the area in late June after incubation started. Females fed in Shallow-*Carex* ponds and shoreward zones of Deep-*Arctophila* ponds throughout the nesting season, some of them in areas near known active nests. Because Lamothe (1973) found that king eider females incubated for extended periods without feeding, females observed feeding during the nesting season at Storkersen Point may have been unsuccessful nesters.

Only females with broods remained on the study area by the second week of August. Broods moved overland feeding in Shallow-*Carex* ponds, Basin-complexes, and Deep-*Arctophila* ponds. Total feeding observations for both sexes of all ages followed the same trend: 46% of 107 observations occurred in Shallow-*Carex* ponds; 40% in Basin-complexes; and 8% in Deep-*Arctophila* ponds.

Feeding behavior of king eiders in freshwater ponds resembled that of dabbling ducks and was described by Lamothe (1973) for birds observed on Bathurst Island. Bottom feeding by submerging the head and neck accounted for 70% of 131 observations at Storkersen Point. Downy young often upended to reach the bottom. Young eiders also dived readily, but diving by adults was observed on only three occasions. Surface dabbling also was employed mostly by downy young. One Class Ib (faded, downy stage) young was observed grabbing at specific targets in a pond where fairy shrimp were abundant.

Information on food habits (Table 14) is in agreement with that from other studies, i.e., that adult king eiders feeding in fresh water have a mixed diet of animal and plant material (Manniche 1910; Hanson et al. 1956; Lamothe 1973). Most vegetation, however, resembled dead material found in bottom detritus of feeding sites, and may have been ingested incidentally. Gizzard contents were included in earlier analyses reported in the literature, biasing results toward vegetative material (Swanson and Bartonek 1970). Manniche (1910) found indeterminable remnants of crustaceans in the stomachs of downy young. Young king eiders fed regularly in Shallow-*Carex* ponds with high populations of fairy shrimp and water fleas; these organisms also were noted in stomach contents (Table 14).

Pintail.—Male pintails, common throughout the summer, used all types of wetlands, but Basin-complexes accounted for 81% of 423 recorded feeding observations. Use shifted from Coastal wetlands and temporary wetlands to the marshy basins and vegetated zones of deep *Arctophila*-rimmed ponds and stream pools as the spring thaw progressed. Large areas with good emergent cover were important to pintails during the molt period in July. During late July and early August, there was increased use of Shallow-*Carex* ponds where fairy shrimp and tadpole shrimp were concentrated.

Table 14. *Percentage volume (ml) of some foods of 17 birds collected at Storkersen Point, 1972 and 1973.*

Digestive contents	Species:	Oldsquaw					King eider				Pintail					Red phalarope		
	Number:	1	2	3	4	5	1	2	3	4	1	2	3	4	5	1	2	3
Acari		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	tr	0.0	0.0	0.0	0.0	0.0	0.0
Anostraca		0.0	0.0	0.0	0.0	0.0	tr[a]	23.1	0.0	4.5	0.0	0.0	0.0	0.0	0.0	0.0	96.9	0.0
Araneae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	27.0
Cladocera		0.0	tr	tr	tr	tr	tr	tr	0.0	2.2	tr	tr	0.0	tr	0.0	0.0	tr	tr
Copepoda		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	tr	tr	tr	0.0	0.0	0.0	0.0	0.0
Muscidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	tr	6.6	0.0	0.0	0.0	0.0	0.0
Chironomidae		tr	tr	52.4	61.3	36.5	1.5	0.0	4.9	0.0	7.9	17.4	6.6	0.0	0.0	tr	0.0	61.0
Tipulidae		0.0	3.6	0.0	0.0	tr	0.0	0.0	0.0	0.0	0.0	0.0	30.6	0.0	0.0	77.8	0.0	5.5
Other Diptera		0.0	0.0	0.0	0.0	0.0	tr	0.0	0.0	tr	tr	0.0	tr	0.0	0.0	tr	0.0	tr
Gastropoda		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	tr	0.0	0.0	0.0	tr	0.0	0.0
Nematoda		0.0	tr	tr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notostraca		0.0	0.0	0.0	0.0	0.0	0.0	tr	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oligochaeta		0.0	0.0	tr	tr	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.6	0.0	0.0	tr	0.0	1.4
Trichoptera		80.2	39.2	tr	tr	tr	24.3	tr	tr	0.0	0.4	tr	0.0	tr	2.3	tr	0.0	0.0
Unknown animal		tr	tr	4.3	0.5	tr	tr	tr	0.9	6.7	20.0	8.2	8.8	tr	tr	11.1	1.6	1.6
Vegetation		tr	3.0	3.5	2.5	19.0	13.2	1.5	33.6	tr	26.8	33.6	22.8	44.0	41.9	tr	1.6	0.8
Gravel		19.8	54.2	39.8	35.7	44.4	30.8	75.4	60.8	86.5	41.3	40.8	12.4	56.0	55.8	11.1	tr	2.7
Total volume (ml)		5.30	4.15	5.15	5.55	6.3	3.25	3.25	9.25	4.45	6.30	5.75	6.05	2.50	2.15	0.45	1.60	3.65

[a] Less than 0.1 percent.

Pintails utilized a variety of invertebrate foods (Table 14). On 24 July 1973, two males that could not be observed before collection, were taken in wing molt. Attempts to collect pintails feeding where fairy shrimp and tadpole shrimp were abundant were unsuccessful. Krapu (1974) found fairy shrimp to be an important food resource of pintails in North Dakota, and these easily obtainable items probably are important in tundra areas as well. The few nesting attempts by pintails at Storkersen Point were unsuccessful, and information on preferences of broods for feeding areas was not obtained. Broods were seen on large, marshy lakes inland about 13 km east and 85 km south of the Colville River delta (Lat. 70° 40′N, Long. 151° 15′W).

Other waterfowl.—Spectacled eiders nested in limited numbers near Storkersen Point, but no information on feeding was obtained. Nests and sightings were near Deep-open lakes. Green-winged teal, mallards, and shovelers also used the Basin-complex wetlands preferred by pintails. American wigeon *(Anas americana)* were numerous in Coastal ponds (Class VIII) in June of most years of the study, and were seen ingesting vegetation in areas dominated by *Carex subspathacea* and *Puccinellia phryganodes*. Black brant and white-fronted geese also seemed to rely on these plants. Nesting whistling swans preferred large water areas with substantial vegetative cover where observations of feeding were difficult.

Loons.—Red-throated loons relied on fish from the nearby Beaufort Sea to feed their young, rarely feeding in inland waters. Arctic loons also made flights to sea but more commonly fed in fresh water. Deep-*Arctophila* ponds were the preferred habitat where young were fed invertebrates by their parents. Two young Arctic loons collected for food habits information had eaten caddisflies and tadpole shrimp, and a young red-throated loon contained Arctic cod *(Boreogadus saida)*. An adult arctic loon had eaten tadpole shrimp, caddisfly larvae, fairy shrimp, and water fleas (Cladocera).

Phalaropes.—Shallow-*Carex* ponds accounted for 66% of 102 recorded feeding observations of red and northern phalaropes *(Lobipes lobatus)*. Large, well-vegetated Basin-complexes were second in importance. Shallow-*Carex* ponds received heaviest use in August, when reduced water levels concentrated free-swimming invertebrates; flocks of 20 to 30 were common. Feeding behavior indicated that free-swimming organisms, benthic organisms, and emerging aquatic insects all were eaten. Birds took fairy shrimp and water fleas from shallow ponds and often picked food items from emergent vegetation. Stomach contents of a specimen which had fed in this manner included adult midges and spiders.

Other shorebirds.—Shorebirds at Storkersen Point made use of exposed bottom areas and extremely shallow waters of drying ponds, but no birds were collected for food habit studies. The diet of four species of genus *Calidris* near Barrow, Alaska, relied on midge larvae, cranefly larvae, adult insects, and arachnids (Holmes and Pitelka 1968). Stilt sandpipers *(Micropalama himantopus)* stopped during migration in August and used shallow ponds extensively. Late season feeding concentrations of shorebirds are composed mostly of young birds.

Discussion and Recommendations

The avian community of the Alaskan Coastal Plain at Storkersen Point is characterized by (1) a small number of breeding birds relative to lower latitudes, (2) few resident species, (3) a high percentage of water-related birds, (4) relatively low-density populations that are widely distributed, and (5) dominantly invertebrate feeders with lesser numbers of grazers. Compared with the bird fauna at Point Barrow (Pitelka 1974), there are fewer species breeding and fewer accidentals, especially Asiatic forms.

The Arctic Coastal Plain is of great importance for species restricted in breeding to the arctic, such as red phalaropes, many other shorebirds, whistling swans, white-fronted geese, brant, king eiders, oldsquaws, and arctic and red-throated loons. Recognition of the importance of the coastal plain to usually non-breeding segments of waterfowl populations, particularly pintails, has been increased by the knowledge that drought-displaced prairie ducks often migrate to northern habitats (Hansen and McKnight 1964; Smith 1970; Henny 1973). Several other species of waterfowl and shorebirds use the wet tundra for feeding during migration and seem also to breed in small numbers periodically.

Efforts to preserve the fauna and flora of tundra wetlands are complicated by our incomplete understanding of the roles of moisture levels, frost action, and other physical forces in the creation and continuity of the wet tundra ecosystem. Unfortunately, human-induced change may create permanent damage before we can study, assess, and predict the complications. Much of the damage from human activity on the tundra will take the form of esthetically displeasing local effects on vegetation. Equally uncertain is the effect of the vast network of roads and collecting pipelines that may alter water levels and form new wetlands, thereby influencing vegetative growth and succession.

First order damage resulting from oil development will be direct effects of oil pollution on vegetation and wetland systems. Although most public concern has related to potential damage along the proposed route of the Trans-Alaska Pipeline, oil spills and disturbances will be more frequent in oil or gas fields where pipeline systems and roads link wells to the main pipeline. Oil spills almost anywhere in this area, where slopes are gradual and drainage patterns indefinite, could result in the deposition of oil in many basins during the spring thaw when melt water flows over the impermeable tundra surface. Any major reduction of food organisms through degradation of preferred habitats by industrial activity will be detrimental to local aquatic bird populations.

The results of severe oil pollution are indicated by the destruction of all invertebrate and plant life in the contaminated pond at the Storkersen Point well; the basin is useless to water birds for food, and the contaminated sediments contain pollutants which may spread to adjacent wetlands. Petroleum compounds in bottom sediments break down slowly, especially in cold climates, and oil-loaded sediments can be lethal to important and abundant midge larvae (Bengtsson and Berggren 1972) and small, shrimp-like crustaceans (Blumer et al. 1971). Repopulation of waters over polluted sediments by free-swimming invertebrates is unlikely because most aquatic invertebrates will be subjected to contact with toxic sediments on the bottom of wetlands during the egg or overwintering stage of their life cycle.

Because petroleum development and production may occur over most of the Alaskan wet tundra ecosystem adjacent to the Beaufort Sea, it is vital that efforts be made to (1) preserve some large and totally undisturbed blocks of this unique habitat, and (2) prevent unnecessary destruction of bird populations and habitats even in areas developed for oil or gas removal.

Total protection of large tracts of tundra, including protection from all-terrain vehicles even in winter (see Plate I), is essential to preserve the integrity of these units as reserves and areas for further study.

Although there are other extensive moist tundra areas in Alaska, the northern coastal plain is unique in its geographic position, its climatic regime, and its possible importance to birds moving in east-west migration. We favor saving some large, undisturbed blocks of habitat that will preserve the unique wetlands and upland habitats that vary from the coast into the foothills of the Brooks Range.

In addition, smaller units that are well distributed throughout oil development areas should be preserved. So little is known about habitat requirements and home ranges of resident birds that the optimum size of such preserve units is uncertain. The Storkersen Point study area was large enough to include one pair of whistling swans, but rather small for aggregations of nesting brant or eiders. Therefore, comparable blocks of 42 km^2 would be minimal to satisfy home-range requirements of mobile species like whistling swans. These blocks should be selected from the most diverse and productive areas, irrespective of their potential for oil development. Such units will preserve the essential diversity of organisms and physical features of the plain for bird production and for scientific investigation. The number of such units essential to significantly maintain a specific level of bird production is uncertain.

Throughout the oil development areas, it should be feasible to preserve key water-bird production areas with little modification of operational procedures. Based on data from this study, Deep-*Arctophila* ponds and lakes (Class IV), Basin-complex wetlands (Class VI), and Coastal wetlands (Class VIII) are most intensively used by water birds. While wetlands in other classes are more abundant (Table 10) and less intensively used by loons and waterfowl, their value to other water birds is great.

The following recommendations are based on general observations of the wet tundra ecosystem and could help to minimize conflicts between water birds and petroleum development on the Arctic Coastal Plain: (1) With current drilling technology, it may be possible to choose well sites some distance from choice Class IV, VI, and VIII wetlands to reduce impact on reproductive activity of the larger water birds. (2) Pipeline pump stations, oil wells, and other facilities containing oil should be restricted to sites where leaking oil cannot enter flowing waters or wetlands in Class IV, VI, and VIII. (3) Where facilities must be in watersheds, regular inspection is essential and contingency plans should be ready for rapid containment of oil. (4) Other pollutants such as drilling mud, solid wastes, and fluid wastes should not be discarded into wetlands. (5) During 15 May to 1 October, major construction activities should be prohibited within 1 km of wetlands in Classes IV, VI, and VIII. (6) New roads and pipelines should be constructed so that a minimum number of Class IV, VI, and VIII wetlands are affected by water blockage. (7) Activities that will drain wetlands of high value to water birds should be prohibited. (8) Low-level aircraft activity should be minimized during the breeding season.

Future studies relevant to understanding relationships between birds, wetlands, and petroleum and gas development should include studies of: (1) the use of classes of wetlands by phalaropes and other species of shorebirds; (2) a comparable classification system for uplands, especially in reference to use by plovers and sandpipers; (3) techniques for rapidly and accurately appraising bird production values of wetlands of the coastal plain;

(4) the capacity of melt water to transport oil over the impermeable tundra surface during spring thaw; (5) the toxicity of oil to aquatic food resources of birds; (6) the effect of disturbance on populations and reproductive success of tundra birds; (7) the impact of water-level changes on vegetation and invertebrates in tundra wetlands; (8) determination of the optimal size and distribution of small production units; and (9) an evaluation of the role of barrier islands and lagoons for birds that use the coastal plain as well as those that exclusively nest on these islands or feed in the lagoons.

Summary

Water-related birds and aquatic habitats dominate the natural ecosystem at Storkersen Point in Alaska's Prudhoe Bay oil fields. Of the 25 species of birds that nested in the study area, 11 were swimming birds (loons, waterfowl, and phalaropes) and 4 were sandpipers (*Calidris* spp.) that often wade. Phalaropes and sandpipers were the most abundant species.

A wetland classification system is presented that is based on characteristics of basin morphometry, vegetation, specific conductance of water, and water movement. Eight classes of wetlands are defined: Flooded Tundra (Class I); Shallow-*Carex* (Class II); Shallow-*Arctophila* (Class III); Deep-*Arctophila* (Class IV); Deep-open (Class V); Basin-complex (Class VI); Beaded Stream (Class VII); and Coastal Wetland (Class VIII). Wetlands of Classes I through V represent progressive stages of basin development resulting from thawing of ground ice, and Class VI wetlands form after Class V basins are partially drained. Beaded Streams (Class VII) are the only type of fluvial waters at Storkersen Point and are a widespread feature of the Arctic Coastal Plain. Coastal Wetlands (Class VIII) are distinguished from other classes, because they are periodically flooded by sea water, have unique vegetation, and tend to be brackish.

Deep-*Arctophila* (Class IV) and Basin-complex (Class VI) wetlands were used most frequently by loons and waterfowl. Shores and waters of Deep-open lakes (Class V) were molting-areas for geese and female oldsquaws, and Coastal Wetlands (Class VIII) were preferred nesting and feeding habitats of black brant. The more abundant, smaller wetlands were intensively used by phalaropes and sandpipers.

Data on numbers and volume of invertebrate organisms associated with emergent vegetation support general observations on feeding and other use of wetlands: (1) Classes III, IV, and VI wetlands are of greatest importance to waterfowl and loons that utilize invertebrates, and (2) Class VIII wetlands are of greatest value to herbivorous brant. Production of invertebrates reaches its peak during late summer when shorebirds and waterfowl broods are most abundant. Use of invertebrates by water birds stresses the importance of protecting wetland habitats from disturbance if the avian community is to be perpetuated.

Undisturbed tundra preserves of a size sufficient to support nesting by all bird species are a vital need. Recommendations to reduce conflicts between water birds and oil or gas development are focused primarily on minimizing oil-related activities near wetlands in Classes III, IV, VI, and VIII because these classes are limited in numbers and are intensively used by water birds. Comparable data on habitat selection by upland-nesting shorebirds are of high priority for further research.

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7 THE USE OF PRAIRIE

ABSTRACT

FOR many species of ducks, the prairie pothole region is considered to be their most important production area in North America. Each spring, throughout a large portion of the waterfowl production areas of Canada and the United States, the population of ducks, their reproductive success, and the condition of the habitat are estimated using comparable methodology. We analyzed this data set to determine the numbers, proportions, productivity, and sources of variation, for the 12 species of ducks that commonly breed in the prairie pothole region portion of the total surveyed area.

Between 1955 and 1985, an average of 21.6 million ducks used the region, representing about 51.1% of the total estimated surveyed population. Over 50% of the total numbers of 8 of the 12 species are found in the region. There is striking variation in bird use within and among years and among subdivisions of the region. Habitat quantity and quality, as measured by the number of ponds available in May, seem to be the dominant factors controlling duck numbers; correlating positively with the distribution, abundance, and reproductive success of ducks. There have been significant shifts in the relative abundance and total numbers of individual species within subdivisions and for the whole region. Massive changes in land-use are dominant factors producing these changes, but extrinsic factors during the nonbreeding season also may be operant. Conservation of waterfowl in North America is closely tied to the fate of the prairie pothole region.

KEY WORDS: prairie pothole region, ducks, temporal variation, regional variation, productivity, May ponds, waterfowl populations.

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POTHOLES BY NORTH AMERICAN DUCKS

INTRODUCTION

Wetlands of the prairie pothole region of North America are intimately linked to the life cycles of a great variety of wildlife. There are species representing all five classes of vertebrates that are obligate users of prairie wetlands and the mosaic of land and water that they form (Clark 1978; Murkin and Batt 1987). Perhaps the most widely recognized wildlife species using this habitat are waterfowl (e.g., Sugden 1984), although other chapters in this volume identify the importance of prairie wetlands to fish (Peterka, Chap. 10) and mammals (Fritzell, Chap. 9).

Historically, prairie potholes have not received much attention from scientists, perhaps because they produce few obvious economic benefits in a region where land that is not in agricultural production is considered to be "wasteland" by most of society. The greatest efforts by individuals, industries, and governments have been focused on removing wetlands by filling or draining. The only opposition to this has come from the politically weaker voices of sports enthusiasts and naturalists who defend these areas for their importance to wildlife.

For most species of ducks, this region is considered to be the most important production habitat in North America (Canadian Wildlife Service 1986). The region frequently is touted as producing from 50 to 80% of the continent's main game species. These claims form the basis of numerous, but as yet largely ineffective, programs to preserve this resource.

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The prairie pothole region extends over approximately 300,000 square miles in the western plains of Canada (≅80%) and the United States (≅20%). This huge area is not homogeneous as there are major differences among regions in geological history and soil types, topography, climate (e.g., precipitation, frost-free period), the history of human settlement, and intensity of land-use. Several of these elements have not been stable over long periods of time. Human factors have changed dramatically throughout the region during the past several decades. Furthermore, waterfowl using different portions of the region may winter in widely different localities across the continent (Bellrose 1980; Johnson 1986), and these areas too have been impacted by humans in disparate ways, which may affect the survival or condition of wintering ducks. Finally, natural climatic variation has resulted in distinct but nonuniform wet and dry periods.

This chapter will attempt to quantify the use and significance of this region for breeding waterfowl. We will describe trends in individual species populations and productivity over the last three decades, explore possible cause-and-effect relationships of these trends, and describe year-to-year variations in use patterns. We will offer some thoughts on future prospects for waterfowl in this region, particularly in relation to conflicts with agriculture.

BASIC ECOLOGICAL RELATIONSHIPS OF WATERFOWL AND PRAIRIE WETLANDS

Before examining data on the region's duck populations, it seems useful to describe briefly those species that use it and factors that make this area especially attractive to breeding ducks. Of the 34 species of ducks breeding in North America, 12 are common in the region. These are discussed under the general categories of dabbling ducks (*Anas* spp.) and diving ducks (*Aythya* spp. and *Oxyura* sp.). Seven of the 12 are dabbling ducks: mallard (*Anas platyrhynchos*), northern pintail (*A. acuta*), gadwall (*A. strepera*), blue-winged teal (*A. discors*), northern shoveler (*A. clypeata*), green-winged teal (*A. crecca carolinensis*), and American wigeon (*A. americana*). Five are diving ducks: canvasback (*Aythya valisineria*), redhead (*A. americana*), lesser scaup (*A. affinis*), ring-necked duck (*A. collaris*), and ruddy duck (*Oxyura jamaicensis*). The greater scaup (*Aythya marila*) is also present in the area and is not separated from the lesser scaup during population inventories. However, only a very low proportion of the scaup counted are known to be greater scaup. Other species that occur, but never beyond trace numbers in continental surveys, are: cinnamon teal (*Anas cyanoptera*), black duck (*A.*

rubripes), wood duck (*Aix sponsa*), white-winged scoter (*Melanitta fusca*), common goldeneye (*Bucephala clangula*), bufflehead (*B. albeola*), and mergansers (*Mergus merganser* and *M. serrator*). Data from these species are not included in this analysis.

For prairie ducks, several critical events occur in pothole habitat. Reproduction is the most important of these; indeed, all other events (e.g., feather molt) appear to adjust to the timing and success of reproduction.

Different species exploit the mosaic of prairie wetlands in different ways (e.g., Stewart and Kantrud 1973; Kantrud and Stewart 1977) and waterfowl communities vary considerably across the prairies (e.g., Stewart and Kantrud 1974; Nudds 1983) and over time (e.g., Smith 1971; Stoudt 1971; Trauger and Stoudt 1978; Leitch and Kaminski 1985; Johnson 1986). However, for all species carefully studied thus far, the birds appear to be attracted to the high levels of primary and secondary productivity characteristic of pothole basins (e.g., Murkin, Chap. 11). The high productivity of prairie potholes is likely a result of the fortuitous combination of fertile soils, diverse complexes of mostly shallow basins, moderately long growing seasons, and seasonal and year-to-year variability in water levels (Williams 1947; Smith 1971; Sugden 1984).

During the breeding period, including brood-rearing, all species appear to exploit the protein- , lipid- , and calcium-rich food provided by abundant aquatic invertebrates (Murkin and Batt 1987; Swanson, Chap. 8). Invertebrates appear to be critical for breeding females as sources of nutrients for egg production and body maintenance (e.g., Bartonek and Hickey 1969; Swanson et al. 1979; Swanson, Chap. 8) and for developing young waterfowl (Sugden 1973). Invertebrate communities themselves are dependent upon wetland dynamics in the prairie ecosystem (e.g., Voigts 1976; Murkin 1983).

Another commonly cited characteristic of potholes, which makes them attractive to breeding waterfowl, is their physical heterogeneity that allows breeding pairs to isolate themselves in defensible pieces of habitat where they can secure resources for breeding and are relatively undisturbed by other birds (e.g., Hochbaum 1944). Selection for reduced competition is probably relevant in a broader sense, too, for ducks and other migratory birds presumably journey to such breeding areas partly because there are fewer resident competitors for necessary resources than at low latitudes (e.g., Lack 1968).

Following breeding, most ducks quickly leave the potholes for larger lakes and marshes where they undergo a complete change in body plumage and prepare for fall migration. With some exceptions (e.g., molting blue-winged teal), males of most species leave the potholes as soon as there is no longer a chance to breed (Hochbaum 1944; Salomonsen 1968; Bergman 1973; Dubowy 1980; Stoudt 1982; Anderson 1985). Some nonbreeding females and those whose nests have been lost also join these postbreeding flocks (Bailey 1981). By midsummer, the only birds left in most potholes are incubating and brood-rearing females and young-of-the-year. Soon after fledging, even these birds abandon small potholes for larger water, usually long before freeze-up makes small wetlands unavailable.

SOURCES OF THE DATA

The data analyzed in this report were obtained during the May waterfowl breeding-ground surveys and the July waterfowl production surveys conducted annually by the U.S. Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service (CWS) (CWS and USFWS 1977). These aerial surveys of waterfowl breeding habitat are arranged in 50 strata (Fig. 7.1), encompassing 50,000 linear miles of transects from South Dakota to Alaska, and have been surveyed annually since 1955. July production surveys have been flown on a variable subset of these transects over a shorter period of time. The 50 survey strata include the majority of the total area used by most of the species, but there is increased evidence that a significant proportion of the mallards may occur outside the surveyed area (Trost, Blohm, and Boyd pers. comm.). The other species for which this factor may be important are: northern pintail, green-winged teal, lesser scaup, and ring-necked duck.

Counts are flown with light aircraft at an altitude of 30–50 m, using two observers (Hanson and Hawkins 1975). Simultaneous ground surveys are run over a portion of the transect route to generate corrections for visibility of various species, pond conditions, etc. (Martinson and Kaczynski 1967). Henny et al. (1972) and Pospahala et al. (1974) provide more detailed discussions of survey techniques and the resulting data.

May breeding pair counts typically included all 50 strata (although long-term means were used for northern Ontario from 1974 to 1985). In the event that weather or other exigencies prevented flying a transect, long-term averages were substituted for missing values. We calculated from CWS files that this occurred with about 7% of the total data set, mostly in the early years of the survey. Data from outside the 50 strata surveyed area have been added by the USFWS to yield total estimated populations for northern pintails and mallards beginning at various times during the 31-year interval. These data were not used because they represent an unequal expansion of the information base and bias comparisons over the full period of this analysis. July production surveys as of 1985 included 31 of 50 strata but past coverage was variable. Brood

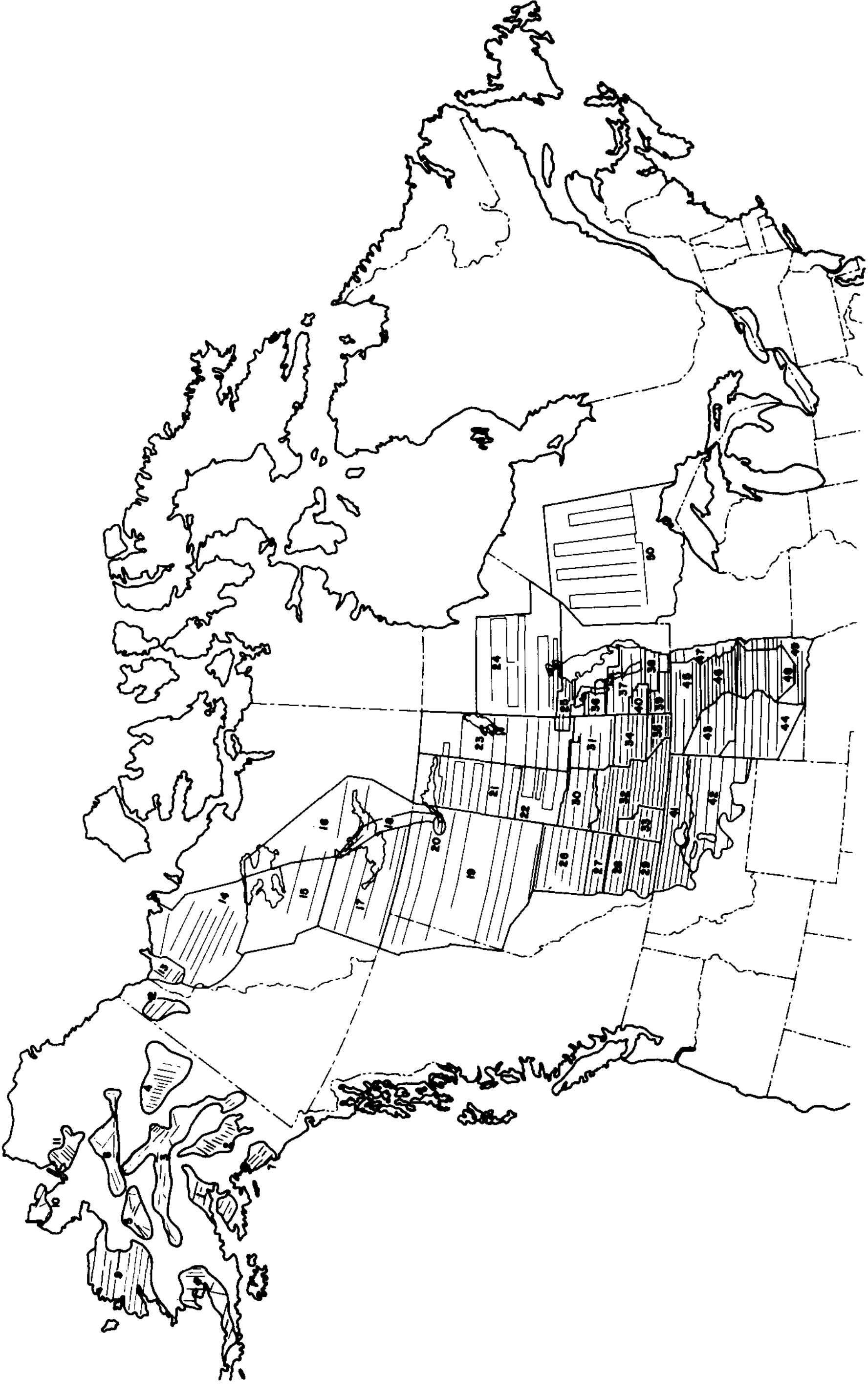

FIG. 7.1. Transects and strata of annual aerial surveys of waterfowl breeding grounds by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service.

data are not available for all regions in all years. Consequently, opportunities for comparisons are more limited with brood data. In all cases where we made comparisons (See Tables 7.7–7.10), available brood data were matched with breeding pair and habitat data for the same individual strata and year, thus providing comparable, consistent comparisons despite imbalances in the data set. We assumed that, although regional coverage varied among years, each sample within each region provided unbiased samples of that region, which would thus allow comparisons among regions and over time.

For purposes of this report, we define the prairie pothole region to be 24 of the 50 strata of the total surveyed area, including southern Alberta (strata 26–29), southern Saskatchewan (30–35), southern Manitoba (36–40), eastern Montana (41–42), North Dakota (43, 45–47) and South Dakota (44, 48–49). This region includes some habitats (lakes, rivers) that do not fit the definition of potholes, but these are of relatively minor importance. Also, portions of Minnesota, Nebraska, and Iowa include important prairie wetland habitat and many breeding ducks, but data for these regions are scattered and lack long-term consistency that allows clear comparisons. Similarly, we did not include data from the earliest comprehensive surveys (1947–1954), which are not strictly comparable with the present data set. For habitat comparisons, we used May pond counts unadjusted for visibility biases, because annually adjusted data are not available before 1961. The timing of the annual surveys obtains the best data for mallard, northern pintail, and canvasback. The other species typically nest later in the season, and during the survey period they may not yet have arrived to be enumerated, or may be on their way to breeding grounds elsewhere. This fact will account for some of the variability obtained in annual population estimates.

Statistical tests follow Sokal and Rohlf (1981) and Wilkinson (1985). Percentage data were arcsine transformed before regressions or analyses of variance. Tukey's HSD test was used when comparisons of means were made after analysis of variance. Smoothing and time series analyses, based on three-year moving averages, were done to search for patterns in certain highly variable population data (Velleman and Hoaglin 1981).

RESULTS

Duck Populations

There has been considerable variation in mean total duck numbers (combined total for all surveyed species) in the region between 1955 and

1985 (21.6 ± 4.75 million, CV 22.1%), and in the mean proportion of all ducks estimated to be in the prairie pothole region portion of the 50 surveyed strata (51.1 ± 1.4%, CV 15.2%) (Table 7.1). The peak estimated population of 33.6 million birds occurred in 1956 and was followed by a rapid decline to 17.6 million in 1959. Populations since then have varied greatly, with the lowest population of 15.3 million recorded in 1985.

Species Composition

The number of ducks present varied considerably within and among species over the 31-year period for which comparable data are available (Table 7.1). The most abundant ducks were the mallard, blue-winged teal, and northern pintail, which together averaged 62% of the birds present. Annual fluctuations in numbers were considerable, with coefficients of variation falling between 20.3 and 71.4%. The most uncommon species, the ring-necked duck, was the most variable in number. On average, about 87% of the ducks were dabbling ducks and 13% were diving ducks.

While the relative numbers of each species present give the clearest picture of the community of ducks, a different picture is obtained when the importance of the region to each species is considered (Table 7.1). For 8 of the 12 species, over 50% of their mean total estimated numbers occurred in the region. The American wigeon approached this category at 49.3%.

Coefficients of variation for the proportion of the estimated populations of various species in the prairie pothole region ranged widely from

TABLE 7.1. Average duck populations in the prairie pothole region and the percentage of each species' total surveyed population found in the region (1955-1985)

Species	Breeding population (x10^6) $\bar{X}$ ± *SD* (*CV*)	Percent of total surveyed population $\bar{X}$ ± *SD* (*CV*)
Mallard	5.4 ± 1.67 (31.1)	67.3 ± 7.6 (11.3)
Blue-winged teal	4.3 ± 0.95 (21.8)	88.1 ± 6.7 (7.6)
Northern pintail	3.7 ± 1.75 (47.8)	62.1 ± 16.4 (26.4)
Northern shoveler	1.6 ± 0.37 (23.2)	80.9 ± 10.6 (13.2)
American wigeon	1.6 ± 0.32 (20.3)	49.3 ± 8.1 (16.5)
Gadwall	1.4 ± 0.32 (22.9)	94.7 ± 3.4 (3.6)
Green-winged teal	0.7 ± 0.21 (28.6)	35.5 ± 9.4 (26.3)
Scaup	1.1 ± 0.38 (32.9)	16.9 ± 4.8 (28.5)
Redhead	0.6 ± 0.19 (31.4)	81.8 ± 11.5 (14.0)
Canvasback	0.4 ± 0.10 (28.3)	64.3 ± 12.6 (19.5)
Ring-necked duck	0.1 ± 0.05 (71.4)	13.9 ± 7.9 (56.8)
Ruddy duck	0.5 ± 0.21 (43.5)	86.7 ± 8.5 (9.8)
Total ducks[a]	21.56 ± 4.75 (22.1)	51.1 ± 7.8 (15.2)

[a] Combined total for all surveyed species.

3.6 to 56.8% (Table 7.1). This could be considered as an additional index of the dependence of a species on the region. Presumably, birds not tied to it, or to a strategy of precise homing, may successfully settle in other areas readily when habitat conditions are adequate. Obligate users could not do so. Thus, species least dependent on the region should show the greatest year-to-year variation (higher CV). Those species most closely tied to it should show the least variation among years (lower CV). This prediction is supported by a significant Spearman Rank Correlation ($r = 0.938$, $P < .001$) between ranks of the mean percentage of species present and ranks of coefficients of variation. Thus, the mean percentage of a species' population present in the region seems to be a strong indication of the dependence of that species on it, regardless of its comparative abundance. Using this criterion, the rank of dependence is (from most to least dependent): gadwall, blue-winged teal, ruddy duck, redhead, northern shoveler, mallard, canvasback, northern pintail, American wigeon, green-winged teal, scaup, and ring-necked duck.

Historical Trends in Duck Use

The proportions of each species present in the prairie pothole region over the 1955–1985 period were plotted (Fig. 7.2) and simple linear regressions were calculated (Table 7.2). These standardize the size of the total estimated population of each species and are thus a relative measure of bird distribution during the survey period. The distribution of total ducks, and of 9 of the 12 species, showed no significant temporal ($P > .05$) change. Only redheads showed a significant ($P < .01$) increase, while gadwalls ($P < .05$) and American wigeons ($P < .05$) significantly declined. Significant decreases were approached by total ducks, mallards ($P < .06$) and blue-winged teal ($P < .07$).

TABLE 7.2. Regressions of the proportions of each species' total surveyed population present in the prairie pothole region (1955-1985)

Species	Slope	r^2	P
Mallard	−0.292	0.121	.055
Blue-winged teal	−0.245	0.110	.069
Northern pintail	−0.291	0.026	.386
Northern shoveler	−0.151	0.017	.488
American wigeon	−0.393	0.193	.013
Gadwall	−0.168	0.198	.012
Green-winged teal	−0.197	0.037	.302
Scaup	−0.049	0.009	.617
Redhead	+0.601	0.227	.007
Canvasback	+0.046	0.001	.859
Ring-necked duck	+0.231	0.071	.148
Ruddy duck	+0.055	0.003	.753
Total ducks[a]	−0.286	0.112	.066

[a] Combined total for all surveyed species.

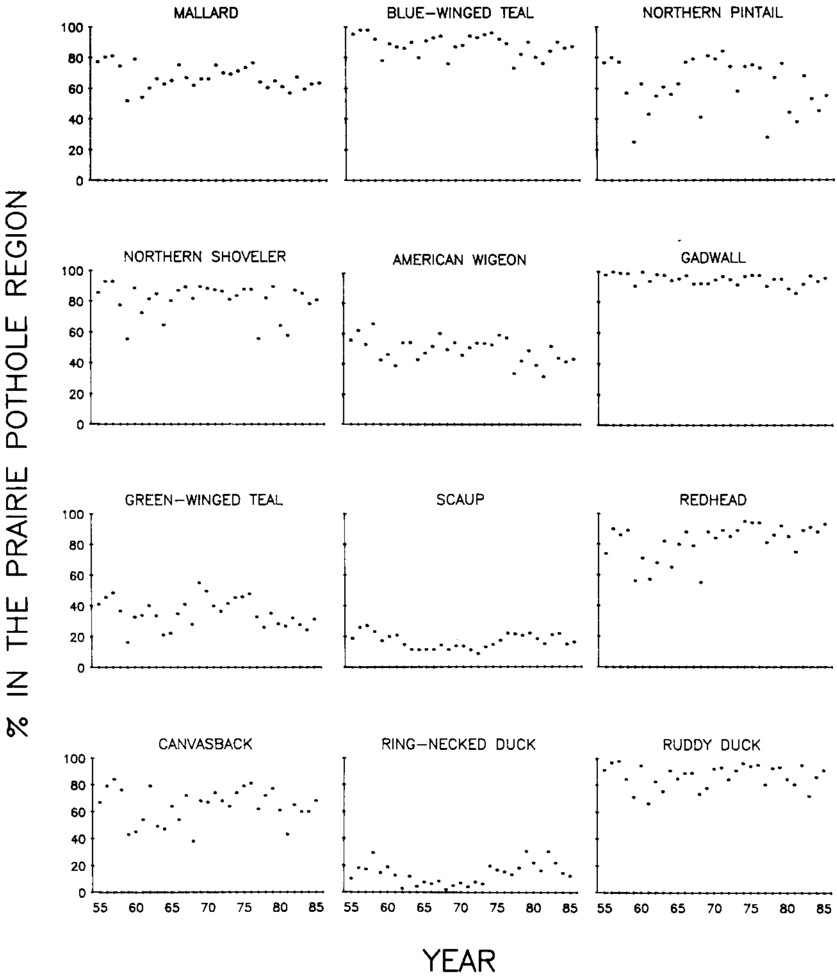

FIG. 7.2. Scatterplots of the percentage of a species' total population from the surveyed area estimated to be in the prairie pothole region each year for 1955–1985.

Because of the wide scatter in these data (Fig. 7.2), we searched further for patterns in proportion of each species settling in the region by using time-series analysis with three-year moving averages (the first and last data points of the series, 1955 and 1985, are only two-year averages) and included the data for the number of ponds present each May. Smoothed plots for the marginally declining species (mallards, blue-winged teal, and total ducks) look very different than plots of raw data. Although the raw data were suggestive of declines, the smoothed plots are distinctly nonlinear and resemble smoothed data for May ponds (Fig. 7.3). Smoothed plots for other species more closely resembled plots of raw data (Fig. 7.2), though the scaup, ring-necked duck, northern pintail, and green-winged teal series also appeared more nonlinear. The steady declines in American wigeon and gadwall and the rise in redhead proportions remained distinct in the smoothed data.

Relationship to Wetland Numbers

The most probable factor affecting the proportions of each species using the region in a given year is habitat quality (Fretwell and Lucas 1969). However, variation in female philopatry and over-winter survival of birds from different portions of the breeding range may also have effects (Johnson 1986). The breeding ground surveys provide only a single index of habitat quality, the number of May ponds, collected at the same time as the data for breeding population estimates. Pond and duck numbers have varied greatly over the 31-year period of the survey

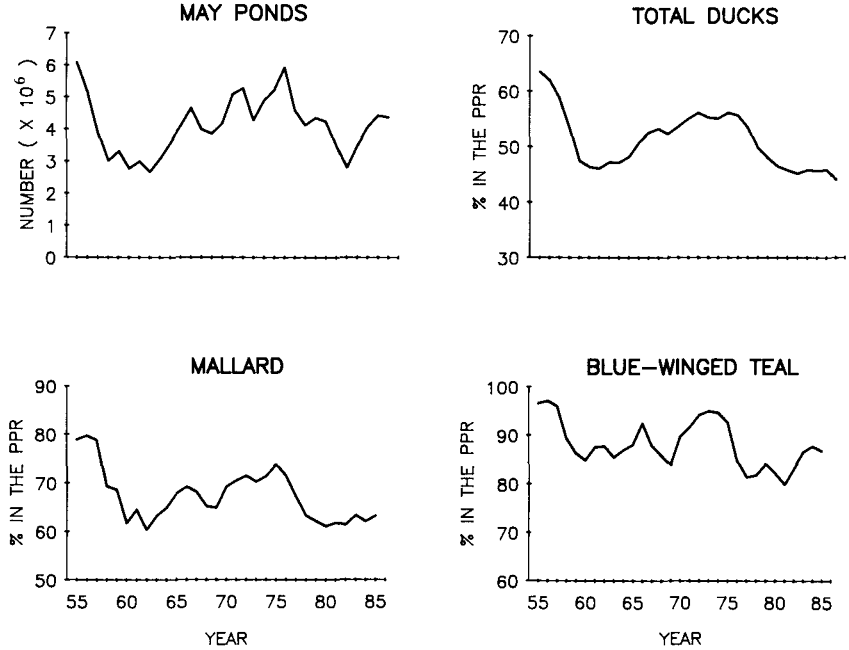

FIG. 7.3. Moving-average plots of the estimated number of May ponds and the percentages of total ducks, Mallard, and Blue-winged Teal present in the prairie pothole region for 1955–1985. Each point is the mean of years *t*, *t* − 1, and *t* + 1; for 1955 the point is the mean of *t* and *t* + 1; for 1985 the point is the mean of *t* and *t* − 1.

(Fig. 7.4). There is a significant linear relationship between the total number of ducks and the number of May ponds ($y = 13.0 + 0.002x$, where y = total ducks and x = May ponds, $r^2 = 0.41$, $P < .001$). The proportions of total ducks and of all species individually, except the lesser scaup and ring-necked duck, also showed significant positive relationships to May ponds (Table 7.3). For significant relationships, coefficients of determination (r^2) ranged between 0.19 for the American wigeon and 0.57 for the northern pintail. The five strongest ($P < .001$)

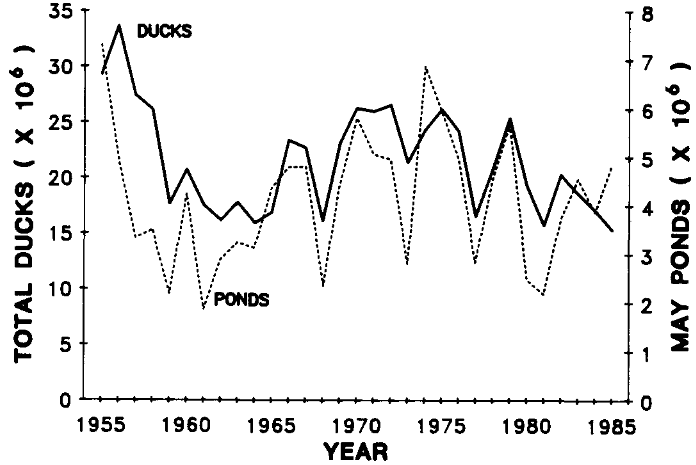

FIG. 7.4. Estimated number of unadjusted May ponds and total ducks present in the prairie pothole region for 1955–1985.

TABLE 7.3. Regressions of the proportions of each species' total surveyed population present in the prairie pothole region in relation to the numbers of May ponds

Species	Slope (×1000)	r^2	P
Mallard	0.030	0.296	.002
Blue-winged teal	0.030	0.371	.001
Northern pintail	0.089	0.571	.001
Northern shoveler	0.048	0.392	.001
American wigeon	0.026	0.191	.014
Gadwall	0.013	0.267	.003
Green-winged teal	0.032	0.229	.006
Scaup	−0.001	0.000	.965
Redhead	0.047	0.320	.001
Canvasback	0.048	0.285	.002
Ring-necked duck	0.005	0.007	.650
Ruddy duck	0.037	0.359	.000
Total ducks[a]	0.037	0.446	.001

[a] Combined total for all surveyed species.

relationships were for the northern pintail, northern shoveler, blue-winged teal, ruddy duck, and redhead.

Geographic and Temporal Variations

To search for patterns of change within the region, we calculated the relative proportion of each species in the community (number of each species x/number of all species combined) for the six administrative regions: Montana, North Dakota, South Dakota, southern Manitoba, southern Saskatchewan, and southern Alberta. Three ten-year time periods were selected (1955–1964, 1965–1974, 1975–1985) for statistical comparisons. The data then are measures of the relative abundance of each species at a given time and place. Two-way ANOVAs for each species showed that there were significant differences for both major factors and interaction effects for all but 6 of 36 possible comparisons (Table 7.4). All species varied significantly among the subdivisions of the region. All species, except the American wigeon, varied significantly among time periods and 7 of the 12 possible interaction comparisons yielded significant effects.

The data were regrouped by the three time periods for analysis of trends in relative proportion of each species summed over the entire region. All species, except the blue-winged teal and the American wigeon, showed significant changes (Table 7.5) over time periods. Mallards and northern pintails showed significant declines over the three periods, while the other six species were found in higher proportions in the later years.

Table 7.6 presents the relative abundance of 12 species in 6 subdivisions of the region summed over all years. For each species, regional averages differed greatly (*P* < .001).

TABLE 7.4. Significance of ANOVA comparisons for six regions of the prairie pothole region over three time periods of the relative abundance of each species in the regional population

	Comparisons		
Species	region	period	region × period
Mallard	***	***	*
Blue-winged teal	***	***	***
Northern pintail	***	***	NS
Northern shoveler	***	***	**
American wigeon	***	NS	***
Gadwall	***	**	NS
Green-winged teal	***	***	**
Scaup	***	***	**
Redhead	***	***	NS
Canvasback	***	**	NS
Ring-necked duck	***	***	***
Ruddy duck	***	***	NS

Note: * *P* < .05, ** *P* < .01, *** *P* < .001.

TABLE 7.5. Relative abundance (mean ± *SD* percentage composition) of each species in the prairie pothole region for three time periods

Species	Period				Pattern of change
	1955–1964	1965–1974	1975–1985	*P*[a]	
Mallard	27.8 ± 3.9 (a)[b]	24.2 ± 2.7 (b)	22.4 ± 3.1 (b)	.002	decrease
Blue-winged teal	21.4 ± 2.3 (a)	20.3 ± 2.4 (a)	19.2 ± 2.0 (a)	.095	no change
Northern pintail	16.5 ± 4.7 (ab)	18.7 ± 3.9 (a)	13.5 ± 3.9 (b)	.029	decrease
Northern shoveler	6.4 ± 1.2 (a)	7.9 ± 0.9 (b)	8.5 ± 1.8 (b)	.006	increase
American wigeon	7.5 ± 1.1 (a)	7.3 ± 0.9 (a)	7.2 ± 1.1 (a)	.857	no change
Gadwall	5.5 ± 2.6 (a)	7.4 ± 2.0 (ab)	7.6 ± 1.2 (b)	.041	increase
Green-winged teal	2.9 ± 0.6 (a)	3.7 ± 0.8 (b)	3.7 ± 0.5 (b)	.008	increase
Scaup	5.7 ± 1.4 (a)	3.6 ± 0.7 (b)	7.2 ± 1.3 (c)	.000	decrease/increase
Redhead	2.1 ± 0.4 (a)	2.5 ± 0.5 (a)	3.8 ± 0.7 (b)	.000	increase
Canvasback	1.6 ± 0.3 (a)	1.6 ± 0.3 (a)	1.9 ± 0.3 (b)	.025	increase
Ring-necked duck	0.2 ± 0.2 (a)	0.2 ± 0.1 (a)	0.6 ± 0.2 (b)	.000	increase
Ruddy duck	1.8 ± 0.6 (a)	2.1 ± 0.5 (ab)	3.1 ± 1.5 (b)	.018	increase

[a] Probability for overall *F* statistic for test of hypothesis that means do not differ among time periods.

[b] In each row, means followed by the same letter are not significantly different (*P* > .05).

TABLE 7.6. Relative abundance (mean ± *SD* percentage composition) of each species in six subdivisions of the prairie pothole region summed over all years (1955-1985)

Species	Region					
	Southern Alberta	Southern Saskatchewan	Southern Manitoba	Montana	North Dakota	South Dakota
Mallard[a]	25.7 ± 4.6 (a)[b]	27.9 ± 5.4 (ad)	21.3 ± 5.6 (b)	29.6 ± 5.0 (cd)	18.3 ± 4.6 (b)	19.8 ± 4.4 (b)
Blue-winged teal	13.6 ± 4.0 (ac)	17.1 ± 3.3 (a)	25.9 ± 8.1 (b)	11.3 ± 4.0 (c)	28.4 ± 6.6 (b)	38.1 ± 9.2
Northern pintail	19.2 ± 6.5 (a)	16.6 ± 5.3 (ab)	8.3 ± 3.8	18.7 ± 4.0 (ac)	15.3 ± 5.8 (bcd)	12.5 ± 4.5 (d)
Northern shoveler	7.3 ± 1.5 (a)	7.2 ± 1.8 (a)	5.4 ± 1.6	7.4 ± 2.9 (a)	9.0 ± 3.0 (a)	8.4 ± 3.1 (a)
American wigeon	7.5 ± 2.1 (ac)	8.6 ± 2.3 (a)	3.9 ± 2.0 (b)	12.1 ± 4.1	4.9 ± 3.8 (b)	5.1 ± 4.8 (bc)
Gadwall	6.4 ± 2.3 (a)	6.6 ± 2.7 (a)	3.8 ± 2.1	7.6 ± 2.8 (a)	10.0 ± 3.4	7.4 ± 2.7 (a)
Green-winged teal	4.3 ± 1.3 (a)	3.5 ± 1.0 (a)	4.7 ± 2.8 (a)	4.9 ± 2.3 (a)	1.6 ± 1.2 (b)	2.0 ± 1.6 (b)
Scaup	8.5 ± 2.9 (a)	5.4 ± 2.6 (b)	8.7 ± 3.9 (a)	4.3 ± 2.0 (b)	2.1 ± 1.8 (c)	1.6 ± 1.0 (c)
Redhead	2.6 ± 1.3 (a)	2.4 ± 1.1 (ab)	4.0 ± 1.5 (c)	1.4 ± 1.6 (bd)	4.6 ± 2.0 (c)	2.3 ± 1.1 (ad)
Canvasback	1.6 ± 0.5 (a)	2.2 ± 0.6	3.4 ± 1.4	0.5 ± 0.3 (b)	1.1 ± 0.5 (a)	0.4 ± 0.2 (b)
Ring-necked duck	0.1 ± 0.1 (a)	0.4 ± 0.3 (a)	1.2 ± 1.1	0.2 ± 0.4 (a)	0.4 ± 0.4 (a)	0.3 ± 0.5 (a)
Ruddy duck	1.6 ± 0.8 (a)	1.4 ± 0.9 (a)	6.7 ± 3.4	1.7 ± 1.8 (a)	4.3 ± 3.0	2.2 ± 2.6 (a)

[a] For each species, regional means are significantly different (ANOVA, *P* < .001) overall.

[b] For each species, regional means followed by the same letter are not significantly different (Tukey's HSD test, *P* > .05).

Occupancy Rates of Ponds

To test for possible changes in use of prairie pothole region habitat, we divided the total estimated number of ducks in the region by the total number of unadjusted May ponds estimated for the same region each year. A simple linear regression over time yielded the equation: $y = 128.164 - 0.062x$, where y = occupancy rate and x = years, $r^2 = 0.13$, $P < .05$. This relationship is relatively weak but indicates an overall decline in pond occupancy rate over the 31-year time period.

In an effort to deal with the extreme variation in these data, we ran linear and quadratic regression models on three-year running means (i.e., each point represented the mean of itself plus the population estimate of the year before and the year after). Both simple linear regression ($y = 11.90 - 0.0924x$, where y = occupancy rate and x = three-year running mean, $r^2 = 0.75$, $P < .001$) and quadratic models ($y = 37.276 - 0.829x + 0.005x^2$, $r^2 = 0.906$, $P < .001$) explained a much greater proportion of the variation present in the smoothed data than in the raw data.

Testing for functional relationships using "built-in" sampling correlations or correlated estimators may yield regression results that reflect sampling covariation as well as true correlation between the variables of interest. Thus, these large increases in r^2 should be interpreted cautiously. Nevertheless, we conclude that there has been a decline in pond occupancy rate since the beginning of the data set. The best-fit of the quadratic equation indicated a steeper decline until the mid-1960s and a decreasing rate of change since that time.

Patterns of Duck Productivity

We examined survey data for the entire region for relationships between productivity indices and wetland abundance, and trends over the time span of the data set. Two statistics were available: an index of class II and III broods (Gollop and Marshall 1954) (all ducks combined), and average brood size. Regressions of mean brood size and May ponds showed a significant positive relationship for three of six subdivisions of the region but not for all regions combined (Table 7.7). Brood index/total ducks showed no relationship to water conditions.

To standardize the brood index among years, we matched data across transects for May and July surveys within the same year and calculated brood index/total ducks as a crude index of productivity for all ducks in the population. Regression analyses were run to test for trends over time for each region.

Brood index/total ducks has declined significantly both for the whole region and for northern Canada (though data there are less extensive) (Table 7.8). A steep decline in productivity in southern Alberta was the primary cause of the significant decline in the region as the other five subdivisions showed no significant changes. Northern Saskatchewan and northern Manitoba combined also showed a significant decline over this time period but northern Alberta, British Columbia, and the Northwest Territories did not.

Average brood size has declined in the prairie pothole region overall but not in northern Canada (Table 7.9). The steepest declines occurred in southern Alberta, South Dakota, southern Saskatchewan, and southern Manitoba.

TABLE 7.7. Results of regression analyses for changes in brood index/total ducks and mean brood size in relation to the number of May ponds

Parameter	Region	Years of data	Slope	r^2	P
Brood index/ total ducks	S. Alberta	31	+0.95[a]	0.020	.456
	S. Saskatchewan	31	+0.08	0.012	.566
	S. Manitoba	31	−0.44	0.050	.234
	Montana	19	+1.43	0.006	.768
	North Dakota	28	−0.39	0.018	.498
	South Dakota	27	+0.89	0.033	.372
	Total	31	−0.07	0.040	.279
Mean brood size	S. Alberta	31	+0.95[b]	0.127	.053
	S. Saskatchewan	31	+0.30	0.171	.023
	S. Manitoba	31	+0.47	0.063	.184
	Montana	19	+2.41	0.235	.041
	North Dakota	28	+1.29	0.200	.019
	South Dakota	27	+0.17	0.001	.872
	Total	31	+0.11	0.084	.113

[a] For brood index/total ducks calculated slope is × 10^5.
[b] For mean brood size calculated slope is × 10^3.

TABLE 7.8. Results of regression analyses for changes in brood index/total ducks for the prairie pothole region and northern survey regions (1955-1985) (Brood data are not available for all regions in all years)

Region	Slope (× 100)	N[a]	r^2	P
Prairie pothole region				
S. Alberta	−0.155	31	0.79	.000
S. Saskatchewan	−0.019	31	0.07	.152
S. Manitoba	+0.011	31	0.03	.354
Montana	−0.075	19	0.14	.119
North Dakota	−0.005	28	0.01	.727
South Dakota	−0.011	27	0.02	.455
Total	−0.033	31	0.34	.001
Northern region				
N. Alberta, B.C., and N.W. Territories	−0.065	17	0.22	.061
N. Saskatchewan and N. Manitoba	−0.088	24	0.36	.001
Total	−0.075	24	0.39	.002

[a] Years of available brood data for each region.

These data were examined further by ANOVA to isolate better the nature of these declines. Data were divided by region and time period. Only two time periods were used because of limited brood data available for the north and other areas (e.g., strata 41, 42, etc.) early in the study period. Two-way ANOVA revealed that brood index/total ducks differed between time periods ($P < .001$) and in time × region interaction ($P = .032$) but not between regions ($P = .082$). Mean brood size did not differ by regions ($P = .178$) but did differ by time period ($P = .001$) and time × region interaction ($P < .001$). Individual pairwise comparisons are presented in Table 7.10.

TABLE 7.9. Results of regression analyses for changes in average brood size for the prairie pothole region and northern survey regions (1955-1985) (Brood data are not available for all regions in all years)

Region	Slope (×10)	N[a]	r^2	P
Prairie pothole region				
S. Alberta	−0.504	31	0.55	.000
S. Saskatchewan	−0.325	31	0.22	.008
S. Manitoba	−0.286	31	0.23	.007
Montana	−0.086	19	0.02	.528
North Dakota	−0.162	28	0.05	.258
South Dakota	−0.431	27	0.29	.004
Total	−0.426	31	0.64	.000
Northern region				
N. Alberta, B.C., and N.W. Territories	−0.588	17	0.28	.030
N. Saskatchewan and N. Manitoba	−0.017	24	0.00	.907
Total	−0.050	24	0.01	.576

[a] Years of available brood data for each region.

TABLE 7.10. Mean (± SD) brood index/total ducks and average brood size for the prairie pothole region and northern Canada for the first and second halves of the survey period

Parameter	Region	1955–1969	1970–1985
Brood index (×100)/total ducks	Prairie	2.10 ± 0.58 (a)[a](A)[b]	1.58 ± 0.27 (b)(A)
	North	2.71 ± 0.90 (a)(B)	1.51 ± 0.44 (b)(A)
Mean brood size	Prairie	5.72 ± 0.37 (a)(A)	5.03 ± 0.30 (b)(A)
	North	5.23 ± 0.26 (a)(B)	5.26 ± 0.39 (a)(A)

[a] For each parameter, values in each row followed by the same lowercase letter are not significantly different ($P > .05$).

[b] For each parameter, values in each column followed by the same uppercase letter are not significantly different ($P > .05$).

DISCUSSION

A striking feature of the prairie pothole region for ducks is the variability of habitat conditions, as indexed by the number of pothole basins flooded in May, and associated variations in duck use and productivity. The first year of the series, 1955, was a year of peak pond numbers and waterfowl populations, unmatched in any year since. The 31-year period has included dramatic changes in water and duck abundance. Our analyses support a great deal of earlier work by others that indicates that population variations result from several, presumably interacting, factors: the habitat preferences and basic characteristics of each species, natural variations of climate and geological history within the region, and man-induced changes in the landscape. To these must be added extrinsic factors that impact duck numbers in diverse ways during the portion of the year (more than half for most species) that birds are not present in the prairie pothole region.

Each species has a unique set of habitat requirements that cause birds to prefer particular regions over others during the breeding season, and the availability of these habitats presumably will affect settling patterns in spring. Resources that are important for ducks are assumed to fluctuate widely, more or less correlated with the only available long-term measure of habitat quality, May ponds. The portions of all species, except scaups and ring-necked ducks, settling in the region showed significant positive relationships to the number of May ponds. These two species appear to be the least closely tied to the region during the breeding season as only 16.9% of scaups and 13.9% of ring-necked ducks are found there in the spring. The main breeding range of these two species is further north in the forested region (Bellrose 1980).

Correlations between the percentage of a species' population settling and spring water conditions are highest in species that are only poorly, or variably, philopatric (northern pintails, blue-winged teal, and redheads, but not northern shovelers) (Table 7.3). There are almost no data on dispersal of ruddy ducks (for reviews, see Johnson 1986; Anderson et al. in press).

In a separate analysis, Johnson (1986) showed that 10 of the 12 species included in our analyses (excluding ring-necked ducks and ruddy ducks) exhibited some degree of displacement to other areas when the region was dry. This was usually in a northerly direction, but one species, the American wigeon, was displaced in a southeasterly direction. Overflights to northern areas during drought have been described previously by Hansen and McKnight (1964), Smith (1970), and Derksen and Eldridge (1980). Johnson (1986) suggested that three general strategies are used by breeding ducks to decide where to settle: a homing strategy wherein adults return to the area used the previous year and yearlings return to their natal area; an opportunistic strategy by which birds simply settle in the first suitable area encountered during spring migration; or a mixed strategy in which birds first home, but if the habitat is not suitable, they move on to other areas.

The data show significant differences in the relative abundance of all 12 species among six administrative subregions, and for 11 of 12 species, among the three time periods analyzed. The details of relative abundance by species for each time period and each region are presented in Tables 7.5 and 7.6. We did not search for detailed correlations between these data and possible cause-and-effect factors. However, it seems most likely that consistent regional differences are the product of species-specific habitat requirements. Changes in relative abundance over time might be the result of land-use changes that favor some species over others, or due to species-specific imbalances in factors extrinsic to the region, such as winter survival. For instance, all the diving ducks, which nest over water and generally are more successful than upland nesting ducks on intensively farmed land, have increased in relative abundance (Table 7.5). Shifts in relative abundance of individual species on small study areas across the prairies have been discussed by Trauger and Stoudt (1978), Leitch and Kaminski (1985), and others.

Along with annual variation in water abundance, the intensification of agriculture, which has resulted in drainage of potholes and destruction of upland nesting cover, probably has been the most dominant factor affecting the distribution, abundance, and reproductive success of the region's ducks. For the Dakotas and the three prairie provinces, estimates of pothole loss due to drainage range from 17 to 71% (Kiel et al. 1972; Schick 1972; Adams and Gentle 1978; Millar 1981; Rounds 1982; Rakowski and Chabot 1984; Tiner 1984; Turner et al. 1987). Conversion of native cover to small grain production and pasture has been extensive throughout the region (Cowardin et al. 1983; Sugden and Beyersbergen 1984; Boyd 1985). Other more subtle changes have occurred on the pothole margins through road construction (Kiel et al. 1972), burning (Fritzell 1975), and soil erosion (Canada 1984).

The result most obvious for waterfowl has been a massive loss and deterioration of habitat, both aquatic and upland. Associated effects result from the concentration of nesting ducks in very limited habitat, such as fence rows, roadsides, and narrow fringes around potholes, and from shifts in predator communities with intensive farming. The most alarming consequence has been the widespread decline of nesting success, and therefore recruitment, documented at numerous intensive study sites (Sellers 1973; Higgins 1977; Johnson and Sargeant 1977;

Cowardin et al. 1985; Greenwood et al. 1987).

Evidence of decreased reproductive success also was found in our analysis of brood production relative to population size and of average brood size. The brood index/total ducks decreased dramatically in southern Alberta and to a lesser degree throughout the region and in survey strata across northern Canada. Average brood size also decreased throughout the prairie pothole region but not in the northern regions. Similar results have been reported from an independent analysis of recent production data (Reynolds 1987).

The data show some significant positive relationships between May ponds and average brood sizes, suggesting that factors that cause birds to settle and breed are also related to the productivity of individual successful nesting attempts. That is, in wetter years, more birds settle and successful nests produce more young than in drier years. However, the brood index/total ducks parameter and May ponds showed no relationship, indicating that the effect of water availability is primarily on settling rates. Subsequently, the relative hatching success of the birds that do settle appears to be unchanged between wet and dry years. Alternatively, broods may be less visible to surveyors in wet years, thereby biasing comparisons of productivity and water levels (Blohm pers. comm.; Anderson pers. obs.). Field studies are needed to examine these biases.

The lower brood index/total ducks and the smaller brood size in recent times are consistent with the general pattern of reduced nesting success resulting from agricultural impacts. However, the lower index in the north cannot be explained by this relationship. The latter finding is somewhat surprising and will require a more intensive analysis to search for potential cause-and-effect relationships. Some extrinsic factor(s) during the wintering or spring migration periods may be affecting these parameters.

Agricultural impacts should be greatest on early nesting species (those that nest before there is appreciable new growth by crops or pasture grasses). Correspondingly, the earliest nesters, northern pintail and mallard, were the only two species that showed a significant decline in relative abundance over the three time periods of this analysis. Furthermore, upland nesters, in general, tended to settle in the region in declining proportions (Table 7.2). The species showing the steepest decline, the American wigeon, is often associated with grasslands (Bellrose 1980; Wishart 1983). Only species nesting over water showed any tendency to settle on the prairies in increasing proportions (Table 7.2). The lower average brood size in recent years may be related to a much larger portion of annual production coming from birds that had lost their first nests to predators or agriculture, and were forced to renest later in the season. Renest clutches are smaller in size and thus will produce fewer ducklings per successful hen (Sowls 1955; Johnsgard 1973; Batt and Prince 1979).

Among waterfowl biologists, there is considerable discussion about whether empty habitat exists in the prairie pothole region (i.e., areas with populations far below their presumed carrying capacity). Our analysis shows a reduced occupancy rate of potholes by ducks since 1955. The debate is whether this is simply a result of there being too few birds to fill the available habitat, or a result of the real carrying capacity being far below the apparent carrying capacity, as indexed only by May ponds. In view of escalating human impacts, there can be little doubt that this landscape should not be as productive as during the early years of the survey. However, there are also data to support the contention that at least some effects on populations have resulted from lower duck survival away from the prairie pothole region (Caswell et al. 1985).

These questions cannot be answered clearly with simple correlation studies such as this, but rather require direct experimentation with recruitment and survival. We consider this to be a critical issue that must be resolved if future waterfowl management is to be effective. We concur with Cowardin et al. (1985) that in order for waterfowl to thrive on the prairies, management must succeed in three areas: preservation and management of essential habitat, regulation of harvest, and maintenance of a recruitment rate that will compensate for annual mortality.

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HENRY R. MURKIN

11 THE BASIS FOR

ABSTRACT

FOOD CHAINS in prairie wetlands are complex, involving a diverse group of producers and consumers. The important factor limiting secondary production in any ecosystem is the net primary production of that system. The nutrient and energy resources of primary production are exploited by heterotrophic consumers through herbivory and detritivory. The vegetation of prairie wetlands changes with climatic conditions causing major fluctuations in both primary production and litter accumulation over time. Accurate estimates of total primary production are not possible at present due to a lack of information on belowground macrophyte production and algal productivity in wetland systems. These gaps in our understanding hamper detailed studies of wetland secondary production and food chains. High emergent primary production in prairie wetlands results in large quantities of litter entering the system. The processing of this litter by a variety of consumers is assumed to be the base of food chains associated with prairie wetlands. There have been, however, no detailed studies of detrital consumption and utilization by detritivores in prairie wetlands. A number of recent studies have reported that herbivory by birds and mammals on macrophytes may contribute significantly to the secondary production of these systems. Future research on grazing of algae by invertebrates is also required before the overall role of herbivory in prairie wetlands can be established in detail. Herbivory may be more important in these systems than previously thought, particularly during some stages of the wet-dry cycle.

KEY WORDS: aboveground production, algae, belowground production, detritivory, detritus, food chains, herbivory, invertebrates, life history, macrophytes, primary production, secondary production.

FOOD CHAINS IN PRAIRIE WETLANDS

INTRODUCTION

WHILE food chains in estuaries, coastal marshes, and associated marine areas have received considerable attention (Livingston and Loucks 1978; Hamilton and Macdonald 1979; Kennedy 1980; Pomeroy and Wiegert 1981; Boesch and Turner 1984), very little effort has been spent developing our understanding of food chains in northern prairie wetlands. Simple textbook models exist for some freshwater wetlands (Odum et al. 1984), however, food chains in these systems are complex, involving a wide array of consumers including bacteria, fungi, invertebrates, amphibians, reptiles, birds, and mammals (Clark 1978; Crow and Macdonald 1978). Because they fix carbon through photosynthesis and incorporate inorganic nutrients from the environment into organic forms, primary producers are the link between consumers and the resources of the system. As a result, the critical factor ultimately limiting secondary production is net primary production within the ecosystem.

In general, there are two basic avenues by which the nutrient and energy resources of primary production are made available to heterotrophic consumers. The first involves direct consumption of living plants by herbivores, and the second, the utilization of plant litter by various detritivores. The habitat provided by both living and dead plants is also important to the survival and reproduction of consumers within the system (Orth et al. 1984). The purpose of this chapter is to review our current knowledge of food chains in northern prairie wetlands and attempt to evaluate the relative importance of herbivory and detritivory to

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overall secondary production in these systems. The complexity of food chain interactions in these wetlands, which themselves are extremely complex, both spatially and temporally, ensures that there is no simple answer to this objective.

COMPONENTS OF THE FOOD CHAINS IN WETLANDS

Study of food chain interactions in prairie wetlands is complicated by the characteristics of the consumers themselves. The temporal use patterns of consumers associated with these wetlands vary greatly (Sather and Smith 1984). Some consumers are completely dependent on wetlands for all of their annual requirements, whereas other species use wetlands for only some of their requirements. Some groups complete their entire life cycle within a single wetland. Others are present for only short periods in the life cycle or during the year. Still others travel from wetland type to wetland type. Those species that use wetlands throughout the year may be restricted to a particular habitat within the wetland or may use two or more habitats over the course of their life cycle. Attempting to determine the role wetlands play in the productivity of a species that occurs in the wetland for short periods during the day, the year, or maybe its entire life is certainly difficult, if not impossible.

Another major problem limiting work on food chain interactions and secondary production is the lack of information on the basic life history and ecology of the consumers present in the wetland (Murkin and Batt 1987). Although some information is available on waterfowl (Swanson and Duebbert, Chap. 8), fur-bearers (Fritzell, Chap. 9), and fish (Peterka, Chap. 10) use of these systems, data on many of the other groups is essentially nonexistent. Microbiological research involving bacteria, fungi, and other microconsumers in prairie wetlands is certainly lacking. A symposium addressing the use of freshwater wetlands by aquatic insects (Rosenberg and Danks 1987) concluded that very little is known about any of the insect families inhabiting these systems. Murkin and Batt (1987) suggest that secondary production work in freshwater wetlands is impossible at present because we lack basic life history information on most of the dominant invertebrate groups within these wetlands. This lack of background information requires compilation of species lists and basic life history information before food chain or production work can be attempted. Understanding wetland food chain interactions and secondary production also requires information on the trophic status of the species of interest. For many of the important consumers in the wetland ecosystem, such as invertebrates, this information is simply not available. These problems are complicated by the fact that some of the consumer groups for which we do have information may change their trophic status over the course of their life cycles (see Merritt and Cummins 1984). In addition, many wetland consumers are basically opportunistic omnivores eating whatever is available in the habitat (Montague et al. 1981; Smith et al. 1984).

PRIMARY PRODUCTION

Net primary production is normally high in wetlands (Richardson 1978), and can be very high in prairie glacial marshes at times (van der Valk and Davis 1978a). There are significant variations in macrophyte primary production within and among wetlands (Table 11.1) due to differences in climate, water levels, fertility, and so on (van der Valk and Davis 1980; Sather and Smith 1984). In prairie wetlands, there are also changes in primary production associated with wet-dry cycles (van der Valk and Davis 1978b; Kantrud et al. Chap. 5) (Table 11.2). A wet-dry cycle may take from 5 to 30 years to complete.

One aspect that is often overlooked during consideration of overall primary production within a wetland is belowground production by aquatic macrophytes. Emergent macrophytes, in particular, produce extensive systems of belowground roots and rhizomes that serve as stores for nutrients between growing seasons. These rhizomes are also the principal means of vegetative propagation for these species. Belowground macrophyte production is high in prairie marshes (Table 11.1). This belowground tissue represents a large pool of nutrients and energy that is usually ignored when considering wetland food chains. In temperate areas of North America, belowground biomass may be the only source of living plant material available to consumers during the winter.

Another area of neglect in the study of wetland production has been the contribution by algae to the overall primary production (see Crumpton, Chap. 6). Because algae do not have large standing crops at any point in time, they are usually considered unimportant to overall primary production. Hooper and Robinson (1976) and Shamess et al. (1985) have shown, however, that algae production in prairie wetlands can be quite high. Although standing algal biomass may be small, turnover rates are very high resulting in significant annual production (Table 11.1).

There are four important groups of algae in northern prairie wetlands: epiphyton, epipelon, phytoplankton, and metaphyton. Epiphytic algae grows on the surface of submersed plant material. In the Delta Marsh, a large northern prairie marsh in south-central Manitoba, the epiphytic algae belong to Chlorophyceae (green algae except Chara),

TABLE 11.1. Biomass estimates of the various primary producers in northern prairie marshes

Component	Annual production[a] (gC/m^2/yr)	Reference
Emergent macrophytes		
Above ground		
Typha glauca	341–576	van der Valk and Davis (1978a)
	772–1075	van der Valk and Davis (1980)
	1351–1762	Neely and Davis (1985)
Scirpus validus	109–175	van der Valk and Davis (1978a)
	392–486	van der Valk and Davis (1980)
Scolochloa festucacea	135	Neckles (1984)
Sparganium eurycarpum	271–543	van der Valk and Davis (1980)
	637–1185	Neely and Davis (1985)
Below ground		
Typha glauca	525–649	van der Valk and Davis (1978a)
	1300–1779	Neely and Davis (1985)
Scirpus acutus	543–841	van der Valk and Davis (1978a)
Phragmites australis	504–704	van der Valk and Davis (1978a)
Sparganium eurycarpum	681–1123	Neely and Davis (1985)
Submersed macrophytes		
Several species combined	41–117	van der Valk and Davis (1978a)
Potamogeton pectinatus	5–112	Anderson (1978)
Algae		
Epiphytic on *Scirpus*	43.5	Hooper and Robinson (1976)
Epiphytic on *Typha*	22.9	Hooper and Robinson (1976)
Epiphytic on *Potamogeton*	11.8–48.5	Hooper and Robinson (1976)
Epipelon	100–300	Robinson, pers. comm.
Phytoplankton (water depth = 50 cm)	5.6–77.6	Hosseini (1986)
Metaphyton	8.8–69.0	Hosseini (1986)

[a] Biomass data has been converted to gC by assuming a 45% carbon content of plant tissue.

TABLE 11.2. Contribution of macrophytes and algae to overall primary production during the various stages of the wet-dry cycle of prairie wetlands

Vegetation	Drawdown	Regenerating	Degenerating	Lake marsh
Macrophytes				
Annuals	High	. . .	. . .	. . .
Emergents	Low	Moderate to high (increases as vegetative growth increases)	Moderate (decreases as marsh opens up)	Low to very low
Submersed	. . .	Low to moderate	Moderate to high (increases as marsh opens up)	Low to high (depends on amount of wind and wave action present)
Algal				
Phytoplankton	. . .	. . .	Low	Low
Epiphytes	. . .	Moderate to high (depends on amount of flooded substrate)	Moderate to high (depends on amount of flooded substrate)	Low to high (depends on submersed macrophyte development)
Epipelon	Low	Low to moderate (will decrease as marsh closes up)	Low to moderate (will increase as marsh opens up)	Low to high (depends on shading by submersed marcrophytes)
Metaphyton	. . .	Low to moderate	Low to high	Low to moderate (depends on amounts of wind and wave action present)

Cyanophyceae (blue-green algae), and Bacillariophyceae (diatoms) (Hooper-Reid and Robinson 1978). Annual production values of epiphytes in the Delta Marsh are shown in Table 11.1.

Perhaps most important due to its contribution to overall wetland productivity, yet virtually unstudied, are the epipelic algae. These are the algae in the top few millimeters of the sediments within the wetland. The epipelic community in northern, shallow water bodies is dominated by Bacillariophyceae (diatoms) (Shamess et al. 1985). Preliminary work on the epipelon in wetlands shows that this community is very productive (Table 11.1).

Phytoplankton refers to the algal suspended in the water column. Although a large number of species are found within the phytoplanktonic community (Shamess et al. 1985), overall annual production in wetlands is thought to be low during all stages of the wet-dry cycle (Robinson, pers. comm.).

The most conspicuous algae community in wetlands with respect to standing crop is the metaphyton or flooding mats of filamentous algae. While techniques are still being developed to study the production of metaphyton in prairie wetlands (Hosseini 1986), initial estimates from work on the Delta Marsh indicate substantial primary production within the metaphyton community (Table 11.1).

The final producer group that has received even less attention than algae are the chemosynthetic bacteria. The importance of these organisms in freshwater wetland production and ecology is unknown.

DECOMPOSITION IN PRAIRIE WETLANDS

The high primary production in prairie wetlands ensures that a considerable amount of material enters the system as detritus. There are three components of the detritus pool in prairie wetlands: standing litter, fallen litter, and dissolved organic compounds that leach from both standing and fallen litter. Material enters the standing litter compartment with the death of the leaf and/or shoots (Davis and van der Valk 1978a). While a great deal of tissue enters the standing litter stage with senescence at the end of the growing season, leaf and shoot death occur throughout the growing season. Timing of shoot death varies greatly among the dominant emergent species. *Carex atherodes* shoots and leaves begin to die in the spring soon after new growth begins and continues throughout the growing season (Davis and van der Valk 1978a). In some of the bulrushes (*Scirpus* spp.), shoots begin to die in midsummer. For *Typha glauca,* Davis and van der Valk (1978a) report that 80% of the shoots alive during the periods of peak standing crops were killed by the first frosts of fall.

Litter decomposition involves three processes that take place simultaneously: (1) leaching of soluble substances occurs rapidly following death of the plant tissue and accounts for much of the weight loss during the early stages of decomposition; (2) mechanical fragmentation due to weathering or animal activities such as trampling, house building, and grazing; and (3) biological decay from the oxidation of detritus by bacteria, fungi, and other consumers (de la Cruz 1979).

In prairie marshes, litter is transferred from the standing litter compartment to fallen litter through fragmentation by wind, snow, and ice action (Davis and van der Valk 1978a). During periods of high muskrat populations, feeding and house building can cause living plant tissue to bypass the standing litter stage and directly enter the fallen litter compartment (Nelson 1982). While some leaching of nutrients takes place during the standing litter stage through rainfall and wave action, any soluble materials remaining in fallen litter are leached out soon after being submersed. Nutrients like sodium and potassium are loosely held within the plant tissue and are rapidly lost through leaching (Davis and van der Valk 1978b). Most nutrients other than calcium, iron, and aluminum show some leaching loss from standing litter.

Once within the fallen litter compartment, nitrogen may actually accumulate in the litter for the first few weeks. This increase can be attributed to the buildup in microbial populations (bacteria, fungi, diatoms, and various protozoa) on the litter (Polunin 1984; Rice and Hanson 1984) and direct absorption and complexing of nitrogen compounds by the litter particles (Lee et al. 1980). Evidence for increased microbial levels is the increased oxygen demand by decomposing plant tissues (Hargrave 1972). This nitrogen accumulation indicates that levels of nitrogen within the litter are too low to support microbial growth and reproduction; therefore, available nitrogen is extracted from the surrounding water (Melillo et al. 1984). Tissues rich in nitrogen are probably more suitable for microbial colonization than detritus with lower nitrogen levels (Davis and van der Valk 1978a). This would suggest that living tissue cut by animals such as muskrats and introduced directly into the fallen litter compartment would serve as excellent substrates for microbial activity (Nelson 1982).

As decomposition proceeds within the water, litter particle size becomes smaller due to further fragmentation caused by mechanical forces such as wave action and animal feeding activities. Various animals, primarily invertebrates, feed on detritus, fragmenting it into smaller particles. The resulting feces are again colonized by microbial populations (Turner and Ferrante 1979). As a result, there is a gradual decrease in detrital particle size and biomass over time. As the various organic compounds are digested through a series of consumers, the chemical structure of the detritus also becomes less complex (Polunin 1984).

As particle size is reduced, transport by water currents serves to alter the distribution of litter within the wetland (Nelson and Kadlec 1984). While the transport of detritus among salt marshes, estuaries, and adjacent marine areas has been suggested to have ecological implications with respect to overall estuarine secondary productivity (Nixon 1980; Gallagher et al. 1984), transport of detritus in freshwater wetlands has received very little attention. As litter particle size is reduced, it becomes more susceptible to transport in suspension by low velocity wind-induced currents (de la Cruz 1979). In lacustrine or riverine marshes, there may be a net export of litter from the wetland. This may be true for any wetland with an outlet through which water leaves the wetland. Many of the prairie potholes do not have an outlet; however, litter may be transported within the wetland through water currents (Nelson and Kadlec 1984). This results in detrital material being transported from areas of production to areas where there is little or no plant production.

As decomposition proceeds, the more refractory particulate and amorphous detritus become incorporated into the sediments (Wetzel 1984). The fate of this material in the sediments requires investigation. Another process requiring attention is the decomposition of the below-ground biomass. There have been no published studies on the decomposition of roots and rhizomes within the prairie wetland ecosystem.

HERBIVORY IN PRAIRIE MARSHES

Herbivores consume living plant tissue. Many researchers suggest that herbivory is relatively unimportant in wetlands and that only a small percentage of the overall primary production is consumed by herbivores (Gallagher and Pfeiffer 1977; Parsons and de la Cruz 1980; Simpson et al. 1983). There have, however, been few tests of this hypothesis (Pfeiffer and Wiegert 1981), nor has any attention been paid to the effects of herbivory on the various algal communities within freshwater wetlands. Herbivory obviously affects the energy and nutrients available to detrital food chains and ultimately the overall function of the wetland ecosystem (Smith and Kadlec 1985). Herbivores using wetlands range from the moose (*Alces alces*) feeding on submersed aquatic vegetation to micro-crustaceans filtering algae from the water column.

A number of cases have been documented where grazing has had a significant impact on the primary production within wetlands. Smith and Kadlec (1985) found that waterfowl and muskrats (*Ondatra zibethicus*) grazing in a Utah marsh reduced production and standing crops of *Typha latifolia*, *Scirpus lacustris*, and *S. maritimus* by 47.5, 25.4, and

8.9%, respectively. Because the exclosures used in this study did not exclude insects or small mammals, the overall effect of grazing may be higher than actually reported.

One of the dominant herbivores in freshwater wetlands is the muskrat (Fritzell, Chap. 9). Complete eat outs of wetland vegetation by muskrats have been documented many times (Errington et al. 1963; Weller and Spatcher 1965; Van Dyke 1972; Sipple 1979). Van der Valk and Davis (1978b) cite muskrats as one of the dominant factors reducing vegetation during the degenerating phase of the marsh vegetation cycle. McCabe (1982) showed that muskrats had a marked effect on vegetation densities and reproduction within a wetland in Utah through repeated grazing. Through selective feeding, muskrats can affect vegetation species composition within a wetland (Fuller et al. 1985) and, therefore, overall primary production rates within the wetland. During periods of optimal habitat conditions, muskrat population levels can increase very rapidly (Errington 1963). The normal phases of muskrat population development are low muskrat numbers, increasing population size as the food supply becomes established (regenerating marsh), overpopulation, range damage (degenerating marsh), and finally starvation (Lowery 1974). There is no doubt that during a muskrat eat out of a prairie marsh, herbivory is a dominant factor in the system's food chain (Perry 1982). Muskrats utilize the belowground portion of macrophytes as well as the aboveground material. Roots and rhizomes are the main food of muskrats during the winter (Dozier 1953). During eat outs, muskrats may dig to depths of 50 cm to uncover rhizomes (Lowery 1974). Besides vegetation directly consumed, muskrats use large quantities of plant material for building winter lodges, feeding huts, and feeding platforms. As a result, a great deal of uneaten plant material is introduced to the marsh through muskrat activity. This has definite implications for detritivores within the wetland. Green and growing shoots cut by muskrats for lodges and shelters have higher nutrient concentrations than dead leaves and stems that fall into the water following senescence and fragmentation (Nelson 1982). Muskrats tend to use the most available plant species for feeding and house building and, therefore, species utilized may vary among wetlands (Allen and Hoffman 1984). In the United States and Canada, cattails (*Typha* spp.) and bulrushes (*Scirpus* spp.) appear to be preferred foods and habitats (Willner et al. 1975). MacArthur and Aleksiuk (1979) found muskrat lodges in the Delta Marsh were usually constructed of cattails or bulrushes interspersed with pondweeds and bottom detritus. Not all plant species are capable of supporting equal populations of muskrats. In Manitoba, cattails can support approximately seven times as many muskrats as equivalent areas of bulrush

(Allen and Hoffman 1984). Carrying capacity near Mafeking, Manitoba, ranged from 7.4 muskrats/ha for *Carex* spp. to 64.2/ha for *Phragmites* (Butler 1940).

Among the other herbivorous mammals, many inhabitants of upland sites (such as hares and voles) make feeding forays into wetlands (Crow and Macdonald 1978). While small mammals are abundant in wetland areas, there has been no research reported on their productivity or their effect on overall wetland primary production. In terrestrial habitats, small mammals may have a major impact on annual primary production (Golley 1973). Working in Iowa, Weller (1981) reported higher densities of meadow voles (*Microtus pennsylvanicus*) and short-tailed shrews (*Blarina brevicauda*) in wet meadows along marshes than in drier upland sites. The effects of these high population levels on wetland primary production, particularly seed production, requires investigation.

Other important herbivores present in prairie freshwater wetlands are the waterfowl. One of the primary herbivores reported by Smith and Kadlec (1985) in their study on a Utah marsh was the Canada goose (*Branta canadensis*). The geese grazed on aboveground plant parts during spring and summer. Smith and Odum (1981) reported that snow geese (*Chen caerulescens*), feeding primarily on roots and rhizomes during winter, removed 58.1% of the available standing crop within a *Spartina* spp., *Distichlis spicata*, and *Scirpus* spp. marsh. Cargill and Jefferies (1984) documented that snow geese consumed approximately 80% of the net aboveground primary production within a *Puccinellia-Carex* marsh in northern Canada. An interesting sidelight to this study was that grazing by the geese actually increased the net aboveground primary production by about 30%. Waterfowl removed most of the aboveground biomass and 70% of viable seeds from the soil of coastal flats in the Netherlands affecting not only nutrient and energy dynamics of the area but also species composition of the vegetation surviving from year to year (Joenje 1985).

Feeding by mallards (*Anas platyrhynchos*) and blue-winged teal (*Anas discors*) completely eliminated sago pondweed (*Potamogeton pectinatus*) aboveground biomass from a shallow pond in the Delta Marsh (Wrubleski 1984). This removal of the pondweed had significant implications beyond the nutrient and energy considerations of the biomass removal. The elimination of the pondweed disrupted the major structural component of the open-water habitat, which in turn influenced the chironomid community structure of the pond. Removal of the pondweed eliminated the epiphytic chironomid species and appeared to benefit the larger, benthic dwelling species.

Invertebrates also feed on submersed and emergent vegetation in wetlands (Berg 1950; McDonald 1955; Skuhravy 1978), however, few large eat outs of emergent vegetation by invertebrates have been documented. Beule (1979) described the destruction of a large area of cattail in a waterfowl management area due to mining by the moth *Leucania scirpicola*. The actual amount of plant material consumed by the moth larvae was not recorded. Skuhravy (1978) noted that in a wetland in Czechoslovakia, one-third of the stems of *Phragmites* were damaged by insects. This resulted in a 10–20% loss of annual primary production. Smirnov (1961) reported a 0.4–7.0% loss of above ground macrophyte production to invertebrate herbivores in a shallow lake in the USSR. It appears that rather than consuming significant biomass within the wetland, invertebrate feeding causes only local damage to the plants involved. Simpson et al. (1979) also concluded that insect grazing on macrophytes in freshwater tidal marshes was minimal.

A major unstudied area of herbivory in wetlands has been the consumption of algae by primary consumers. Aquatic invertebrates are abundant in prairie wetlands, yet little is known about their feeding habits or trophic status. Cladocerans are abundant in the Delta Marsh (Murkin 1983) and other prairie wetlands. Porter (1977) reported that cladocerans and copepods feed primarily on phytoplankton in the water column. During periods of peak abundance, these crustaceans are potentially able to graze over 100% of the daily phytoplankton production (Smirnov 1961). Haney (1973), working in lakes, showed that cladocerans were responsible for 80% of the overall grazing activity by the zooplankton community. Porter (1977) found that cladocerans control both algal abundance and species composition by selectively grazing on the most palatable algal species present. To complicate matters, not all cladocerans feed exclusively on algae. Coveney et al. (1977) found that in an eutrophic lake, one species of Daphnia fed primarily on phytoplankton while another species fed almost exclusively on bacteria.

In many prairie wetlands, larva of the chironomidae (O. Diptera) are the most abundant invertebrate group present. Many of the species within this family are filter feeders that build tubes on plant material or in bottom sediments (Lamberti and Moore 1984). Planktonic algae and detritus are apparently their main food sources. It appears, however, that algae make up the majority of their diet during spring and summer when algal productivity is high. In addition, larvae inhabiting the littoral areas of lakes consume more algae than those in deeper profundal areas. Stomach contents of the chironomidae larva (*Procladuis nietus*) collected in the Delta Marsh contained primarily diatoms (Wrubleski, unpubl. data). Cattaneo (1983) reported that chironomid assemblages significantly reduced the biomass of lentic epiphytic algae.

Hunter (1980) found that the freshwater snails, *Lymnaea*, *Physa*, and *Helisoma*, all common inhabitants of prairie marshes, greatly reduced the standing crop of pond periphyton. Most of the evidence for invertebrates feeding on algae comes from studies other than wetlands. Before progress can be made toward understanding secondary production and food chains in prairie wetlands, further research into the trophic status of wetland invertebrates is urgently needed.

Vertebrates feeding on algae in wetlands has not been documented in any detail; however, American coots (*Fulica americana*), gadwalls (*Anas strepera*), and mallards (*A. platyrhynchos*) have been observed feeding on mats of metaphyton in the Delta Marsh (Murkin, pers. observ.). Dickman (1968) found that densities of filamentous green algae in a lake in British Columbia were controlled by the grazing activities of tadpoles (*Rana aurora*) within the lake.

DETRITIVORY IN PRAIRIE MARSHES

Although not very well documented in the literature, the "freshwater marshes are detritus-based systems" axiom is widely accepted by analogy with salt marshes. The idea is that the major trophic structure of the wetland ecosystem proceeds from plant detritus, to microorganisms, to a variety of invertebrate consumers, and then in some cases on to vertebrate predators (see Swanson and Duebbert, Chap. 8). This reasoning follows very closely the current theories on streams (Vannote et al. 1980) and salt marshes (Odum and Heald 1975). It appears aquatic macroinvertebrates are the key link in secondary production of these wetland systems. Few vertebrates in prairie wetlands have been described as detritivores, although bottom feeders such as carp are likely to ingest plant litter incidental to foods removed from the substrate. Bacteria, fungi, and other microorganisms are essentially the first-level consumers of dead plant material. However, the detritus and the associated microbes are normally considered to be the base of detrital food chains, with secondary production occurring at higher trophic levels (Darnell 1976).

Once dead plant material enters the fallen litter compartment as coarse particulate organic matter (CPOM), it is colonized by microorganisms, which increase its nutritive quality for secondary consumers. Detritivores may actually select litter with higher overall nutrient levels (Valiela and Rietsma 1984). The nutritive quality of the original litter may be of minor importance compared to the nutrients associated with the colonizing microorganisms (Ward and Cummins 1979; Findlay and Tenore 1982; Lawson et al. 1984). Motyka et al. (1985) found that colonized detritus was selected much more readily by aquatic detritivores than uncolonized litter. For many consumers, CPOM serves both as food and habitat. In prairie wetlands, CPOM normally enters the marsh as a pulse in spring; however, as mentioned earlier, there is also continuous input for many plant species throughout the year.

Cummins (1973) described the functional groups of invertebrates with respect to processing litter in streams. Nelson (1982) has shown that these concepts are useful in marshes as well. Shredders and grazers (or scrapers) are the first invertebrate groups to respond to CPOM and its associated microbial communities. An important shredder in prairie wetlands is the amphipod *Hyalella azteca* (Nelson 1982). De March (1981) describes *H. azteca* as primarily a detritivore; however, it will consume algae if they are available. Various snails are important grazers (scrapers) in prairie wetlands (see Pip 1978).

Early invading functional groups serve to reduce the particle size of the litter by their feeding activities. Some authors argue that detritivorous invertebrates do not actually digest detritus at all. They simply assimilate the microorganisms associated with the litter, then egest the dead plant material (in smaller particle sizes), which is then recolonized by decomposer microorganisms (Montague et al. 1981). As the litter particle size is reduced, this fine particulate organic matter (FPOM) becomes available to another set of consumers. Filter feeders remove the fine litter particles from the water column, while collectors gather FPOM from the substrate surfaces. The family Chironomidae in wetlands has representatives in both these functional groups. As the litter particle size is reduced through successive trophic functional groups, the residual material resistant to decomposition by micro-organisms and invertebrates is incorporated into the sediments of the wetland.

Another important detritus pool in aquatic environments is the dissolved organic molecules or complexes released during leaching or incomplete digestion by consumer organisms. Most research has focused on the large particulate detritus; however, the much smaller amorphous organic complexes and dissolved molecules may be more abundant in aquatic systems (Bowen 1984). Similar to particulate detritus, dissolved organic matter consists of a more labile fraction that is readily utilized by bacteria and a more refactory component that is utilized more slowly (Roman and Tenore 1984). Dissolved organic matter may be the primary food source for suspended bacteria, microflagellates, and protozoa within these environments (Linley and Newell 1984; Taylor et al. 1985). This consumption of dissolved nutrients by these microorganisms is an important mechanism in the transformation of dissolved nutrients into microbial biomass, which then can be utilized by higher consumers (Murray and Hodson 1985; Riemann 1985).

Unlike the few studies of herbivory with actual estimates of total primary production consumed by primary consumers, there are no estimates of detrital consumption and utilization in wetlands. Because of the vast amounts of plant litter observed in prairie wetlands and the often high densities of assumed detritivores (i.e., the abundant invertebrate groups), it has been assumed that detritivory forms the base of the food chains in these systems.

FOOD CHAINS AND THE VEGETATION CYCLE

The vegetation cycle of prairie marshes (see Kantrud et al., Chap. 5 for details) will certainly provide very different resources to secondary consumers during each of the stages (Table 11.2). These changes in available resources would also result in changes in the roles of herbivory and detritivory in food chains during the wet-dry cycle (Table 11.3).

During the drawdown stage, aquatic invertebrate and vertebrate production is nonexistent. It appears that the terrestrial conditions would be most suitable for terrestrial herbivores and detritivores. During the first growing season of the drawdown, there would be little surface litter present on the exposed mudflats, so basic food-chain support would be herbivory on the primary production of the rapidly growing mudflat annuals and perennials. If the drawdown persists for more than one growing season, there will be some buildup of plant litter and the potential of detritivore support within the terrestrial food chain.

With the return of standing water and the development of a regenerating marsh, there would be some potential for detritivore food-chain support as the mudflat annual litter is submersed and decomposes. The primary production by rapidly growing and expanding emergent vegetation beds would provide potential for herbivore support. The large surface areas provided by submersed mudflat annual litter and the expanding macrophyte stands would also provide the potential for high epiphytic algae production during these periods. Maximum algae growth would occur on the flooded annual litter before the emergent vegetation stands become too dense and cause shading of the water column. The vast surface area provided by flooded annual plant litter for epiphytic algae growth and invertebrate habitat may be one of the primary reasons for the high overall productivity associated with newly flooded wetlands. It appears that food chains in the regenerating marsh may be dominated by the vast amounts of primary production during this stage of the marsh cycle.

As the regenerating marsh shifts to the degenerating marsh stage, the amount of living plant material in the wetland declines and the detritus added to the water column increases. Nelson (1982) suggests that the

TABLE 11.3. Contribution of herbivory and detritivory to food chains during the various phases of the wet-dry cycle of prairie wetlands

Function	Drawdown	Regenerating	Degenerating	Lake marsh
Herbivory				
Macrophytes	Low	Low	High	Low
Algae	. . .	Moderate	Moderate to high (depends on epiphyton)	Low to high
Detritivory	Low	Low to moderate	High	Low to moderate

litter added to the water by factors such as muskrats will be of high quality and further enhance detritivore production during these periods. This may imply a shift from primarily herbivore support of the food chains to detritivory; however, the surface area provided by the increased litter input to the water column may again increase algal production, particularly as the emergent vegetation stands thin out and light once again penetrates the water column. The nutrients leached from the newly submersed litter are also readily utilized by algal cells.

As the degenerating marsh opens to the lake marsh stage, both macrophyte primary production and litter production are at a minimum. The lake marsh characteristically consists of a shallow lake with a muddy bottom surrounded by a thin border of emergent vegetation. Some submersed vegetation persists in the open-water areas, however, the overall productivity of submersed plant species is lower than emergent vegetation (Table 11.1). The flocculent sediments consist of fine litter particles that are resistant to further decomposition. The emergents around the border of the lake would provide only minor amounts of living plant tissue and potential litter to the system. While normally considered unproductive, lake marshes often support large populations of Chironomidae larva. Murkin and Kadlec (1986) documented the highest densities of chironomid larva during the lake marsh stage of an artificially created wetland vegetation cycle. One possible source of food-chain support during this stage may be epipelic algae. This algae group prefers shallow, open pond situations with soft sediments and few macrophytes to shade the substrate. As shown earlier, epipelon may not have a large standing crop at any time; however, its rapid turnover rates result in relatively high levels of primary production over the course of a season. The epipelon may well be the main support of the available food chains during the lake marsh stage of the prairie wetland vegetation cycle.

CONCLUSIONS

There is no doubt that detritivory is an important component of the food chains in prairie wetlands. This review, however, suggests that herbivory is also a factor in wetland food chains, especially during some stages of the wet-dry cycle (Tables 11.2 and 11.3). I agree with Smith and Kadlec (1985) that grazing and herbivory require further investigation to establish their importance to overall wetland secondary production. Another area requiring attention is the role of algae in support of primary consumers. Algal contribution to overall wetland productivity may be much higher than presently anticipated. Even in salt marshes where detritus is generally considered to be the basis for the food chains of both the marsh and associated marine areas, algae are becoming recognized as important factors to the consumer production in these systems (Montague et al. 1981; Kitting 1984). Levinton et al. (1984) suggest that plant detritus contributes little to nutrition of secondary producers in a *Spartina* marsh, while microalgae form the bulk of foods used by consumers. The primary role of detritus in the secondary production and food chains of prairie wetlands may be to provide the habitat necessary for algae and invertebrate growth and reproduction.

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DIETARY SELECTIVITY IN RELATION TO AVAILABILITY AND QUALITY OF FOOD FOR GOSLINGS OF CACKLING GEESE

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ABSTRACT.—Food selection by and diet of Cackling Goose (*Branta canadensis minima*) goslings were studied in relation to the quality and availability of food during brood rearing, 1977–1979. Arrowgrass (*Triglochin palustris*) was the most important food in the diet of goslings before wing-molt of adults and sometimes during molt. *Carex mackenziei* was the most common sedge in the diet but was less important than arrowgrass. Leaves of other species were relatively unimportant during premolt. Arrowgrass declined, while *Carex* seeds and crowberries (*Empetrum nigrum*) increased, in the diet as brood rearing progressed. Arrowgrass was highly preferred, whereas other sedges and grasses (except *C. mackenziei*) were avoided in areas for which both availability and consumption were measured. Preference for arrowgrass was related to its higher protein and energy content and lower cell-wall content compared to other forage species. Thus, geese benefitted nutritionally from selecting their preferred diet. Seeds and berries contained high levels of lipids and carbohydrates relative to green leaves. Less arrowgrass was consumed in a year when brood densities were higher than in the other 2 years of the study. Arrowgrass availability declined as brood rearing progressed in another year. Thus, Cackling Geese may have been reducing the availability of their most nutritious food, at least at high brood densities. Food quality in breeding areas may be influencing population dynamics of geese despite the high overall availability of green plants. *Received 16 May 1983, accepted 7 November 1983.*

GEESE are primarily herbivorous during the breeding season (Owen 1980: 127). Plant foods are generally lower in protein and energy content and are usually less digestible than animal foods. For geese, the relatively poor nutritional quality of green vegetation is exacerbated by their simple gastrointestinal tracts. Adult geese must replenish fat and protein reserves, which are at annual lows during hatching or early molt (Hanson 1962, Ankney and MacInnes 1978, Raveling 1979), and goslings must grow under these nutritional constraints. Nutrition during the brood-rearing period may affect such life history parameters as overwinter survival or future reproductive success. Poor food quality, in conjunction with the importance of nutrition following nesting, should have resulted in selection for foraging behavior that maximizes nutrient intake.

There have been few studies of the summer foraging ecology of geese that nest in the Arctic of North America other than general or food-habits investigations (Barry 1967, Mickelson 1975, Eisenhauer and Kirkpatrick 1977). Lieff (1973) reported associations between preferred foraging areas and the presence of particular plant species for both Lesser Snow Geese (*Chen caerulescens caerulescens*) and Canada Geese (*Branta canadensis*), and both he and Harwood (1975) demonstrated preferences for fertilized vegetation by grazing geese. None of these studies related the nutrient content of particular plant species to their importance in the diet, however. In view of the potential importance of summer foraging behavior, we undertook a study of this aspect of the ecology of Cackling Geese (*B. c. minima*) in order to describe their diet in relation to the availability and nutrient content of foods. The study was conducted from the first week of June through mid-August 1977–1979.

STUDY AREA

Our study area was located within the Clarence Rhode National Wildlife Range (now Yukon Delta National Wildlife Refuge) on the Yukon-Kuskokwim Delta, Alaska in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak (61°N, 165°W). The primary study plot was a 40.4-ha area surrounding a cabin and observation tower between the Onumtuk slough and Kashunuk River (see Mickelson 1975 for further description).

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We classified two main types of habitat on the study area: upland and lowland. Upland habitat consisted of relatively well-drained areas about 1.3–1.7 m above mean high-tide levels that were dominated by lichens, moss (*Sphagnum* spp.), *Empetrum nigrum*, *Rubus chamaemorus*, *Salix fuscescens*, and *Ledum palustre*. Areas about 0.5 m above mean high-tide levels were defined as lowland. About 50% of the lowland area consisted of small ponds (i.e. <0.8 ha in area). We recognized two subtypes of terrestrial lowland habitat, mudflat and meadow. Mudflats, adjacent to ponds, comprised 5% of terrestrial lowland habitat and were characterized by bare mud or small, nearly pure patches of either *Puccinellia phryganodes* or *Carex subspathacea*, which were less than 5 cm tall. Nearly pure stands of *C. mackenziei* and *Hippuris tetraphylla* also occurred adjacent to ponds and mudflat areas. Meadows consisted of vegetation up to 20 cm in height, dominated by *C. rariflora*, *C. ramenskii*, *Calamagrostis deschampsioides*, and *Dupontia fisheri*. Scattered individuals of *C. mackenziei* occurred in both mudflats and meadows. *Triglochin palustris* (arrowgrass) occurred in small numbers in both lowland subhabitats and in stands of *C. mackenziei*.

METHODS

Plant species density.—Densities of plant species in meadows commonly used by wild geese were estimated by counting all individual shoots within a 14.5 cm² wire square, randomly placed 11 times along each of three 30-m-long transects (definition of individual shoot as in Chapin et al. 1980). Sampling locations along the transect line were selected before the first sampling date and were used for subsequent dates. Approximately the same transects were sampled three times during both 1978 and 1979, and the total numbers of individuals of each plant species at each sampling location (33 locations in each year) were recorded. We then calculated the mean percentage of total leaves contributed by each species. On mudflats, the wire square was tossed arbitrarily 62 times, and all arrowgrass individuals in the square were counted. The density of all other mudflat species combined was determined by counting all individuals within samples clipped from 15 0.1-m² quadrats during 1979.

Diet.—Goslings were removed from nests at hatching, imprinted on humans, and allowed to graze on the principal study area in both 1978 and 1979. The diet of these goslings was augmented with commercial poultry starter for their first 10 days. Imprinted goslings were periodically sacrificed after being allowed to feed in areas of known plant-species density. These feeding trials allowed a comparison between the abundance of plant species and their presence in the gosling diet. In addition, wild geese were collected by shooting on a 12.7-km² area adjacent to the principal study area during 1977, 1978, and 1979.

After all collections, esophageal contents were removed immediately, rinsed with 80% ethyl alcohol, and placed into vials. Within 3 h, esophageal samples were rinsed with water and returned to vials. Samples were refrigerated following rinsing and frozen within 24 h. Esophageal samples were sorted by plant species at the University of California, Davis, and freeze-dried to constant weight. Contributions of foods to the diet are reported as a percentage of dry weight.

Collection and chemical analysis of plant samples.—Mixed-species samples from mudflats and meadows, along with pure samples of *C. mackenziei* and *C. subspathacea*, were collected for chemical analyses by clipping from 0.1-m² quadrats randomly placed within previously delineated 3 × 5-m plots during 1978 and 1979. These previously delineated plots were located in areas where grazing geese had been observed. Mixed-mudflat samples (nearly entirely *P. phryganodes*) included only erect shoots and leaves. Samples were clipped to litter level. Litter and standing dead material were removed in the laboratory and mixed-mudflat and *C. subspathacea* samples were washed to remove excess mud. Individual arrowgrass plants were removed from mixed-meadow samples collected in 1978 to provide a pure sample of meadow arrowgrass for that year. All other arrowgrass samples were hand-collected.

All sampled plant species were represented in 1978 samples, whereas only *C. mackenziei*, mixed-mudflat, and arrowgrass were sampled in 1979. Plant samples were clipped on 25 June, on 3 and 4, 19, and 29 to 31 July, and on 7 August 1978, with the exception of early July mixed-mudflat samples, which were collected on 11 July 1978. All 1979 clipped samples were collected on 24 June, on 7, 17, and 28 July, and on 9 August. Samples of *T. palustris* were collected from mudflats and meadows on 10 dates through the summer of 1979. The amount of material was insufficient for separate analyses representing each date, however. Therefore five composite aliquots were formed for both mudflat and meadow *T. palustris* by combining material collected on the following pairs of dates: 24 and 30 June; 4 and 7, 17 and 21, 28 and 31 July; and 9 and 12 August. *Carex* seeds were collected only during August 1979, while *Empetrum nigrum* berries were collected on 7 and 29 July and 7 August 1978 and 9 August 1979.

Samples were frozen within 24 h. In Davis, samples were thawed, blotted lightly with paper towels, weighed, freeze-dried to constant weight, and then ground in a Wiley Mill to pass a 40-mesh sieve. Nitrogen was determined by the macro-Kjeldahl method (Horwitz 1975). Crude protein was estimated by multiplying 6.25 times Kjeldahl nitrogen. Crude fat was determined by extracting samples for 12 h with anhydrous ether in a Goldfisch apparatus. Samples were ashed by combustion of ether-extracted samples for 4 h at 500°C. Acid and neutral detergent-insoluble fractions (ADI and cell wall, respectively) were estimated by the Van Soest method (Goering and Van Soest 1970). Neutral detergent-insoluble material was saved, and the nitrogen content of this fraction was estimated by Kjeldahl analysis. Amino acid concentrations were determined on a Durham 500 amino-acid analyzer following 24 h hydrolysis in 6 N HCL (Spackman et al. 1958). Cysteine concentrations were determined using the same technique, except that samples were oxidized in performic acid for 24 h before hydrolysis (Hirs 1967).

Digestibility of protein in cell walls was calculated by assuming that the nonprotein fraction of cell walls was an indigestible marker (Drent et al. 1978). The percentage of protein in the cell-wall fraction of the diet was estimated by calculating a weighted average of the percentage of protein in the cell-wall fractions of the arrowgrass and nonarrowgrass portions of the diet, with the weights consisting of the proportional contributions of arrowgrass and non-arrowgrass foods to total cell wall in the diet. The protein content of cell walls in the feces was determined by Kjeldahl analysis of the fecal cell-wall fractions.

Statistical analyses.—Distribution of dietary data (percentage contribution to diet by a food) was nonnormal and in some cases approached a bimodal distribution (see Fig. 1). For this reason we used Kruskal-Wallace or Mann-Whitney *U*-tests to compare the percentage contribution of a particular food to the diet of groups of goslings. Spearman rank correlation was used to analyze seasonal trends in diet and the correlation between cell-wall and protein content of plants. The dietary preference of imprinted goslings feeding in meadows was determined by means of a Mann-Whitney *U*-test to compare the percentage of leaves of a given type in esophagi versus that in the environment. We did not statistically evaluate the preference of imprinted goslings feeding on mudflats, because the use of different size quadrats for estimating densities of arrowgrasses and nonarrowgrasses precluded an estimation of among-sample variation of the percentage of arrowgrasses on mudflats. We analyzed the chemical constituents of plants by means of a 2-way ANOVA (species X sampling dates, for protein and water) or 1-way ANOVA (other constituents) followed by a protected Least Significant Difference comparison between means (Carmer and Swanson 1973) in cases with a significant *F* value.

RESULTS

DIET

We divided the brood rearing period into three time periods for presentation of dietary data: preceding the molt of adult remiges (premolt), coincident with the adult flightless period (molt), and coincident with fledging of young (fledging). The dividing points between premolt and molt collection periods were 14 July in 1979, 15 July in 1978, and 28 July in 1977. Molt and fledging periods were separated by 2 August in 1978, the only year in which collections were made during fledging. These periods correspond approximately to the following gosling ages: premolt, 1–23 days; molt, 24–41 days; fledging more than 42 days. Contributions of foods to the diet are expressed in aggregate percentages.

Imprinted and wild goslings differed significantly ($P < 0.05$) in diet in only 3 of 16 possible pairwise comparisons (4 food categories × 2 yr × 2 time periods within years, Fig. 1). These differences were due to the single collection during the 1979 molt period of three wild goslings from the same brood, which contained a significantly lower percentage of *T. palustris* and *C. mackenziei* and a significantly higher percentage of *Carex* seeds and *Empetrum* berries than did the tame goslings collected during the same period. There were no foods for which differences between the two groups in the consumption of a food were consistent between years. Because of the lack of differences between wild and tame goslings except for the one collection, we combined results from the two groups for subsequent analyses. (See Appendix for a complete summary of the diet of goslings.)

Because of initial difficulties in identification of plant species, some *C. subspathacea* was included with arrowgrass in the analysis of esophageal contents from goslings collected during 1977. Of the original arrowgrass sample from these goslings (a sample comprised of arrowgrass from all 1977 goslings that contained arrowgrass), 13% was available for reanalysis. *Carex subspathacea* comprised 4% of the dry weight of this material. This error did not have a substantial effect on either the presentation of, or the conclusions drawn from, our data.

Seasonal variation.—Arrowgrass predominated in the premolt diet of goslings, contributing 92% of the diet during this period in 1977, 44% in 1978, and 98% in 1979 (Fig. 1). Other foods were unimportant during premolt in 1977 and 1979, but *C. mackenziei* comprised 28% and other leaves (other *Carex* spp. leaves, grasses, and forbs) 19% of the 1978 premolt diet.

Arrowgrass declined in dietary importance

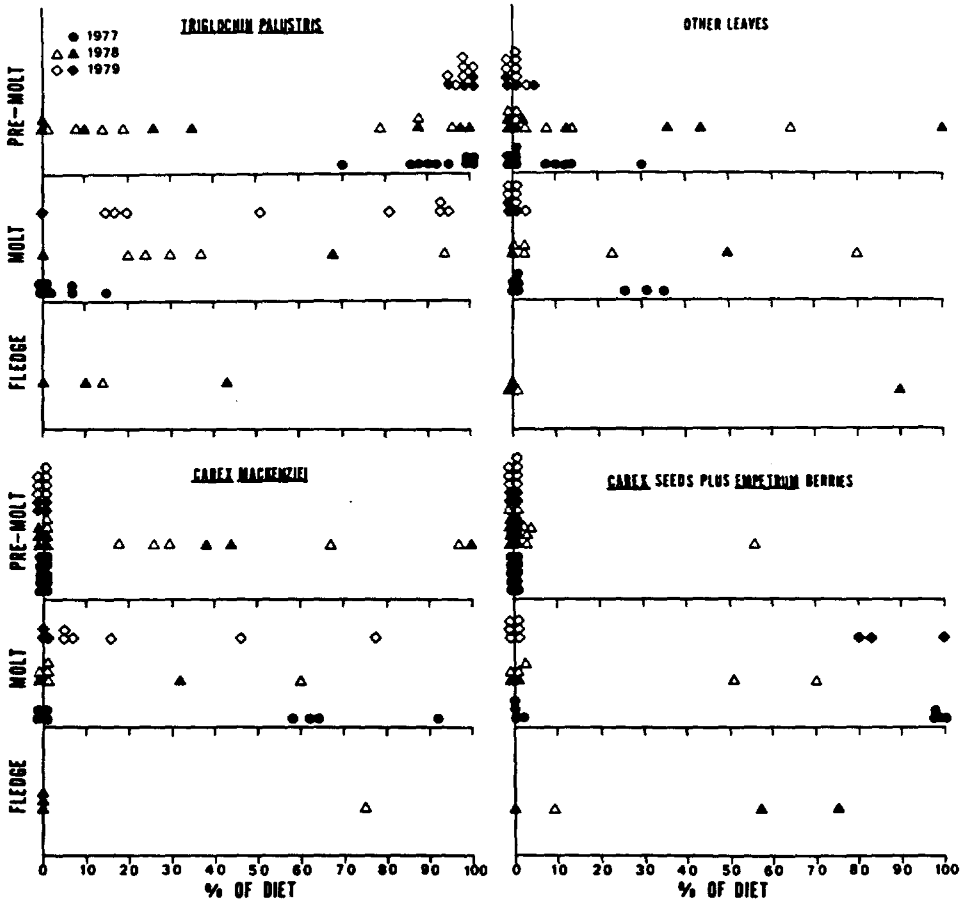

Fig. 1. Diet of Cackling Goose goslings during brood rearing 1977-1979. Each point within a food type corresponds to one individual, and each individual is represented in all four food types. Points are arrayed along the horizontal axis, representing percentage of diet (dry weight). Points representing goslings collected during the molt, premolt and fledging periods (see Results) are plotted separately within each food type. Points representing goslings collected in different years are separated vertically within plots for each of the three time periods. Open symbols represent tame goslings; solid symbols represent wild goslings.

during brood rearing in 1977 ($r_s = -0.71$, $P < 0.005$) and 1979 ($r_s = -0.77$, $P < 0.001$), while a slight nonsignificant negative trend was observed in 1978, the year of lowest premolt feeding on arrowgrass ($r_s = -0.19$, $0.2 < P < 0.4$, Fig. 1). *Carex* seeds and *Empetrum* berries tended to increase in the diet as brood rearing progressed in 1978 and 1979 ($r_s = 0.30$, $0.1 < P < 0.2$ and $r_s = 0.32$, $0.1 < P < 0.2$, respectively), and we observed a significant increase in 1977 ($r_s = 0.72$, $P < 0.001$).

Seasonal variation in the diet resulted in a reduction in the contribution of arrowgrass to 4% of the diet during molt in 1977, 39% in 1978, and 52% in 1979 (Fig. 1), with a further reduction to 17% of the fledging diet in 1978. *Carex mackenziei* was the most important sedge in the diet during molt, comprising between 13% (1978) and 35% (1977) of the diet (18% in 1979). Seeds and berries increased from less than 10% of the premolt diet during all 3 yr to 49% of the molt diet in 1977, 18% in 1978, and 29% in 1979, and to 35% of the 1978 fledging diet. Other leaves combined comprised between 1% (1979) and 23% (1978) of the diet during molt (12% in 1977).

Among-year variation.—Goslings from the premolt period in 1978 contained significantly

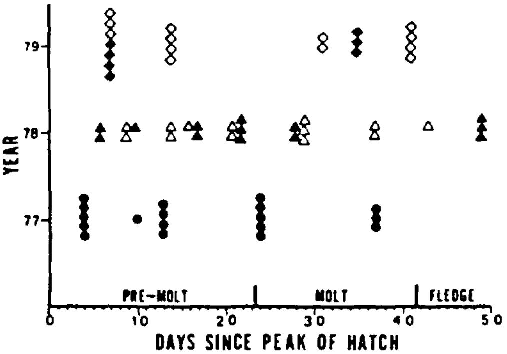

Fig. 2. Timing of collection of Cackling Goose goslings. Peak hatch was 4 July 1977, 21 June 1978, and 20 June 1979. Points from goslings collected within the same year are arrayed along the horizontal axis, while points from different years are segregated vertically. Each point represents one gosling. Open symbols represent tame goslings; solid symbols represent wild goslings.

less arrowgrass ($P < 0.002$) and significantly more *C. mackenziei* ($P < 0.001$) than did goslings from the same period in 1977 and 1979 (Fig. 1). Arrowgrass comprised a slightly (but nonsignificantly) larger fraction of the molt diet in 1979 than in 1978 and was a significantly larger fraction of the molt diet during these 2 yr than during 1977 ($P < 0.002$).

More goslings were collected later in the premolt period during 1978 than during 1977 and 1979 ($P < 0.01$, Fig. 2). This was probably not the cause of the among-year differences in premolt diet, however, for two reasons: (1) goslings from the first 14 days of the premolt period (in which all 3 yr were represented) still contained less arrowgrass in 1978 than in 1977 and 1979 ($P < 0.01$), and (2) goslings collected 15–16 days into the premolt period in 1978 (later than collections in 1977 and 1979) contained between 87% and 97% arrowgrass, among the highest levels recorded for 1978.

Preference.—Imprinted goslings were highly selective of arrowgrass leaves in meadows (Fig. 3, Mann-Whitney *U*-test, $P < 0.0002$), consuming them approximately five times more frequently than they occurred in the environment. Arrowgrass was selected at a similar relative rate on mudflats, although we could not evaluate this statistically, because we had no measure of variability in the availability of arrowgrass on mudflats. Other sedges and grasses comprised a much smaller fraction of the diet than of available individuals.

CHEMICAL COMPOSITION OF VEGETATION

Concentrations of all constituents varied among species ($P < 0.001$, Tables 1, 2). Crude protein ($P < 0.0005$) and water content ($P < 0.01$) varied among sampling dates. Temporal variations in protein and water concentration were parallel among species (Kendall's Test of Concordance $P < 0.01$); the same proportion of each species' samples were collected on a given sampling date. We thus combined data across sampling dates for purposes of presentation. We will report on temporal variation in vegetation constituents in a separate paper.

Results dealing with the water content of vegetation must be interpreted with caution. Samples were collected under variable, but usually wet, conditions. Mixed-mudflat and *C. subspathacea* samples were washed to remove mud associated with these samples. As a result, the apparent water content of these samples was inflated and these data were not analyzed statistically.

Gross nutrients.—Crude protein content was highly variable among species and was highest (30%) in arrowgrass from mudflats (Table 1). Crude protein in arrowgrass from meadows and in *C. subspathacea* averaged 19%, whereas all other types of green vegetation and *Carex* seeds contained between 13.3% and 15% protein. *Empetrum nigrum* berries contained substantially less protein (5%) than did other foods.

Crude fat concentrations were 2–3 times greater in seeds and berries (7.8–9.7%) than in green plants (3.2–4.4%, Table 1). The ash content of seeds and berries (2.4–3.9%) was considerably lower than that of vegetative parts of green plants (6.1–13%, Table 1).

Cell wall.—Arrowgrass contained substantially less cell wall than other green plants, and there was lower cell-wall content in arrowgrass from mudflats than arrowgrass from meadows (Table 2). *Carex subspathacea*, *C. mackenziei*, and mixed-mudflat vegetation did not differ from one another in percentage cell wall. Cell walls constituted the largest proportion (58.3%) of dry weight (among green plants) in mixed-meadow vegetation.

Mean levels of ADI (consisting of cellulose, lignin, and some ash) varied between 21.1% and

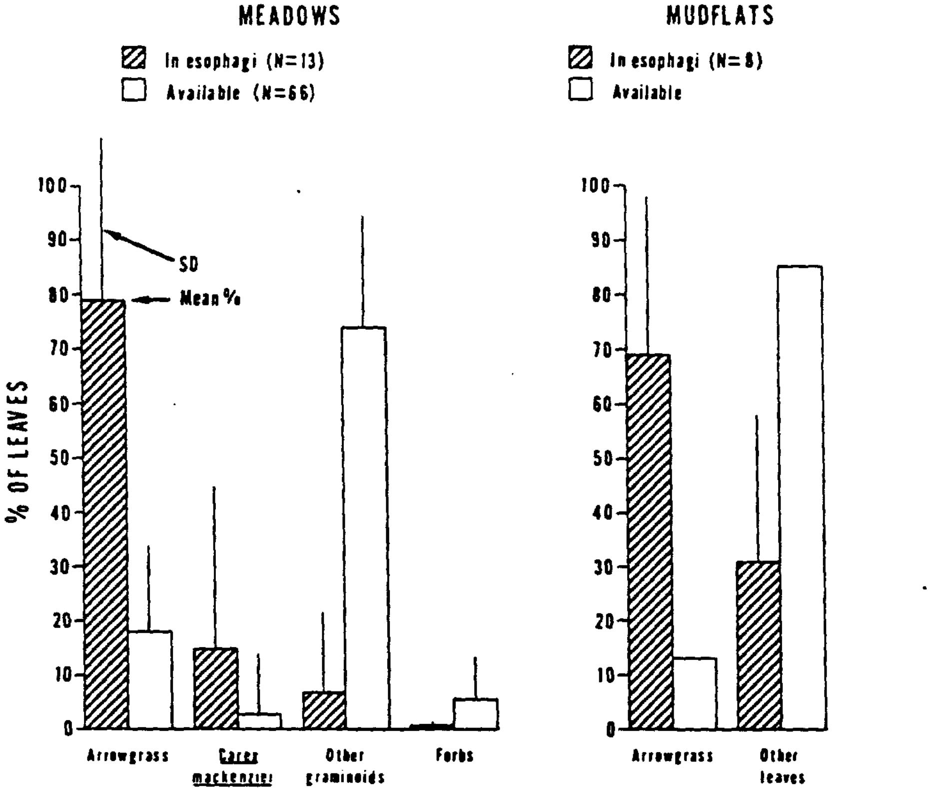

Fig. 3. Dietary selectivity by imprinted goslings in 1978 and 1979. Species composition of leaves in esophagi was determined by counting all leaves in esophagi of goslings that had fed in the vicinity of meadow vegetation transects (13 goslings) or on mudflats (8 goslings). We did not present variability in percentage of leaves available on mudflats, because numbers of arrowgrass leaves were estimated from quadrats of a size different from those for other leaves (see Methods).

29.2% of plant dry weights (Table 2), *Carex mackenziei* and *C. subspathacea* contained significantly less ADI than mixed-meadow vegetation, whereas mixed-mudflat vegetation contained intermediate levels of ADI. Other samples were not compared statistically due to insufficient sample sizes.

Significant differences among species in the percentage of cell wall comprised of protein were not detected (1-way ANOVA, $P > 0.05$, Table 2). When averaged across all species, cell walls contained 0.72% nitrogen, or 4.5% crude protein. This is a slight underestimate, because cell-wall fractions were contaminated with cellite from the NDF procedure. The percentage of cell wall was inversely correlated with total crude protein ($r_s = -0.32$, $P < 0.01$). In conjunction with the constant protein fraction in cell walls, this resulted in a larger fraction of total protein being associated with cell walls in plants that contained less total protein. Cell-wall protein constituted 2–4% of total crude protein in arrowgrasses but 22% of crude protein in mixed-meadow vegetation.

Available protein and carbohydrate.—Protein associated with cell walls is relatively unavailable to nonruminants (Van Soest and Moore 1965). Cackling Geese digested approximately 38% of cell-wall protein (Sedinger and Raveling unpubl. data). Hence, the association of protein with cell walls significantly reduced the protein available for digestion. Available protein was further reduced below crude protein, because the 6.25 multiplier used to calculate crude protein failed to account for nonamino-acid nitrogen in plants (McDonald et al. 1973).

TABLE 1. Nutrient content of foods used by Cackling Geese ($\bar{x}$ ± SE).

Plant species/ type	H_2O (%)	Crude protein[a] (%)	Crude fat[a] (%)	Ash[a] (%)
Arrowgrass (from mudflats)	86.5 ± 1.5 (A)[b] (n[c] = 5)	30.1 ± 1.7 (A) (n = 5)	3.8^{NT} (n = 1)	13.0^{NT} (n = 1)
Arrowgrass (from meadows)	84.9 ± 0.7 (A) (n = 5)	19.5 ± 1.5 (B) (n = 10)	3.9^{NT} (n = 1)	12.5^{NT} (n = 1)
Carex subspathacea	79.6 ± 1.7^{NT} (n = 5)	19.0 ± 1.6 (B, C) (n = 5)	4.4 ± 0.4 (A) (n = 5)	9.2 ± 1.0 (A) (n = 5)
C. mackenziei	78.3 ± 1.1 (B) (n = 15)	14.0 ± 0.7 (D, E) (n = 15)	3.2 ± 0.2 (A) (n = 13)	9.2 ± 0.4 (A) (n = 13)
Mudflat-mixed	82.2 ± 0.6^{NT} (n = 20)	15.2 ± 0.6 (C, D) (n = 20)	3.2 ± 0.2 (A) (n = 17)	7.9 ± 0.7 (A) (n = 15)
Meadow-mixed	70.1 ± 1.0 (C) (n = 15)	13.3 ± 0.6 (E) (n = 15)	3.2 ± 0.1 (A) (n = 15)	6.1 ± 0.1 (B) (n = 15)
C. rariflora seeds	66.1^{NT} (n = 1)	14.9^{NT} (n = 1)	7.8^{NT} (n = 1)	3.9^{NT} (n = 1)
Empetrum nigrum berries	80.9 ± 1.8 (A, B) (n = 4)	5.0 ± 0.4 (F) (n = 4)	9.7^{NT} (8.7-10.6)[d] (n = 2)	2.4^{NT} (2.2-2.6) (n = 2)

[a] Percentage of dry weight.

[b] Entries within a column, not sharing a common capital letter were significantly different ($\alpha = 0.05$). NT indicates entry was not tested (because of small samples or bias in water content data; see text).

[c] n = number of samples from distinct sampling dates and/or areas.

[d] Parentheses indicate range for crude fat and ash of *E. nigrum* berries.

TABLE 2. Cell-wall content (% dry weight) of food plants used by Cackling Geese ($\bar{x}$ ± SE).

Plant species/type	Neutral detergent insoluble (% cell wall)	Acid detergent insoluble (%)	Cell-wall nitrogen[a] (%)
Arrowgrass (mudflat)	23.7 ± 1.2 (A)[b] (n[d] = 4)	23.7^{NT} (n = 1)	0.4 (0.3-0.4)[c] (n = 2)
Arrowgrass (meadow)	29.1 ± 0.8 (B) (n = 5)	28.0 (24.0-32.0)^{NT} (n = 2)	0.5 ± 0.1 (n = 4)
Carex subspathacea	47.6 ± 1.6 (C) (n = 5)	23.1 ± 0.9 (A, B) (n = 5)	0.8 (0.7-1.0) (n = 2)
C. mackenziei	50.4 ± 0.8 (C) (n = 15)	21.1 ± 0.8 (A) (n = 15)	0.8 ± 0.1 (n = 5)
Mudflat-mixed	49.5 ± 1.9 (C) (n = 20)	25.8 ± 1.0 (B, C) (n = 20)	0.9 ± 0.2 (n = 3)
Meadow-mixed	58.3 ± 1.0 (D) (n = 15)	27.1 ± 0.4 (C) (n = 15)	0.8 ± 0.1 (n = 4)
C. rariflora seeds	60.4^{NT} (n = 1)	22.7^{NT} (n = 1)	—
Empetrum nigrum berries	36.8^{NT} (n = 1)	29.2^{NT} (n = 1)	—

[a] No significant, among-species variation (1-way ANOVA, $P > 0.05$).

[b] Entries within a column not sharing a common capital letter were significantly different ($\alpha = 0.05$). NT indicates entry was not tested.

[c] Values in parentheses are the range for entries when $n = 2$.

[d] n = number of samples from distinct sampling dates and/or areas.

TABLE 3. Available protein and carbohydrate content of foods used by Cackling Geese (% dry weight).

Plant species/type	Available protein[a] (%)	Soluble carbohydrate[b] (%)
Arrowgrass (from mudflats)	24.3	35.4
Arrowgrass (from meadows)	15.0	39.8
Carex subspathacea	13.7	25.9
C. mackenziei	9.4	28.7
Mudflat-mixed	10.4	29.8
Meadow-mixed	8.5	24.5
C. rariflora seeds	11.3	17.6
Empetrum nigrum berries	3.3	48.4

[a] Calculated from: % available protein = 5.44·% N − 1.47 − 0.62·% protein in cell walls. For seeds and berries % available protein = 5.44·% N − 0.62·% protein in cell walls (because seeds and berries contained little nonprotein nitrogen).

[b] Percentage soluble carbohydrate = 100% − % cell wall − % non-cell-wall protein − % crude fat − % ash. % non-cell-wall protein = 5.44·% N − 1.47 − % protein in cell walls (except seeds and berries; see a).

We estimated the true relationship between nitrogen and protein by regressing the sum of the percentages of amino-acid concentrations (Sedinger in press) against the percentage of nitrogen, using nine samples of green vegetation. The accurate relationship between protein and nitrogen was:

$$\text{percentage of true protein} = -1.47 + 5.44\,(\text{percentage of nitrogen}).$$

Accounting for cell-wall protein and the conversion from Kjeldahl nitrogen to protein resulted in estimates of protein available for digestion of between 19% (arrowgrass) and 36% (mixed-meadow) below crude protein values (Table 3).

Soluble carbohydrate comprised 48% of *Empetrum nigrum* berries (Table 3), whereas arrowgrass contained the largest fraction of soluble carbohydrate among green plants (35.4–39.8%). Other green plants contained between 24.5% (mixed-meadow) and 29.8% (mixed-mudflat) soluble carbohydrate.

DISCUSSION

Diet.—Arrowgrass dominated the summer diet of young Cackling Geese before they fledged despite its low abundance relative to other graminoid species. Such selectivity resulted both from preferential foraging in mudflats (Sedinger and Raveling unpubl.), where arrowgrasses were more available, and from discrimination among available food plants at particular feeding sites (Fig. 3). The preference for arrowgrass displayed by Cackling Geese means that actual food availability was much lower than one might qualitatively assume from the large extent of sedge meadows on the Yukon-Kuskokwim Delta.

The preference for arrowgrass was associated with its content of protein, water, ash, and soluble carbohydrate being higher than, and its cell-wall content being lower than, that of other graminoids. The relationship between available nutrients and food preference was highlighted by a preference for foraging in mudflats (Sedinger and Raveling unpubl.), where arrowgrass contained more protein and less cell wall than it did in meadows. The choice among grasses and sedges was less clearly related to nutrient content. *Carex subspathacea* contained the highest protein and lowest cell-wall content among grasses and sedges; yet, it was not an important component of the diet. *Carex mackenziei* was consumed at 2–3 times the rate of other grasses and sedges combined; yet, it did not contain higher protein or lower cell-wall content than these other species. *Carex mackenziei* contained less ADI than either mudflat or meadow vegetation. Less cellulose and lignin in cell walls of *C. mackenziei* may have allowed greater mechanical breakdown of plant cell walls, thus rendering nutrients in this species more available and making it a preferred food. Acid and neutral detergent fiber contents of diets were both negatively correlated with growth rates of meadow voles (*Microtus pennsylvanicus*), herbivores with simple gastrointestinal tracts, indicating that cellulose and/or lignin interfered with utilization of nutrients (Russo et al. 1981).

The lack of correspondence between nutrient content and contribution to the diet of foods other than arrowgrass may have been partially due to differences between the chemical composition of vegetation actually consumed by geese and vegetation samples collected for chemical analysis. Arrowgrass from esophageal contents of geese contained an average of 28% and *C. mackenziei* leaves 51% more protein than did hand-collected or clipped leaves of the same species (Sedinger and Raveling unpubl. data). An unknown fraction of this "extra" protein was due to contamination by saliva (Moss 1972), but higher protein levels in esophageal samples were probably at least partially due to selection by geese of higher-quality feeding areas or higher-quality plants or plant parts. Geese have the ability to select plants with higher protein content (Lieff et al. 1970, Harwood 1975, Owen et al. 1977). Geese also select younger and probably more nutritious leaves from within plants (Prins et al. 1980), and McLandress and Raveling (1981a, b) demonstrated that geese grazed in a manner that maximized nutrient intake. If Cackling Geese were capable of detecting patches of vegetation of higher nutrient content, then species that were more variable in nutrient content (e.g. *C. mackenziei*) could have been preferred due to the presence of some plants or plant parts with high nutrient content, even though there were no between-species differences in mean nutrient content in our samples or in the species as a whole.

Carex subspathacea and *P. phryganodes* had low growth forms in which arrowgrass was readily available. Hence, on mudflats, geese were able to maintain a high rate of intake while feeding exclusively on arrowgrass. Arrowgrass was probably less available in stands of *C. mackenziei* due to the longer growth form of the latter species. This could have resulted in *C. mackenziei* being grazed along with arrowgrass in order to increase the rate of intake over what would have been possible if only arrowgrass were being eaten. Thus, *C. subspathacea* and *P. phryganodes* were probably consumed less frequently than expected, because their growth forms allowed a high enough rate of intake of arrowgrass alone, whereas *C. mackenziei* was consumed more frequently than expected from its nutrient content, because its growth form precluded a high enough rate of intake when feeding on arrowgrass alone.

The minimal contribution of invertebrates to the diet (Appendix; Mickelson 1973) is of interest, because such foods provide a concentrated source of protein of high biological value (Krapu and Swanson 1975) known to be important in the early diet of other waterfowl (Sugden 1973). Goslings of Cackling Geese readily consumed insects under enclosed conditions (pers. obs.). A relatively small return from consuming single insects at a time in meadows may select against the consumption of insects except under conditions (e.g. cold weather, M. R. McLandress pers. comm.) in which insects are highly vulnerable and thus available in large numbers. The grazing behavior of geese may also contribute, because search images required for correct selection of preferred food plants may preclude feeding on insects except when superabundant and available.

Nutritional considerations.—Discrimination among potential foods resulted in a clear nutritional benefit to Cackling Geese. If the ability of geese to select more nutritious individuals from within a species is disregarded and only the nutritional advantage of selection among species is considered, the protein content of the actual diet was 37% higher in meadows and 43% higher in mudflats than random selection would have provided. Dietary protein was directly related to the growth rate of domestic and Mallard (*Anas platyrhynchos*) ducklings (Dean 1972, Street 1978). Adult muscle size may be maximized by sufficient dietary protein during early development (Moss et al. 1964, Swatland 1977). Canada Goose goslings grew faster when raised on fertilized vegetation than on unfertilized vegetation (Lieff 1973) and goslings of Bar-headed Geese (*Answer indicus*) grew faster on an artificial diet than they did in the wild (Wurdinger 1975), indicating that diet in the wild was inadequate for maximum rate of growth.

A preference for arrowgrass also increased energy content in the diet because of its higher soluble carbohydrate levels compared to grasses or sedges. Low energy levels in the diet of chicks less than 10 days old may result in both fewer and smaller adipose cells (March and Hansen 1977). Hence, the dietary selectivity displayed by Cackling Geese probably maximized growth rate, final adult body size, and ability to store both fat and protein. These factors could significantly influence their reproductive capacity as adults (Ankney and MacInnes 1978, Raveling 1979). Faster growth may also have reduced susceptibility to predation, and, as Scott et al. (1955) demonstrated, mortality due to cold and wet weather may be reduced by improvement of the diet in gallinaceous birds. Furthermore, Cole (1979) found that larger Lesser Snow Goose goslings survived better than smaller ones in cool summers.

Seasonal and annual variation in diet.—Cackling

Geese ingested less arrowgrass and more energy-rich *Carex* seeds and *Empetrum* berries as summer progressed. This change in diet was possibly in response to an increased requirement for energy to allow premigratory fat deposition and to a decreased growth demand. Reduced arrowgrass consumption, however, began while goslings were still growing rapidly and presumably still requiring a high-protein diet. Esophagi of four imprinted goslings collected on 31 July 1979, approximately 1 week before fledging, contained between 81% and 95% arrowgrass, indicating that this food was readily consumed when available, even during the late brood-rearing period. Biomass of arrowgrass declined in mid-July 1979 (Sedinger and Raveling unpub. data) on mudflats, indicating that declining consumption of arrowgrass was at least partially due to reduced availability of that species.

Arrowgrass comprised a smaller fraction of both the premolt and molt diets during 1978 than during 1979 (Fig. 1), although the difference was significant only during premolt ($P < 0.002$). This was associated with higher densities of geese on our principal study plot during 1978 than during 1979 [an average of 23 Cackling Goose families during 1978 vs. 12 families during 1979 and an average of 1 family of either Brant or Emperor Geese (*Chen canagica*) in each year]. This inverse correlation between goose density and the presence of arrowgrass in the diet, in conjunction with declining arrowgrass biomass through the brood-rearing period, indicates that Cackling Geese were reducing the availability of their preferred food, especially when densities of geese were high. Reduced consumption of arrowgrasses due to reduced availability would reduce protein and energy intake by geese.

Population and distribution considerations.—To the extent that nutrition influences survival and future reproduction, availability of vegetation of sufficient quality may, in conjunction with habitat features providing for safety from predation, determine preferred nesting habitat. Nesting geese are not uniformly distributed throughout arctic areas, and their distribution may be related to the presence of brood-rearing areas with the "proper" plant species composition. Lieff (1973) suggested that different nesting and brood-rearing areas at McConnell River, N.W.T., Canada produced different "quality" goslings, which may have been related to differences in food quality. In view of the ongoing commercial development of arctic areas, it is important to determine the contribution of particular plant species to the maintenance of goose populations and to determine the relationship between these plant species and preferred goose breeding areas.

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APPENDIX. Food of Cackling Goose goslings on the Yukon-Kuskokwim Delta. Results from 64 goslings containing a total of 14.6 g in esophagi (dry weight).

Food species	Frequency of occurrence	Dry weight (%)
Triglochin palustris	88	68
Carex mackenziei leaves	38	18
C. ramenskii leaves	20	1
C. rariflora leaves	5	Trace[a]
C. subspathacea leaves	2	Trace
C. glareosa leaves	6	Trace
Carex (unident.) leaves	5	Trace
Puccinellia phryganodes leaves	6	1
Graminae (unident.) leaves	14	Trace
Hippuris tetraphylla leaves	11	Trace
Potentilla egedii leaves	8	Trace
Empetrum nigrum leaves	6	Trace
Stellaria crassifolia leaves	11	Trace
Ranunculus hyperborea leaves	5	Trace
Chrysanthamum arcticum leaves	2	Trace
Salix ovalifolia leaves	2	Trace
Carex seeds	28	8
E. nigrum seeds	6	1
E. nigrum berries	3	1
Moss (unident.)	2	Trace
Litter	14	Trace
Insects	16	Trace

[a] Trace = <1%.

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TIMING OF NESTING BY CANADA GEESE IN RELATION TO THE PHENOLOGY AND AVAILABILITY OF THEIR FOOD PLANTS

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SUMMARY

(1) This study examined seasonal variation in the foraging behaviour of cackling Canada geese (*Branta canadensis minima*) and in the nutrient content and availability of tundra grasses and sedges (graminoids) and arrowgrass during the nesting and brood-rearing periods, 1977–79 on the Yukon-Kuskokwim Delta, Alaska.

(2) Nitrogen concentrations in nearly all graminoids and arrowgrass began to decline either prior to, or during, hatching of cackling goose clutches. Grazing or clipping of vegetation resulted in higher and prolonged peaks in nitrogen concentration but peak nitrogen levels in these plants still occurred within a week of the end of the hatching period.

(3) Standing crops of graminoids increased until early August while the standing crop of arrowgrass (the most nutritious plant in the diet) in preferred foraging habitat began to decline in mid-July due to grazing by geese.

(4) Peck-rates of adult cackling geese tended to decline as brood-rearing progressed, indicating that preferred foods declined in availability during this period. Also, late in brood-rearing, preferred foraging areas were used less and arrowgrass comprised a smaller proportion of the diet.

(5) Changes in plant nutrient levels and shifts in diet and habitat use reduced the nutritional quality of the diet as brood-rearing progressed. Thus, as a result of both the natural phenology of tundra plants and grazing by geese, late hatching broods were at a nutritional disadvantage compared to those hatching early.

(6) We conclude that a seasonal decline in the quality of foraging conditions is probably an important factor favouring early nesting by geese.

INTRODUCTION

Arctic nesting geese arrive on their breeding areas in early spring when little food is available; thus they are forced to rely heavily on stored reserves for both maintenance and egg formation (Barry 1962; Ankney 1977a; Ankney & MacInnes 1978; Raveling 1979). Whenever the spring thaw is late, average clutch size of these geese is reduced (for various species and populations, see Cooch 1958; Barry 1962; MacInnes *et al.* 1974; Mickelson 1975; Owen & Norderhaug 1977; Raveling & Lumsden 1977; Findlay & Cooke 1982; Ely & Raveling 1984), probably because females have devoted reserves to maintenance prior to

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egg-laying, instead of to egg formation and incubation. Since a later return to breeding areas could theoretically result in maximum clutch size production every year, regardless of the timing of the thaw, there must be counter-selective factors which prevent such a delay from evolving.

Two, not necessarily mutually exclusive, hypotheses, have been proposed to explain early arrival by geese on their nesting areas. Murton & Kear (1973) and MacInnes *et al.* (1974) suggested that early nesting evolved to synchronize grazing by goslings and post-breeding adults with the availability of food of the highest nutritional quality. During the brood-rearing period, geese obtain most, if not all, of their food from green plants (Barry 1967; Owen 1980; Sedinger & Raveling 1984). In addition, the brood-rearing period must be important in the annual protein budget of geese because it represents one of two segments of the annual cycle (the other being the spring pre-migration and migration period, McLandress & Raveling 1981) during which relatively high-protein green plants comprise a large proportion of the diet (see Owen 1980 for review of the annual cycle of food consumption). As yet, however, only Hardwood (1977) has published data which can be used to compare the phenology of plant nutrient composition with the phenology of the breeding season of geese and there are no data available to evaluate the effect of the geese themselves on the availability of the highest quality foods.

The second hypothesis states that the primary function served by geese nesting early is to allow enough time for young-of-the-year to fledge and gain strength for migration prior to freeze-up in the autumn (Cooch 1958; Ryder 1967). Two observations by Barry (1962, 1967) of flightless young brant, *Branta bernicla hrota* and *B. b. nigricans*, which had died when autumn freeze-up occurred, provide the primary evidence supporting this hypothesis. However, early arrival and nesting is observed in geese that nest at lower latitudes with longer growing seasons (MacInnes *et al.* 1974; Mickelson 1975; Raveling & Lumsden 1977; Cooper 1978). If length of the breeding season is the major factor that ultimately determines timing of egg-laying, a delay in nest initiation might be beneficial for these geese. Thus, it seems that the first hypothesis provides a more reasonable explanation for the early arrival on nesting areas, at least for geese that do not nest in the high arctic.

We undertook this study to compare the breeding phenology of cackling geese, *B. canadensis minima* Ridgway, with the phenology and availability of their principal food plants in order to examine the importance of these factors in influencing the timing of nesting by geese. The study was conducted during the nesting and brood-rearing periods from 1977 through 1979.

STUDY AREA AND METHODS

Study area

Our study area was on the Yukon-Kuskokwim (Y-K) Delta, Alaska, in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak (61°N, 165°W). The principal study plot was a 40·4 ha area between the Onumtuk Slough and Kashunuk River (see Mickelson 1975 for further details) that surrounded a cabin and attached observation tower, which could be reached from the cabin without the observer being seen by geese.

We classified the habitat on the study area as either upland or lowland. Upland habitat consisted of relatively well drained areas from about 0·5 m up to about 1·5 m above mean high tide levels, characterized by lichens, moss, *Sphagnum* spp., *Empetrum nigrum*, *Rubus chamaemorus*, *Salix fuscescens* and *Ledum palustre* (Hulten 1968). Areas about 0·5 m above mean high tide levels were defined as lowland. We recognized two subtypes of terrestrial lowland habitat: mudflat and meadow. Mudflats, which were adjacent to ponds, comprised 5% of terrestrial lowland habitat. These areas were characterized by bare mud or small, nearly pure, patches of either *Puccinellia phryganodes* or *Carex subspathacea*, both of which were less than 5 cm tall. Nearly pure stands of *C. mackenziei* and *Hippuris tetraphylla* also occurred adjacent to ponds and mudflats. Meadows consisted of vegetation up to 20 cm in height, dominated by *C. rariflora*, *C. ramenskii*, *Calamagrostis deschampsioides* and *Dupontia fisheri*. Scattered individuals of *C. mackenziei* and *Triglochin palustris* (arrowgrass) occurred in both mudflats and meadows and arrowgrass also occurred in stands of *C. mackenziei*.

Hatch dates

We determined hatch dates of cackling goose clutches either by visiting nests during hatching, or by visiting nests during egg-laying and assuming a 26-day incubation period and an egg-laying rate of one per day (Mickelson 1975). We added 1 day to the laying period for clutches of more than four eggs to account for 'skip-days' between eggs in larger clutches (MacInnes 1962; Mickelson 1975; Cooper 1978).

Vegetation sampling and analysis

In order to estimate vegetation biomass (standing crop) and to provide samples for chemical analyses, we established exclosed and unexclosed areas (7·6 × 7·6 m in 1977 and 3 × 5 m in 1978 and 1979) in a variety of vegetation types (Table 1). Exclosures were constructed of 1 m high plastic mesh (2 cm between strands). Mixed-meadow samples were

TABLE 1. Number of exclosed and unexclosed areas placed in each vegetation type during 1977–79

	1977	1978		1979	
Vegetation type	Excl.	Excl.	Unexcl.	Excl.	Unexcl.
Mixed-meadow	3	3	2	—	—
Mixed-mudflat	—	2	2	2	2
Carex mackenziei	—	1	—	1	1
C. subspathacea	1	1	—	—	—

TABLE 2. Sample sizes for estimation of standing crop and nitrogen content

	Standing crop[*]					% Nitrogen[†]		
Sample type	1977E	1978E	1978U	1979E	1979U	1977	1978	1979
Mixed-meadow	3	6[‡]	4	—	—	3	3[**]	—
Mixed-mudflat	—	4[§]	4	4[¶]	4[¶]	—	2[**]	2
Carex subspathacea	1	2	—	—	—	1	1	—
C. mackenziei	—	2	—	2	2	—	1	2

[*] Sample sizes in 1977 equal the number of exclosures. Sample sizes in 1978 and 1979 result from three (in two of three mixed-meadow exclosure and both mixed-mudflat exclosures on 13 June 1978) or two quadrats (all other areas and dates) clipped in each area. Table 1 contains the number of exclosures and unexclosed areas in each vegetation type.

[†] Samples from quadrats clipped within the same treatment (e.g. mixed-meadow exclosure on the same date were combined prior to Kjeldahl analysis, except in 1978 when samples from one mixed-meadow exclosure were analysed separately from those from the other two. See above for numbers of quadrats per treatment.

[‡] $N = 8$ on 13 June.

[§] $N = 2$, 5 and 2 on 7, 13 and 25 June, respectively.

[¶] $N = 3$ on 7 July.

[**] $N = 2$ and 1, for mixed-meadow and mixed-mudflat, respectively, on 7 June.

comprised of the species occurring in meadows while mixed-mudflat samples consisted almost entirely of *Puccinellia phryganodes*.

Samples of grasses and sedges were clipped to litter level at 7–12 day intervals from 0·01 m^2 (1977) or 0·1 m^2 (1978, 1979) quadrats randomly placed within each of the exclosed or unexclosed areas. No quadrats were clipped more than once. The irregular sampling interval allowed us to clip vegetation coincident with aircraft supply flights so samples could be transported out of the field. Plant sampling from exclosed and unexclosed areas was begun on 23, 7, and 12 June and terminated on 12, 7, and 9 August, in 1977, 1978, and 1979, respectively. Numbers of samples clipped from each area are indicated in Table 2. Exclosures provided samples of vegetation that were ungrazed while vegetation from unexclosed areas and hand-collected samples were available to grazing geese. Standing crop is reported here on a dry weight basis.

Individual arrowgrass plants were removed from 1978 mixed-meadow samples to provide a 'pure' sample of meadow arrowgrass for that year. All other arrowgrass samples were hand-collected from individual plants, in areas grazed by geese, on ten dates through the summer of 1979. The amount of material was insufficient for separate analyses representing each date, however. Therefore, five composite aliquots were formed for both mudflat and meadow arrowgrass by combining material collected on the following pairs of dates: 24 and 30 June, 4 and 7, 17 and 21, 28 and 31 July, and 9 and 12 August.

Productivity of graminoids was determined in 1978 by repeatedly clipping to litter level 0·1 m^2 quadrats (initially randomly selected) in the *C. mackenziei*, both mixed-mudflat exclosures and in two of three mixed-meadow exclosures. Productivity was estimated as the growth (g dry weight) since the previous clipping.

Plant samples were frozen within 24 h and kept frozen until ready for analysis at the University of California, Davis, where they were blotted lightly with paper towels, weighed, and freeze-dried to constant weight. Dry samples were ground in a Wiley Mill to pass a 40 mesh per inch sieve. Nitrogen content was determined by the macro-Kjeldahl method. Sedinger & Raveling (1984) provide more detail regarding sampling and analytical procedures.

The lengths of the longest leaves on individual arrowgrass plants available for grazing were measured (one leaf per individual) to the nearest mm as plants were encountered in mudflats and meadows used by geese. Measurements of the lengths of ungrazed arrowgrass individuals were made on all individuals in five 0·01 m^2 quadrats in the meadow exclosures and on individuals in one of the 3 × 5 m mudflat exlosures. Arrowgrass productivity was estimated by measuring the growth (mm) between clippings to litter level of all individuals within five 0·01 m^2 quadrats in the meadow exclosures and within a subarea of the same 3 × 5 m mudflat exclosure used to measure lengths of ungrazed arrowgrass individuals.

Foraging behaviour

Habitat utilization by cackling geese was estimated by recording approximately once each day, the habitat (meadow, mudflat, or upland) occupied by all feeding cackling goose families on our principal study area. Habitat use was recorded between 04·00 and 24.00 h (the period when geese were actively foraging) immediately upon entering the observation tower, if four or more goose families were visible. If more than one habitat type was occupied by members of a family, the habitat occupied by the majority of family members was recorded.

Rate of pecking at food items by adults of both sexes of cackling geese (peck-rate) was determined by recording on a hand counter the number of pecks which occurred during a continuous bout of feeding, timed to the nearest 0·1 s. We used only those feeding bouts that were uninterrupted by alert behaviour (i.e. intervals in which the head was continuously down searching for, or consuming food). Feeding bouts of less than 5 s were excluded from the analysis because errors in estimation of peck-rate due to miscounting by one peck were >10% for short bouts. Adult males and females were distinguished by the larger body size (cf. Raveling 1978a) and greater frequency of alert and aggressive behaviour exhibited by males (Raveling 1970).

Statistical analyses

We used linear regression followed by *t*-tests to test for significance of seasonal trends in plant protein content and biomass, goose peck-rate and habitat use. Analysis of covariance was used to compare both slopes and adjusted mean levels of regression lines. We compared nitrogen concentrations and standing crops in exclosed *v*. unexclosed vegetation using two-way ANOVA.

RESULTS

Date of hatch

Cackling goose clutches hatched significantly later in 1977 than in 1978 or 1979 ($\chi^2_3 = 43{\cdot}4$, $P < 0{\cdot}001$, 1977 *v*. 1978 and $\chi^2_3 = 60{\cdot}4$, $P < 0{\cdot}001$, 1977 *v*. 1979, Fig. 1). Peak of hatching occurred on 4 July, 21 and 20 June in 1977, 1978, and 1979, respectively. The proportion of clutches hatching late was greater in 1978 than in 1979 ($\chi^2_2 = 7{\cdot}59$, $P < 0{\cdot}025$).

Hatching was highly synchronous, especially in 1977, the year of delayed nesting, when 93% of the clutches hatched over an 8-day period between 30 June and 7 July (Fig. 1). Hatching was less synchronous during 1978 and 1979 with 70% and 83% of clutches, respectively, hatching between 18 and 27 June.

Plant phenology

Standing crop of vegetation on mudflats was greater within exclosures than within unexclosed areas during 1978 ($F_{1,36} = 19{\cdot}57$, $P < 0{\cdot}001$, Fig. 2). Standing crops in exclosed *v*. unexclosed areas did not differ significantly for any other vegetation type × year combination.

Standing crop tended to increase between early June and early August for all vegetation types except 1978 unexclosed mixed-mudflat. These increases were significant ($P < 0{\cdot}05$), except for 1977 exclosed mixed-meadow, 1978 exclosed mixed-muflat and 1979 exclosed and unexclosed *C. mackenziei*. Standing crops were smaller (four areas) or unchanged (one area) on the last compared to the penultimate sampling date in five of twelve areas, suggesting that above-ground standing crops began to decline in August.

Nitrogen content of vegetation (per cent of dry weight) was not different in exclosed *v*. unexclosed areas for any year or vegetation type ($P > 0{\cdot}29$, all comparisons), so results from the two treatments were combined. Peak concentrations of nitrogen in plants either preceded (five cases) or coincided with (four cases) the hatching period of geese in nine of eleven vegetation type × year categories (Figs 3,4). Peak nitrogen concentrations in arrowgrass from meadows in 1978 and mudflats in 1979 may have preceded the hatching period but no arrowgrass samples were collected from those habitats prior to the beginning

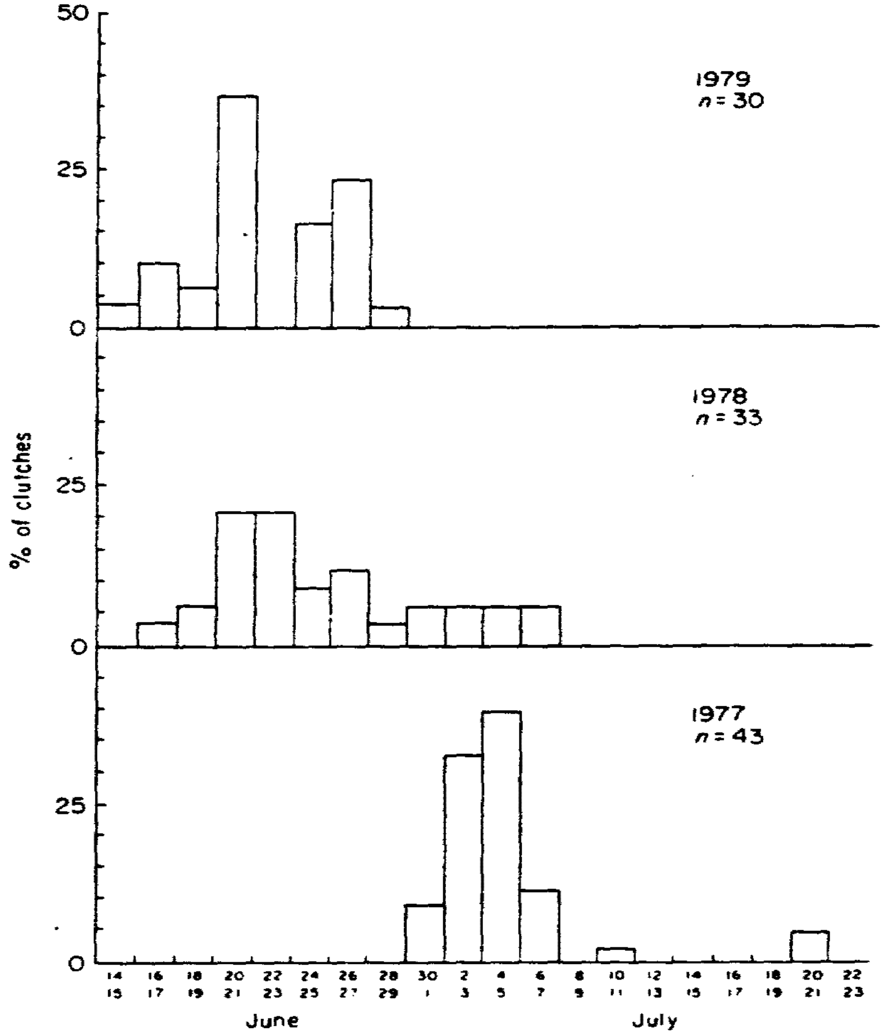

FIG. 1. Hatching dates of cackling goose clutches.

of hatch. Maximum measured nitrogen concentrations in 1978 mixed-mudflat vegetation and 1979 arrowgrass from mudflats occurred approximately 11 and 7 days following the respective hatching periods in the 2 years. Plant nitrogen concentrations declined during brood-rearing (i.e. following the peak of hatch) in all sequences of vegetation samples, significantly so in six of the eleven sequences ($P < 0{\cdot}05$, Figs 3,4). Maximum nitrogen concentrations for vegetation × year categories ranged from 2·6% (1978 mixed-meadow) to 5·4% (1979 arrowgrass from mudflats), while minimum nitrogen concentrations ranged from 1·4% (1977 mixed-meadow) to 3·9% (1979 arrowgrass from mudflats). Maximum nitrogen concentrations in repeatedly clipped grasses and sedges occurred in early July on both mudflats (4·0%) and meadows (3·3%, Fig. 5).

Growth rates of grasses and sedges peaked in mid-July at between 0·08 (mixed-mudflat) and 0·17 g 0·1 m^{-2} day^{-1} (*C.* mackenziei, Fig. 6). Maximum productivity of arrowgrass in meadows occurred in late June (Fig. 6). Growth rate of arrowgrass in mudflats was not

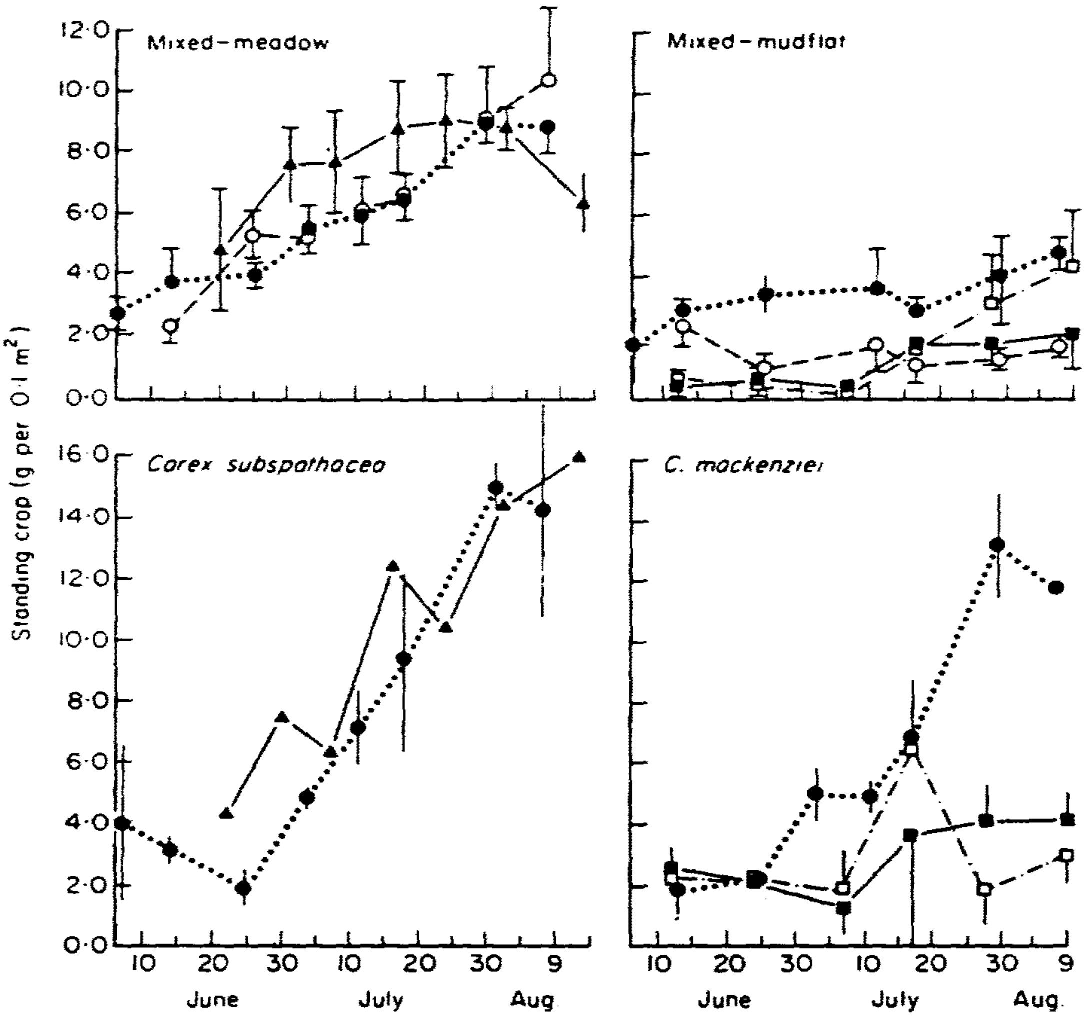

FIG. 2. Seasonal variation in standing crops of graminoids, 1977–79: (▲) 1977, (●) 1978, (■) 1979; open and closed symbols represent exclosed and unexclosed areas, respectively). Each point represents $\bar{X} \pm$ S.E. ($n > 2$) or $\bar{X} \pm$ range ($n = 2$). Sample sizes are in Table 2. Standing crops from 1977 are calculated from results from three 0·01 m² quadrats from each exclosure.

measured prior to early July but maximum recorded growth rate occurred during that period (Fig. 6).

The length of arrowgrass leaves protected from grazing increased until the end of July, then began to decline on both mudflats and meadows (Fig. 7). Those leaves subject to grazing, however, declined in length on mudflats in mid-July. Leaf lengths of grazed arrowgrass plants were significantly shorter ($P < 0{\cdot}05$) than those of ungrazed arrowgrass plants over the entire sampling period on mudflats. Grazed arrowgrass leaves in meadows were not sampled during July but were significantly shorter ($P < 0{\cdot}05$) than ungrazed leaves during August.

Foraging behaviour

Use of mudflats by cackling geese declined as brood-rearing progressed during all 3 years of the study, significantly so in 1977 and 1979 (Fig. 8). Rate of decline did not vary significantly among years ($F_{2,73} = 2{\cdot}42$, $P > 0{\cdot}05$) but the average per cent of foraging time spent on mudflats was greater in 1979 than in either 1977 or 1978

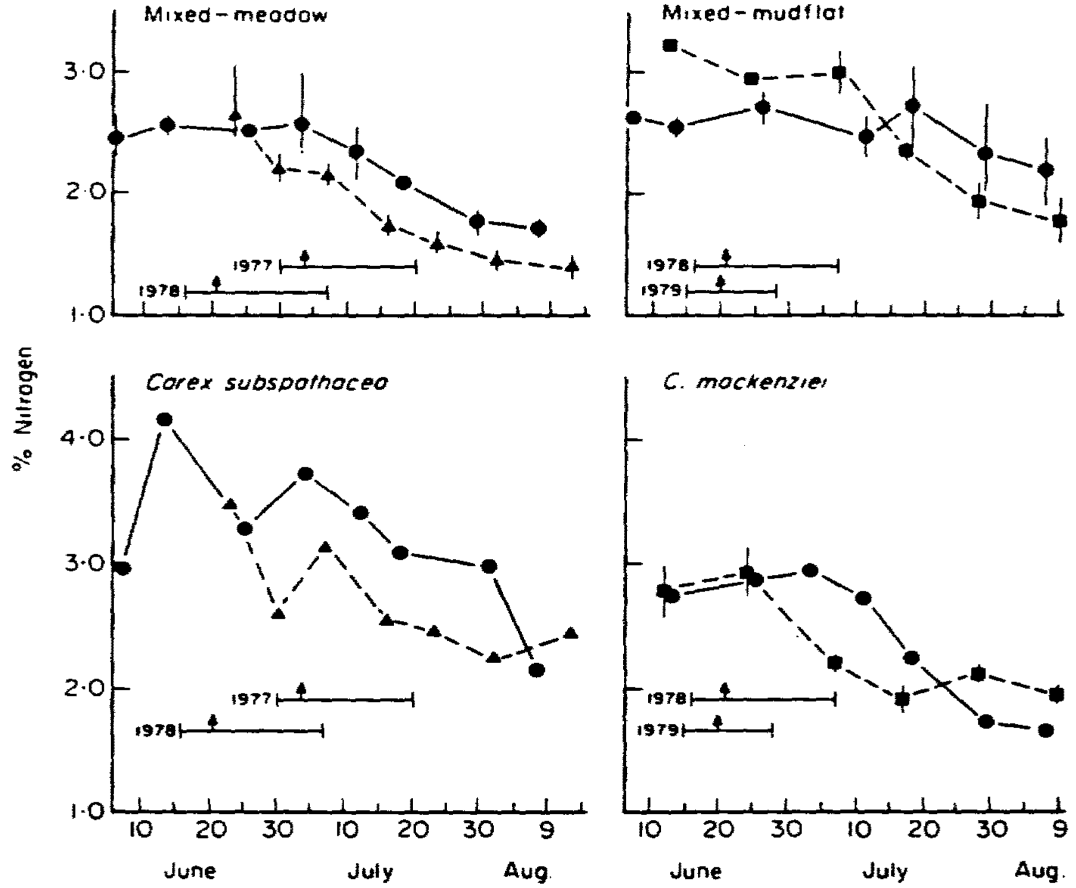

FIG. 3. Seasonal variation in nitrogen content (per cent of dry weight) of graminoids: (▲) 1977, (●) 1978, (■) 1979. Points and vertical bars represent means and ranges, respectively. Sample sizes are in Table 2. Arrows and horizontal bars represent the hatching peaks and hatching periods, respectively.

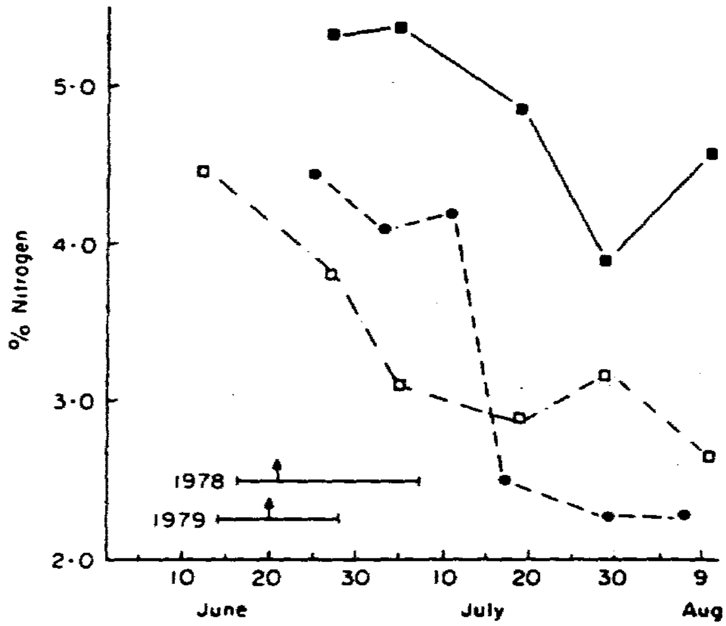

FIG. 4. Seasonal variation in nitrogen content (per cent of dry weight) of arrowgrass (*Triglochin palustris*) leaves from both mudflats (■) and meadows: (●) 1978, (□) 1979. Arrows and horizontal bars as in Fig. 3.

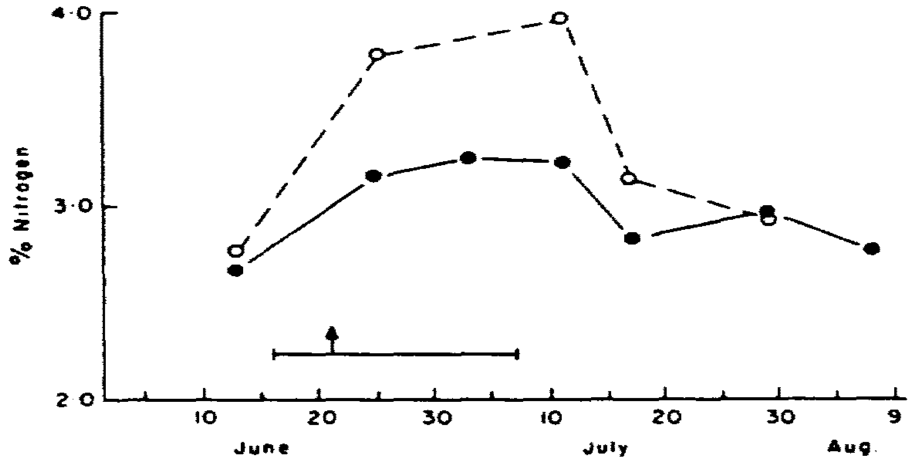

FIG. 5. Seasonal variation in nitrogen content (per cent of dry weight) of repeatedly clipped graminoids in 1978: (●) mixed-meadow, (○) mixed-mudflat. Arrow and horizontal bar as in Fig. 3.

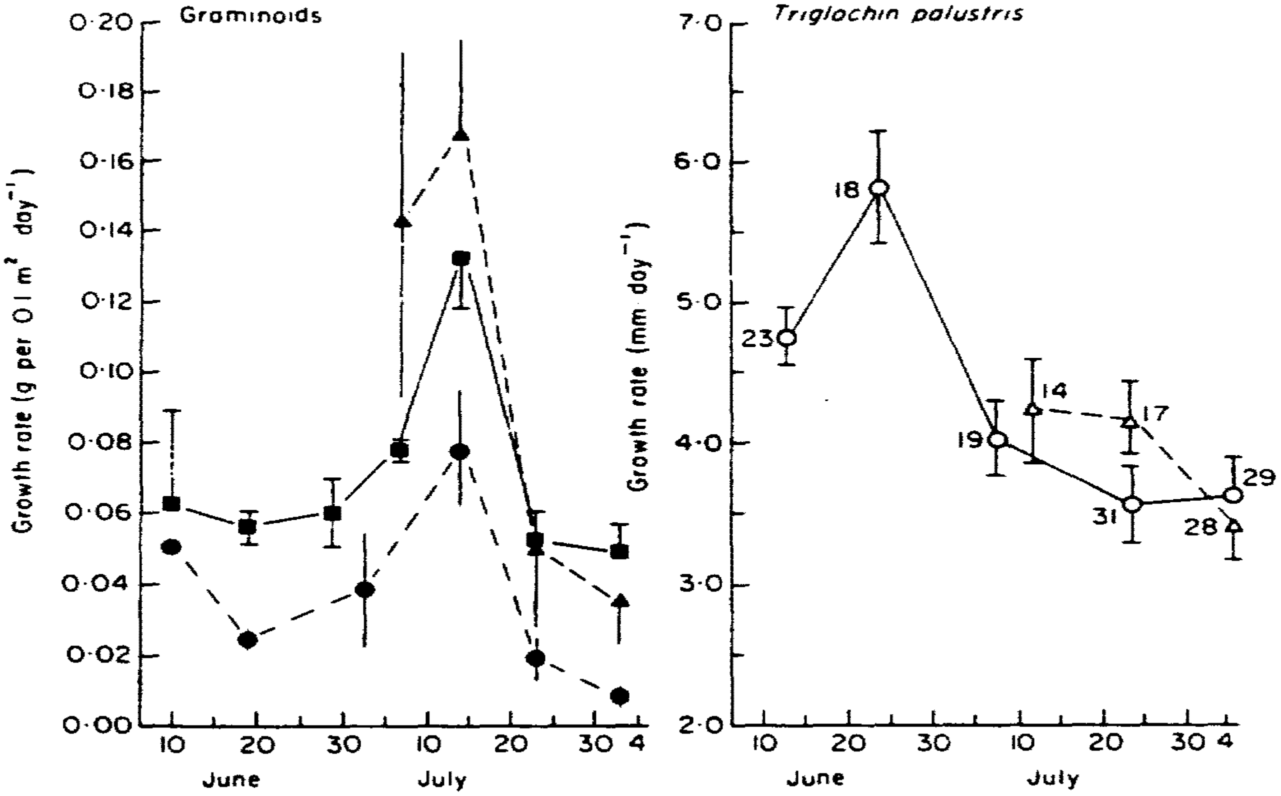

FIG. 6. Productivity (dry weight) of repeatedly clipped graminoids (g 0·1 m^{-2} day^{-1}, (●) mixed-mudflat, (■) mixed-meadow, (▲) *C. mackenziei*); and arrowgrass (mm per day, (○) from meadows, (△) from mudflats) during 1978 and 1979, respectively. Points are plotted on the midpoints of intervals over which growth occurred. Sample sizes for arrowgrass (number of leaves measured) are adjacent to plotted points. Sample sizes for graminoids (number of quadrats clipped) are n = 2, for mixed-mudflat and *Carex mackenziei*, and n = 6 for mixed-meadow. Exceptions are 10 June mixed-meadow and mixed-mudflat (n = 4 and 1, respectively) and 14 July mixed-meadow (n = 5).

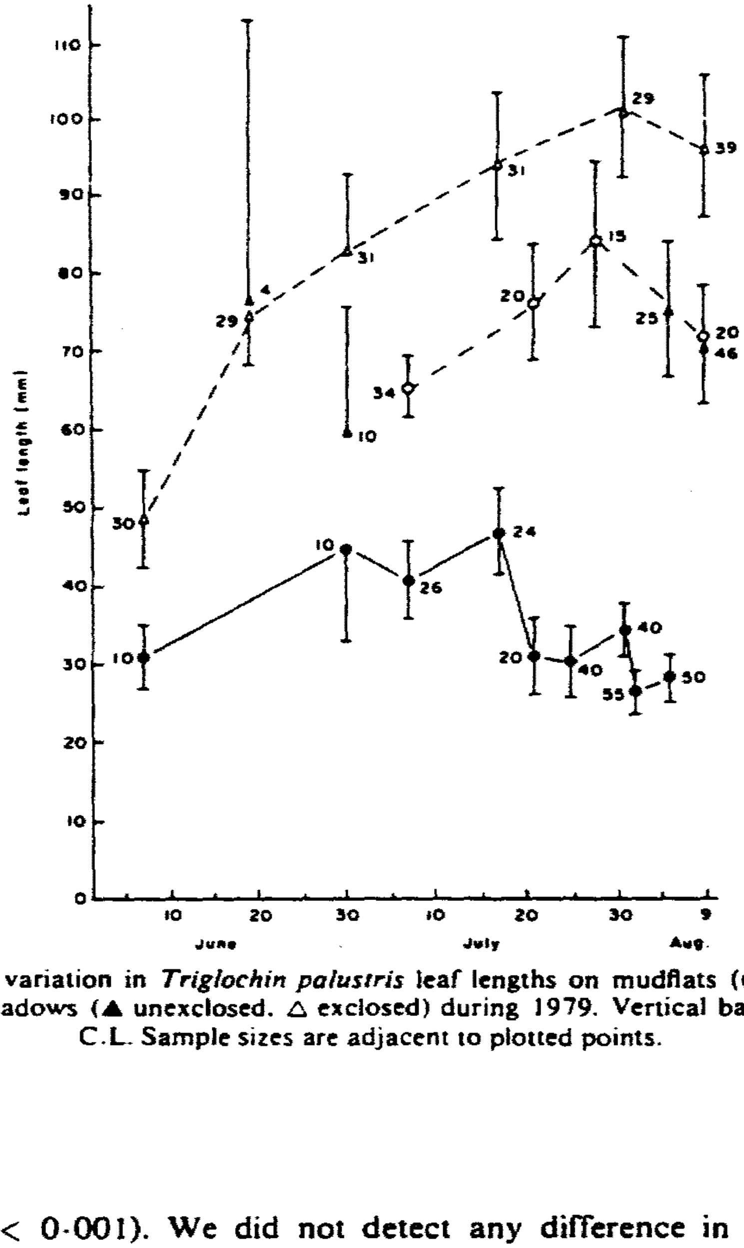

FIG. 7. Seasonal variation in *Triglochin palustris* leaf lengths on mudflats (● unexclosed, ○ exclosed) and meadows (▲ unexclosed, △ exclosed) during 1979. Vertical bars represent 95% C.L. Sample sizes are adjacent to plotted points.

($F_{2,75} = 17\cdot66$, $P < 0\cdot001$). We did not detect any difference in foraging habitat use among different periods of the day for any year of the study ($P > 0\cdot1$ for all 3 years, Kruskal-Wallis Tests). Therefore, daily differences in the time at which habitat use was recorded did not bias our results.

Feeding bout lengths incorporated into the analysis of peck-rates varied from 5 to 50 s and from 5 to 53·2 s for males and females, respectively. Mean lengths of these bouts varied from 10·9 s (males feeding on mudflats in 1979) to 14·1 s (females feeding on mudflats in 1978). Length of feeding bout did not affect our estimate of peck-rate because number of pecks was linearly related to bout length. Thus, long bouts provided the same estimates of peck-rates as short bouts.

Peck-rates of both sexes of adult cackling geese in meadows declined during the brood-rearing periods of both 1978 and 1979, although the relationship was not significant for males in 1979 (Fig. 9). Adjusted mean peck-rates in meadows were higher in 1979 than in 1978 for both males ($F_{1,155} = 6\cdot45$, $P < 0\cdot025$) and females ($F_{1,200} = 6\cdot79$, $P < 0\cdot025$). Peck-rates of geese feeding on mudflats also tended to decrease during brood-rearing for both males and females in 1979 and for males in 1978 although the relationships were

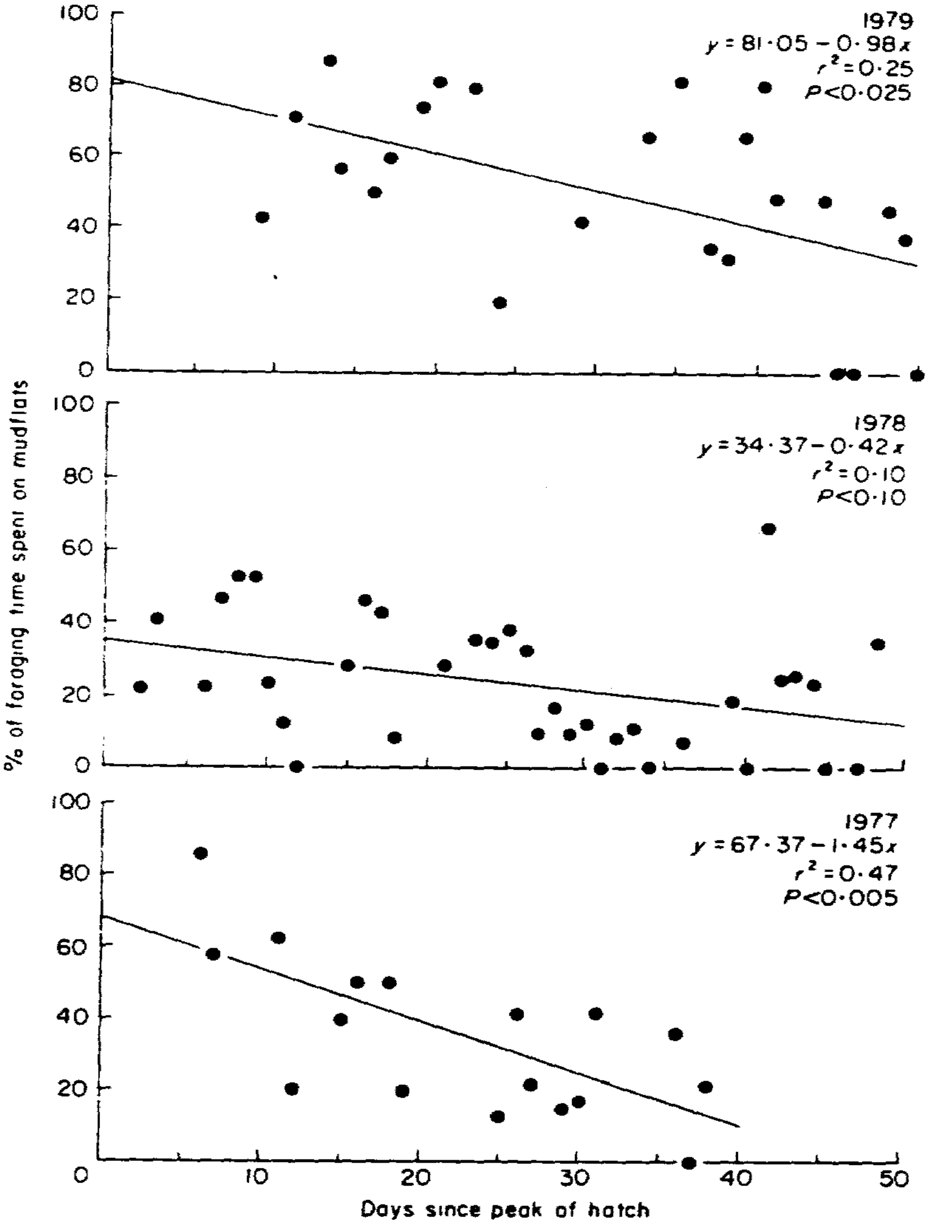

FIG. 8. Per cent of foraging time spent on mudflats by broods of cackling geese, 1977–79. Each point is the percentage of foraging broods on mudflats during mapping of broods (see methods). Mean numbers of broods (with ranges in parentheses) represented by each data point are 12·5 (6–24), 18·9 (5–48) and 9·5 (4–35) for 1977, 1978 and 1979, respectively. P is the probability that slopes differ from 0 by chance.

significant only for 1978 males and 1979 females (Fig. 10). Adjusted mean female peck-rates on mudflats were higher in 1979 than 1978 ($F_{1,152} = 19{\cdot}44$, $P < 0{\cdot}001$), while there was no between year difference for males feeding on mudflats ($F_{1,161} = 1{\cdot}20$, $P > 0{\cdot}10$). Peck-rates of geese were higher, on average, on mudflats than on meadows for males in both 1978 ($F_{1,109} = 36{\cdot}10$, $P < 0{\cdot}001$) and 1979 ($F_{1,207} = 45{\cdot}73$, $P < 0{\cdot}001$) and for females in 1979 ($F_{1,223} = 48{\cdot}21$, $P < 0{\cdot}001$). We did not make this comparison for females in 1978 because the slopes of the peck-rate *v.* time relationships differed between mudflats and meadows.

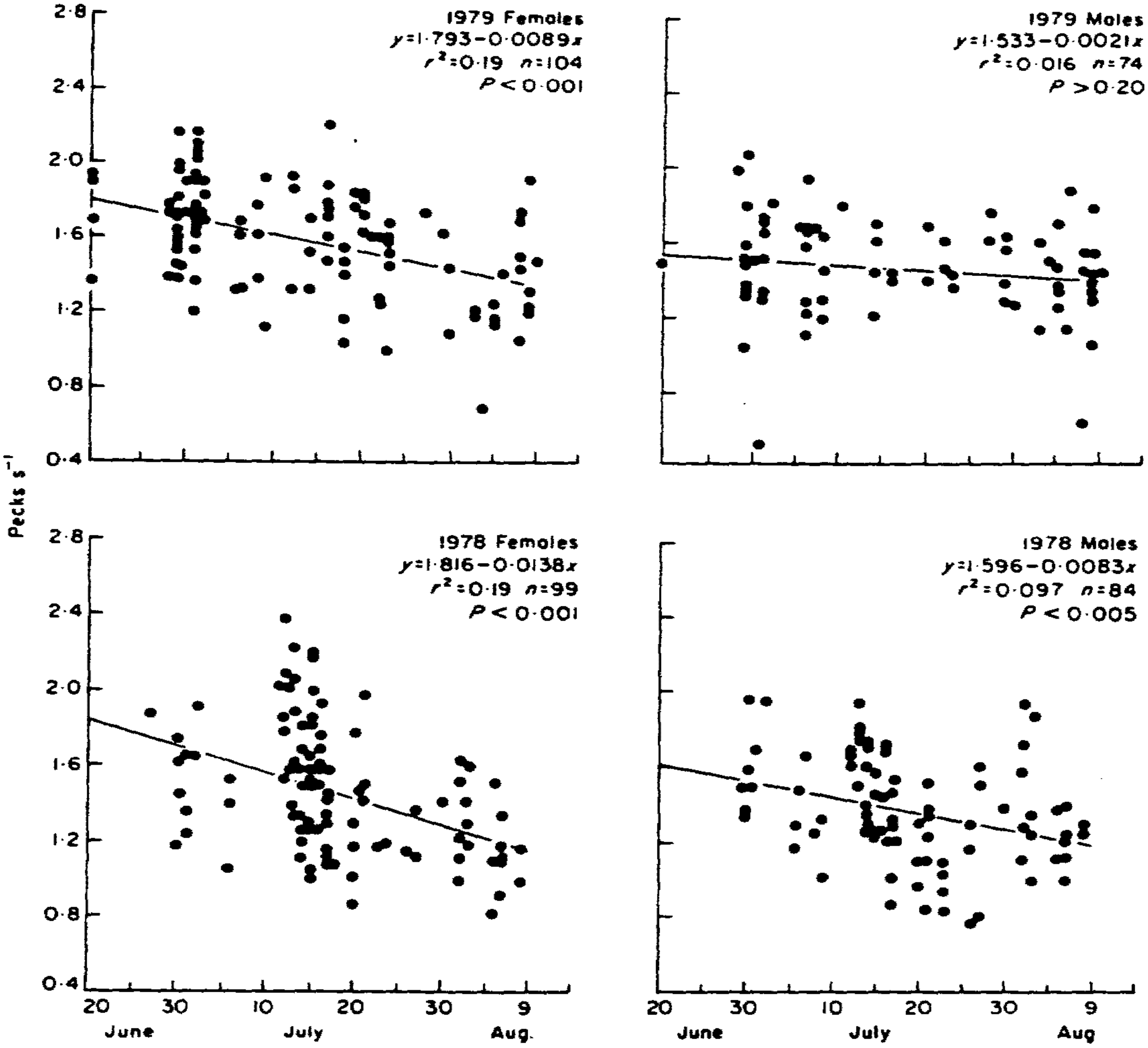

FIG. 9. Seasonal variation in pecking rates (pecks per s) of adult cackling geese foraging on meadows during 1978 and 1979. Day 0 for regressions corresponded to 20 and 21 June, for 1979 and 1978, respectively. *P* as in Fig. 8.

DISCUSSION

Plant phenology

Declining nitrogen, hence protein, concentrations in tundra graminoids, beginning shortly after spring emergence, have been documented at Barrow, Alaska (Chapin 1978) and on the west coast of Hudson Bay (Cargill 1981). High above-ground nitrogen concentrations in graminoids following the spring thaw result from rapid mobilization of nitrogen stored in below-ground organs which maximizes growth during the long days surrounding the summer solstice (Dennis, Tieszen & Vetter 1978). Nitrogen concentrations of whole plants decline because of the 'dilution' of rapidly growing tissue by more mature leaves (Chapin 1978; Mooney & Gulman 1982) and are maintained below potential levels because inorganic nitrogen is in short supply in many tundra areas (Ulrich & Gersper 1978; Chapin *et al.* 1981; Cargill 1981).

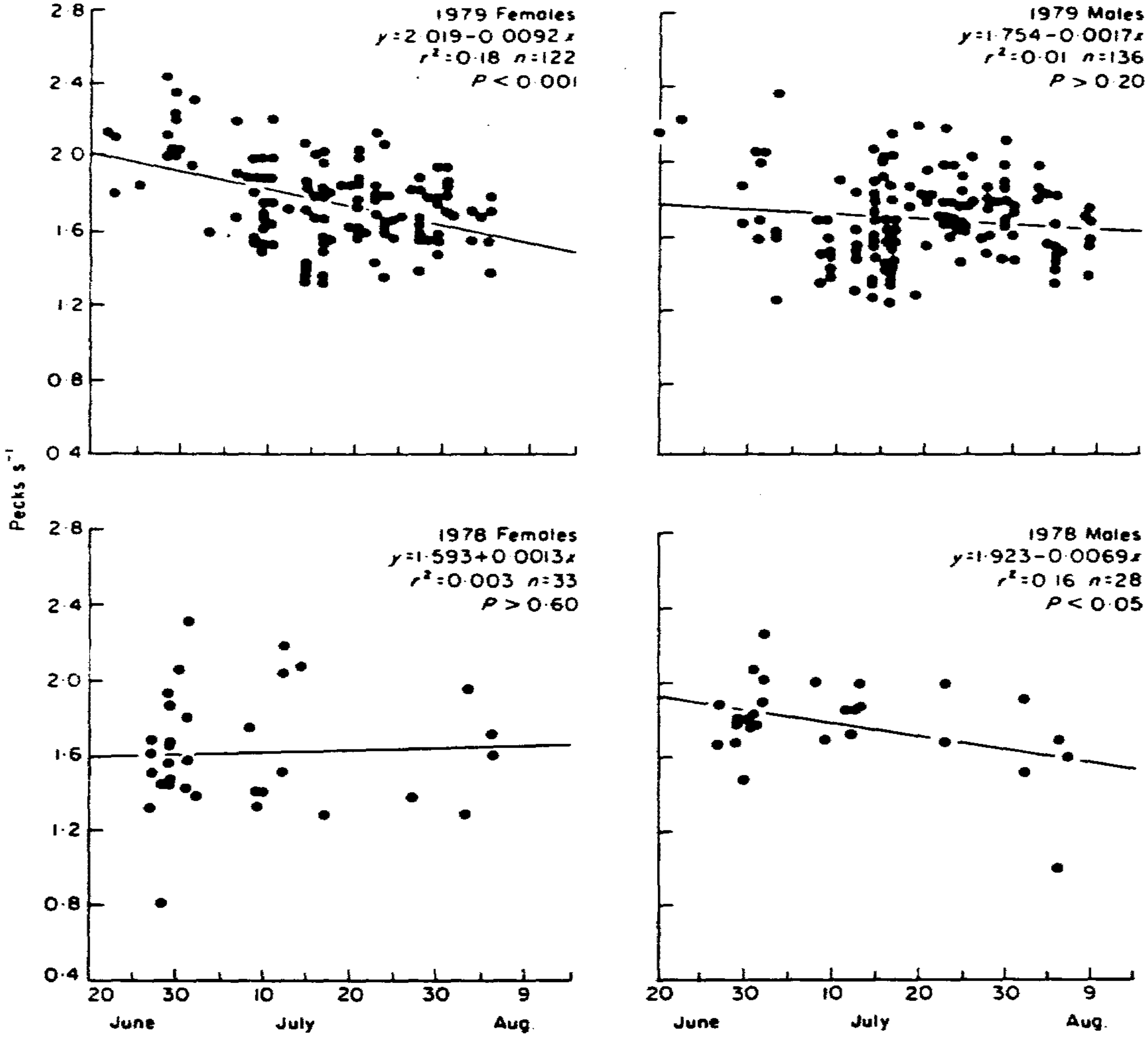

FIG. 10. Seasonal variation in pecking rates (pecks per s) of adult cackling geese foraging on mudflats during 1978 and 1979. Analysis as in Fig. 9.

Grazing may maintain relatively high nitrogen concentrations in graminoids during the growing season (Jameson 1963; Harwood 1977; Cargill 1981; Ydenberg & Prins 1981). This was true in our study as indicated by the delayed nitrogen peak in repeatedly clipped grasses and sedges (Fig. 5) compared with most other samples (Fig. 3). Also, in arrowgrass, which was more heavily grazed on mudflats than on meadows (Fig. 7), the nitrogen concentration peak was higher and lasted longer on mudflats than on meadows (Fig. 4). This delayed decline in nitrogen concentrations in grazed or clipped vegetation may have resulted in higher nitrogen levels in plants when goslings hatched than would have been predicted from data from our exclosures. However, the peak nitrogen concentration in heavily grazed arrowgrass still occurred within a week of the end of hatching in 1979 (Fig. 4), and the decline in nitrogen concentration in repeatedly clipped grasses and sedges began either during or within 4 days of the 1978 hatching period (Fig. 5).

The phenology of arctic graminoids results in their reaching peak nitrogen concentrations from 10 days (at Barrow, 71° N, Chapin, Van Cleve & Tieszen 1975) to an average of between three and seven weeks (La Parouse Bay, 58°N, Cargill 1981; Y-K Delta, 61° N, this study) following the initiation of spring growth which is approximately coincident with snow melt (Tieszen 1972, 1974). Since the initiation of nesting in Canada geese is also usually coincident with or immediately follows snow melt (MacInnes 1962; MacInnes *et al.* 1974; Mickelson 1975; Raveling 1978b) and a minimum of about 31 days (5 days for laying plus 26 days for incubation in cackling geese) is required for a female to hatch a clutch, most plant foods are already declining in nitrogen content before late-hatching broods start feeding. Since all arctic and subacrtic species of geese begin nesting at about the time of snow melt (see Owen 1980 and Bellrose 1982 for reviews), these relationships should have general applicability to their foraging ecology.

Hatch date may be even later relative to peak nitrogen content when nesting is delayed by a late spring thaw, as happened in 1977 (Fig. 1). Peak nitrogen concentrations in *C. subspathacea* and mixed-meadow vegetation, however, were not noticeably later in 1977 than in 1978 (Fig. 3). Plant nitrogen levels thus tended to be lower at a given gosling age in 1977 than in 1978 (and probably 1979).

Variation in nitrogen concentrations among parts of individual plants might have provided opportunities for geese to select foods higher in nutrient content than were our samples, which represented averages of the entire above-ground parts of plants. The nutrient content of various above-ground fractions (e.g. individual leaves, stems, etc.) needs to be measured but available evidence indicates that within-plant variation in above-ground nutrient content may be limited. The known duration of leaf exsertion in arctic sedges ranges from 20 to about 60 days (Tieszen 1978; Chapin 1981) and some new leaves could have appeared during the first 3 weeks of the brood-rearing period. However, younger leaves do not necessarily have systematically higher rates of photosynthesis (Tieszen 1978) and rates of photosynthesis are highly correlated with leaf nitrogen levels because 50–80% of leaf protein consists of ribulose-1,5-biphosphate carboxylase, which fixes CO_2 (Friedrich & Huffaker 1980; Camp *et al.* 1982). Thus, our present knowledge of plant growth dynamics indicates that a steady supply of high protein content food was probably not provided by later exserted leaves. Furthermore, protein concentrations in those plant tissues actually available to geese may have been lower than our estimates (for the area we sampled) because meristem tissue, which was high in protein content (Williams *et al.* 1976), was located at the bases of stems and leaves (Rechenthin 1956) where it was less available to grazing geese. Thus, phenological patterns in plant foods probably resulted in declining nitrogen concentrations in available foods as brood-rearing progressed, especially in those plants that were not grazed until late in brood-rearing. We believe that higher nitrogen concentrations in oesophageal *v.* clipped samples (see below) were due to geese foraging in areas where plants had higher nitrogen concentrations (Ulrich & Gersper 1978).

Intraspecific competition in cackling geese

Arrowgrass predominated in the diet of goslings less than 24 days old (44% and 98% of the diet in 1978 and 1979, respectively. See Sedinger & Raveling 1984 for a description of the diet). Arrowgrass was eaten at four (on meadows) to five (on mudflats) times its frequency of occurrence in the environment which was related to its higher protein levels (compare Figs 3 and 4) and lower cell wall levels (23·7–29·1% of dry weight) than grasses and sedges (47·6–58·3%, Sedinger & Raveling 1984).

Availability of arrowgrass on mudflats declined in mid-July 1979 (Fig. 7). This was the result of grazing by geese, as indicated by shorter leaf lengths of arrowgrass in grazed *v.* ungrazed areas (Fig. 7). Growth rates of repeatedly clipped arrowgrass peaked in late June (meadows) or early July (mudflats) (Fig. 6). Thus, the absolute decline in arrograss biomass by mid-July 1979 was the result of cropping rate exceeding growth rate during this period. This probably occurred even earlier in 1977 and 1978 because brood densities were higher in those years (twelve broods on our principal study area in 1979 *v.* seventeen and twenty-three broods in 1977 and 1978, respectively, J. S. Sedinger & D. G. Raveling, unpublished). Cackling geese also reduced the leaf lengths of arrowgrass in meadows (Fig. 7) which, in conjunction with increasing biomass of less preferred plants, caused the declining peck-rates in meadows later in the summer (Fig. 9).

Reduction in availability of arrowgrass had at least three effects. First, peck-rates declined (meadows, Fig. 9) or had a slight tendency to do so (mudflats, Fig. 10), thus reducing rate of intake. Second, mudflats were used less as brood-rearing progressed (Fig. 8). Finally, arrowgrass comprised a steadily declining proportion of the diet during brood-rearing (17% of the diet of goslings more than 41 days old in 1978, Sedinger & Raveling 1984). The magnitudes of all three of these factors were related to brood densities. Peck-rates were higher in 1979 (lowest brood density year) than in 1978 for females feeding on mudflats (Fig. 10) and for both sexes feeding on meadows (Fig. 9). Mudflats were also used more by feeding broods in 1979 than in 1978 or 1977 (Fig. 8) and arrowgrass comprised a larger fraction of the diet in 1979 than in the other 2 years (Sedinger & Raveling 1984). Because mudflat arrowgrass was the most nutritious food available to cackling geese, these shifts in diet and habitat use and the lower rates of intake resulted in poorer foraging conditions later in brood-rearing and when brood density was high.

We calculated the nitrogen content of the diet of goslings during the brood-rearing period (Fig. 11), taking the following factors into account: per cent of each food type in the diet (arrowgrass, *Carex mackenziei*, mixed-meadow, mixed-mudflat and *Carex* seeds; data

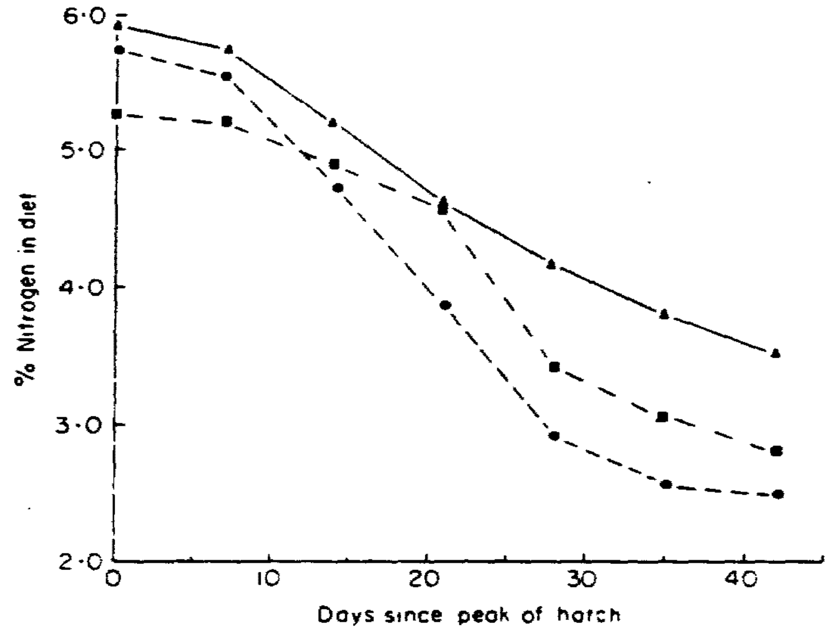

FIG. 11. Seasonal variation in calculated nitrogen content of the diet (percentage of dry weight) of cackling goose goslings: (●) 1977, (■) 1978, (▲) 1979. See text for description of calculations.

from Sedinger & Raveling 1984), per cent time spent feeding in mudflats *v.* meadows and per cent nitrogen content of foods. We calculated per cent time feeding on mudflats from Fig. 8. Nitrogen concentrations were measured directly in oesophageal samples of arrowgrass from goslings which had fed on mudflats ($n = 3$), meadows ($n = 4$) and on *Carex mackenziei* ($n = 5$). Nitrogen concentrations averaged 11, 41 and 51% higher in oesophageal samples than in clipped samples of these three foods, respectively (which we believe to be the result of foraging in areas with higher protein content plants, see above). Because of this difference, we increased our estimates of nitrogen concentrations in clipped samples (data from Figs 3, 4) by the appropriate correction factors (e.g. 11% for arrowgrass from mudflats) to estimate the nitrogen concentrations in foods consumed by geese. We used the correction calculated from *C. mackenziei* for other sedges and grasses. There were no significant seasonal trends in the correction factors. Our estimates of nitrogen concentrations in foods were probably overestimates because some of the differences between oesophageal and clipped samples were the result of contamination of oesophageal samples by saliva (Moss 1972). Composition of the diet was estimated from linear regressions relating per cent contribution to the diet by a food to the number of days following peak of hatch (J. S. Sedinger & D. G. Raveling, unpublished). Calculated dietary nitrogen levels varied from between 5·3% (1978) and 5·9% (1979) at the peak of hatch to between 2·5% (1977) and 3·5% (1979) at the beginning of fledging (Fig. 11).

Calculated seasonal changes in dietary nitrogen were influenced primarily by reduced use of mudflats, where arrowgrass had the highest nitrogen content, and decreased consumption of arrowgrasses. Nitrogen would have declined from 5·6 to 3·9% of the diet (average of declines in 1977–79, a 31% decline) as a result of the observed changes in habitat use and diet alone, even if plant nitrogen levels had been constant (compare with the average 48% decline in Fig. 11). Thus, seasonal patterns in dietary nitrogen were not principally dependent on declining plant nitrogen levels. However, declines in dietary nitrogen late in brood-rearing, due to shifts in diet and habitat use, were exacerbated by lower nitrogen levels in previously ungrazed plants (Hardwood 1977; Cargill 1981, see above).

Scott (1973) recommended between 20% and 22% protein in the diet for maximum growth rates of waterfowl. About 55% of the nitrogen in artificially prepared diets is incorporated into tissue by poultry (Scott, Nesheim & Young 1976). Geese incorporate between 11% and 50% of the nitrogen in their plant foods into tissue (Marriot & Forbes 1970; Sedinger 1984). If we assume that 30% (J. S. Sedinger & D. G. Raveling, unpublished) of dietary nitrogen is incorporated into tissue by geese, maximum growth rates would require overall dietary protein levels of about 40% (55/30 × 22%) or 6·45% nitrogen when feeding on green plants alone. Calculated levels of dietary nitrogen were below this level even under the best foraging conditions (Fig. 11). Thus, even early in brood-rearing, grazing conditions were suboptimal and goslings hatching 1 week after the peak of hatching had between 19% (1979) and 32% (1977) less protein in their diet during the third through to the fifth weeks of age (period of rapid growth) than goslings hatching 1 week prior to the peak (Fig. 11).

Early hatching broods thus experienced a superior nutritional environment at any given age compared with later hatching goslings. The reduction in dietary nitrogen levels was primarily due to shifts in habitat use and diet (see above) in response to reduced availability of high quality foods, which was the result of grazing by the geese themselves. Seasonal patterns in dietary nitrogen thus represented a case of intraspecific competition favouring those broods that hatched early (see below).

Natural selection for hatch date

Nutrition during the growing period may ultimately influence the ability of animals to deposit fat (March & Hansen 1977) and protein (Moss, Simmonds & McNary 1964; Swatland 1977) as adults. Poor early nutrition may result in a permanent reduction in adult body size (Wilson & Osbourn 1960). The ability to accumulate fat and protein reserves is expecially important in geese because the size of the clutch laid by a female is directly related to the size of such reserves (Ankney & MacInnes 1978; Raveling 1979). Final adult body size may also influence the ability of males to attract mates (Ankney 1977b). Improved early nutrition may also reduce the age of first reproduction as indicated by a higher proportion of geese nesting as 2 year olds when they had hatched in a year with early as opposed to late nesting (Finney & Cooke 1978). Finally, early hatching lesser snow geese, *Anser caerulescens caerulescens*, were recruited into the breeding population at a higher rate than those hatching later in a season (Cooke, Findlay & Rockwell 1984). Both Lieff (1973) and Wurdinger (1975) demonstrated that nutrient levels in plants limit growth rates in geese. Thus, poorer nutrition later in brood-rearing, due to intraspecific competition and plant phenology, should provide strong selection pressure favouring early nesting.

Mortality of incompletely developed goslings due to early autumn freeze-up in some years (Barry 1962, 1967) has also been proposed as an important factor favouring early arrival and nesting in arctic geese (Cooch 1958; Ryder 1967). However, such gosling mortality was reported only for years when the brood-rearing period was significantly shorter than 'normal' due to both delayed nest initiation and early autumn freeze-up. The best documented case occurred in 1959, when nesting was delayed 10 days and autumn freeze-up occurred 14 days earlier than the average for the other 8 years of the study (Barry 1967). Despite the abbreviated brood-rearing period in 1959, 55 days separated the hatching of the first clutch and autumn freeze-up. This was 5–15 days longer than the 40–50 days required for brant young to fledge (Barry 1962; Mickelson 1975). Thus, even during a short brood-rearing period, only the very latest hatching goslings were probably prevented from fledging and strengthening flight muscles prior to autumn freeze-up. Furthermore, the failure to fledge in late hatching goslings was probably also the result of slowed growth due to poor diet and so was a result of nutritional factors rather than strictly the shortness of the brood-rearing period.

Early arrival may be disadvantageous in some years because weather delays the availability of nest sites causing females to use stored lipid reserves for maintenance and consequently to lay smaller clutches (Cooch 1958; Barry 1962; Mickelson 1975; MacInnes *et al.* 1974; Raveling & Lumsden 1977). Early nesters may also suffer egg loss due to inclement weather (Raveling & Lumsden 1977), flooding (Cooch 1958; Barry 1962) or predation (Findlay & Cooke 1982). The disadvantages of early arrival and nesting act in opposition to the nutritional advantages of early nesting to produce stabilizing selection favouring dates of arrival on nesting areas that, on average, allow geese to begin nesting as soon as secure nest sites become available. The intensity of these opposing selection pressures has apparently been strong enough to produce the striking synchrony in nest initiation dates observed in arctic geese (Cooch 1958; Barry 1962; MacInnes 1962; Ryder 1972; Mickelson 1975; Raveling & Lumsden 1977).

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Autumn staging of Cackling Canada Geese on the Alaska Peninsula

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Introduction

Knowledge of the biology of breeding and wintering geese has increased dramatically during the last two decades. Until recently our understanding of events occurring on premigration staging areas lagged behind that for breeding birds. This is undoubtedly because geese often stop only briefly at staging areas which are usually quite remote. However, recent studies on spring staging areas showed that geese foraged in a manner that increased protein and energy intake (Ydenberg and Prins 1981; McLandress and Raveling 1981) while Ebbinge *et al.* (1982) demonstrated that spring weight gain on staging areas influenced subsequent reproductive success in Dark-bellied Brent Geese *Branta bernicla bernicla*. In the autumn Lesser Snow Geese *Anser caerulescens caerulescens* also selected foods high in nutrient content (Prevett *et al.* 1979; Thomas and Prevett 1980) and juveniles did not have sufficient lipid reserves to complete autumn migration until after staging on the James Bay coast (Wypkema and Ankney 1979).

Cackling Canada Geese *Branta canadensis minima*, the smallest subspecies of Canada Geese, nest on the coastal fringe of the Yukon-Kuskokwim Delta and winter primarily in the Central Valley of California (Figure 1). In October they leave the Delta and fly directly to the north side of the Alaska Peninsula where they remain for up to three weeks. In most years Cackling Geese fly nonstop from the Alaska Peninsula to the Klamath Basin (2,800 km) on the Oregon-California border in late October (Nelson and Hansen 1959). A direct flight was confirmed in 1984 by observation of a marked individual on the Alaska Peninsula and resighting of the same individual in the Klamath Basin 3 days later (H. McCollum pers. comm.). Since 1980 a significant fraction of the Cackling Goose population has begun wintering in the Willamette Valley of western Oregon (J.C. Bartonek unpub. 1986) reducing the length of the autumn migratory flight by ca. 450 km.

Recent declines in numbers of Cackling Geese (O'Neill 1979; Raveling 1984) have stimulated interest in their biology during all phases of the annual cycle. Autumn staging is likely to be especially important for these geese because of the energetic consequences of their small size and the long overwater migration they undertake. This report concerns the behaviour of Cackling Geese staging at Ugashik Bay on the Alaska Peninsula during autumn. The importance of premigratory staging for this population in view of the energetic cost of autumn migration, as evidenced by weight loss during the flight to California, is also discussed. Detailed accounts of migration chronology in relation to weather patterns and annual variation in the energetic cost of migration are currently under preparation by personnel of the Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service.

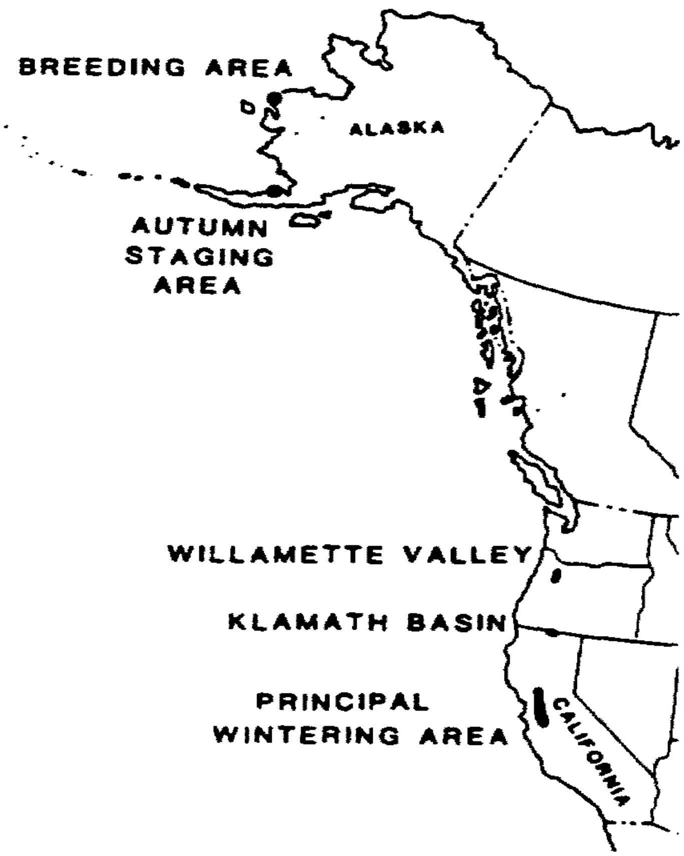


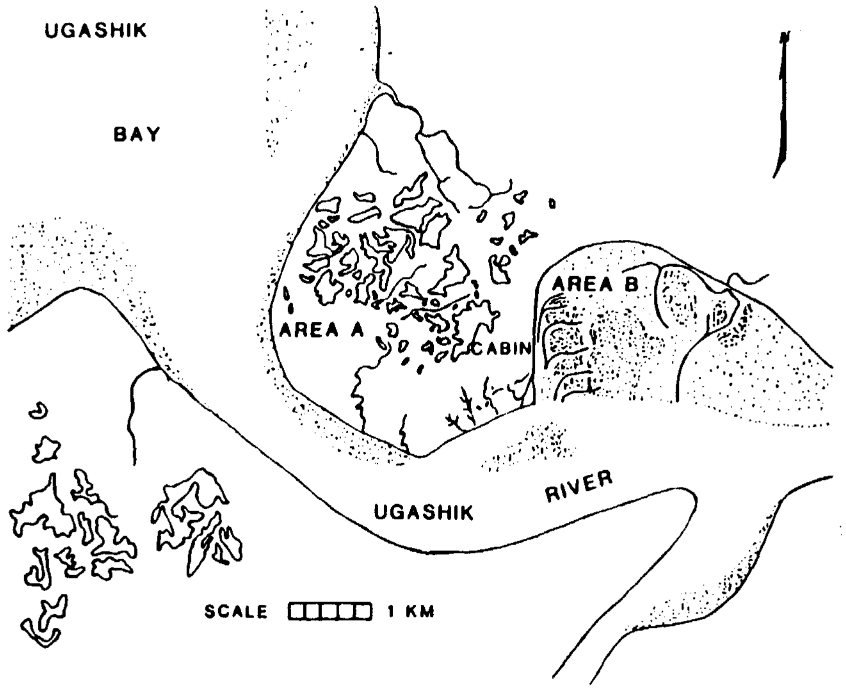
Figure 1. Locations of breeding, autumn staging and wintering areas of Cackling Canada Geese.

Study Area

Virtually the entire population of Cackling Geese is present on the Alaska Peninsula in October and is restricted to two areas, Ugashik Bay and the mouth of the Cinder River (R. Gill pers. comm.). All observations were made at Ugashik Bay where Cackling Geese used two principal areas. The first was a 10 km² peninsula formed by a bend in the Ugashik River as it entered Ugashik Bay (Area A, Figure 2). This area consisted of a tall (1 m) graminoid community interspersed with shallow (10-30 cm deep) brackish ponds. Pond shores had a shallow gradient that supported stands of *Hippuris tetraphlla*, *Spergularia canadensis*, and *Puccinellia phryganodes*. *Triglochin palustris* occurred sporadically in this habitat. Geese also used an extensive tidal mudflat (Area B, Figure 2) which contained pure stands of *H. tetraphylla* and *P. phryganodes*, and occasionally used unvegetated mudflats along the river bank and exposed bars in Ugashik Bay

Methods

Observations were begun on 7th and 5th October in 1983 and 1984, respectively, and finished on 16th and 20th October in the two years. Behaviours of geese were classified as: foraging, drinking, locomotion (walking, swimming and flying), maintenance (preening and bathing), alert, resting and aggressive interactions (chasing and fleeing). In 1984 time spent in these behaviours by individual geese using inland ponds (the only area that could be consistently observed) was estimated by recording their activities at 1 minute intervals for periods ranging from 10 to 180 minutes ($\bar{X}$ = 46 minutes). The percentage of time spent in each behaviour for a given observation period was estimated to be the proportion of 1 minute samples on which each behaviour was recorded. Proportions of time spent in each behaviour during a single observation period thus provided a single data point for statistical anlysis. In 1983 a continuous record was kept of behaviours of focal individuals except that behaviours of less than 1 minute duration were not recorded. Because of the potential bias associated with this method results from 1983 were not subjected to statistical analysis. The number of aggressive interactions during an observation period, in which a focal individual was involved, were counted and the role of the focal individual (aggressor or displaced bird) was noted (1984 only).



Individuals were selected for observation from among geese wearing plastic neckbands with alpha-numeric codes that allowed individual recognition, and consequently identification of age and sex. Neckbands were applied on the breeding grounds by personnel of the U.S. Fish and Wildlife Service, and in California by personnel of the California Department of Fish and Game and the University of California, Davis, as part of a study examining survival. Sex was determined during banding by cloacal examination. Geese were assigned to one of three age categories for analysis of behavioural data: adults, at least 27 months old; second-year, 15 months old; and hatching-year, 3 months old at the time of the study.

Weights of Cackling Geese at Ugashik Bay were obtained from birds shot by hunters in 1980 and 1983. Weights of geese from 1980 were provided by R. Sellers, Alaska Dept. of Fish and Game, while KSB weighed geese in 1983. Hunter-killed geese were classified as either hatching-year (3 months old) or after-hatching-year (>15 months old).

Comparison between sexes of the percentage of time spent in different behaviours by adults and hatching-year birds was made using t-tests. Sample sizes of second-year birds were not sufficient for this analysis. These analyses did not indicate significant differences in behaviour between sexes so data were pooled and a 1-way ANOVA was performed to examine differences in behaviour among age classes. Behavioural data were collected from some individuals on more than one occasion. Since data collected from the same individual on different occasions may not have provided independent samples, data from individuals were nested within age classes in the ANOVA. This analysis produces a χ^2 statistic resulting from a maximum-likelihood test of the hypothesis that there was no variation in behaviour due to age (Dixon 1983).

Results

Sample sizes of Cackling Geese shot by hunters were not adequate for assessment of weight gain while at Ugashik Bay. Because the samples were collected throughout the staging period, weights presented here may underestimate peak departure weights (Table 1). Nevertheless, Cackling Goose adults were at weights equal to, or exceeding pre-laying spring weights given by Raveling (1979) of 1,871 g for males, 1,890 for females; young-of-the-year were between 38% and 47% heavier than fledging weights given by Sedinger (1986), of 1,284 g for males, 1,228 for females. Ingesta were not removed from geese at Ugashik Bay, so weights of these geese were possibly slightly inflated (by about 48 g, if ingesta weight was similar to that in birds during summer, Sedinger 1986). There were no significant differences among age and sex classes in weight lost during the flight between the Alaska Peninsula and the Klamath Basin (t-test, $P>0.05$); Cackling Geese lost between 400-600 gm during the flight, 23-33% of the starting weight.

Foraging was the predominant activity of Cackling Geese while at Ugashik Bay in

Table 1. Weights of Cackling Geese during autumn (X ± SE)

Location	Weight (g) of geese Imm. males	Imm. females	Adult males	Adult females
Ugashik Bay	1775±78 (N=7)	1804±62 (N=9)	2053±39 (N=8)	1912±85 (N=10)
Klamath Basin[a]	1360±24 (N=13)	1200±21 (N=18)	1490±25 (N-26)	1320±26 (N-22)

Table 2. Percentage of time spent performing different behaviours (X ± SE) by Cackling Geese during autumn staging, 1984, at Ugashik Bay, Alaska.

Age class	N*	Feed	Rest	Behaviour Main	Drink	Alert	Loco	Aggress
Adult	32 (46)	53.3 ±6.8	17.2 ±5.2	15.5 ±3.8	0.7 ±0.5	6.5 ±1.9	6.6 ±1.6	0.2 ±0.1
Second-year	8 (12)	73.2 ±11.9	8.0 ±6.6	9.8 ±5.5	0.0 ±0.0	1.4 ±0.9	6.0 ±2.5	1.5 ±1.8
Hatching-year	7 (9)	83.5 ±4.7	0.0 ±0.0	2.7 ±3.0	0.2 ±0.2	3.7 ±1.6	9.6 ±3.4	0.4 ±0.4

*Number of individuals sampled and total number of focal samples in parentheses.

1984 (Table 2). Males and females did not differ in behaviour but birds in the three age classes differed significantly ($\chi^2=6.99$, $P<0.05$) in the proportion of time devoted to feeding, with hatching-year birds spending 84% of the time feeding compared to 73 and 53% for second-year birds and adults, respectively. In 1983 hatching-year geese also spent more time feeding (98% of 5 observation periods, representing 3 individuals) than adults (68% of 13 observation periods, representing 9 individuals). The increased time devoted to feeding by hatching-year birds resulted in their spending less time resting and performing maintenance behaviours than adults or second-year geese, although these differences were not significant.

Analysis of aggressive interactions is restricted to adults owing to small sample sizes for the other age classes (Table 3).

Table 3. Aggressive interactions of adult male and female Cackling Geese at Ugashik Bay.

Sex	No. times aggressor	No. times displaced	Total
Males	22	7	29
Females	8	26	34
Total	30	33	66

Males and females did not differ in the number of aggressive interactions per minute: 0.06±0.02 and 0.04±0.02 interactions for the two sexes respectively (t-test, $P>0.05$). However, a significantly higher proportion of male interactions resulted in displacement of the nonfocal individual than was the case for females, which were usually displaced ($\chi^2=6.41$, $P<0.02$).

Discussion

Autumn staging is essential for premigratory weight gain in Lesser Snow Geese; hatching-year birds did not have sufficient lipid reserves prior to autumn staging to complete autumn migration (Wypkema and Ankney 1979). It is likely that this is also true for Cackling Geese. To estimate the energy cost of the autumn migratory flight from the Alaska Peninsula to the Klamath Basin it was assumed that lipids yielded 9 kcal/g when oxidized (Ricklefs 1974). It was also assumed that flight muscles converted chemical to mechanical energy with an efficiency of 25% (Greenewalt 1975). The latter's models were used to estimate the cost of flight because their predictions were closest to estimates of energy expenditure in flying birds made using doubly-labelled water (Flint and Nagy 1984). Using these models of the energy requirements for flight and assuming that Cackling Geese flew at a speed of 38.9 km/h (thus completing the 2,800 km migration in 72 h as observed) an average of 483 g of lipid were required to power the autumn migratory flight. An additional 35 g of lipid were required to maintain the birds during the flight, based on the model of the relationship between weight and basal metabolic rate of Ashchoff and Pohl (1970). Thus a total weight loss of 518 g is predicted by the models. This estimate is within 5% of the overall average migratory weight loss indicated by the data in Table 1 (543 g). This may have been an underestimate because Alaska weights may not have represented peak premigratory condition and some weight may have been regained in California prior to collection (D.G. Raveling pers. comm.). Considering also that other factors might have affected the cost of migration (e.g. different flight speed, imperfect navigation, wind) there is remarkable agreement. Cackling Geese would require only 392 g of lipid to complete autumn migration if they flew at 58 km/h, the speed of minimum cost of transport.

Before leaving the Yukon-Kuskokwim Delta Cackling Geese feed heavily on *Empetrum nigrum* berries (C.P. Dau pers. comm.) which contain high concentrations of both lipids and soluble carbohydrates (Sedinger and Raveling 1984). Cackling Geese undoubtedly deposit large amounts of lipid before departing. However, given the energy cost of the flight from the Alaska Peninsula to the Klamath Basin it is unlikely that these geese could fly directly from the Yukon-Kuskokwim Delta to wintering areas, which would entail a 20% longer flight. Therefore, the Alaska Peninsula is an essential staging area for Cackling Geese in autumn. This may be especially true for hatching-year birds as indicated by their intensive feeding at Ugashik Bay. The diet there includes tubers of *Triglochin palustris* (D. Timm unpub. 1982) which have been shown to be a good source of energy for geese staging along the coast of James Bay, Ontario (Thomas and Prevett 1980). Nevertheless, one hatching-year bird shot by hunters weighed only 1,400 g, which is barely 100 g above average fledging weight (Sedinger 1986). Given the average weight loss during migration it seems unlikely that this individual contained sufficient reserves to complete the migration. However, at present we have no estimate of the number of individuals that fail successfully to complete the flight from the Alaska Peninsula to wintering areas.

Raveling (1970) showed that larger social units were dominant to smaller ones in wintering flocks of other Canada Geese *B. c. interior*. We observed associations of marked birds that were banded together and likely represented families. However, associations were seen at a lower rate than would have been expected, using unpublished data, if most families were still intact. If Cackling Goose families had been intact at Ugashik Bay, we should have observed a more even distribution of outcomes of aggressive interactions between males and females (Table 3) owing to the association of females with other family members. The disparity between males and females in the outcomes of aggressive interactions suggests that members of pairs were not associated with their mates. The observations of weak family associations during autumn staging were consistent with those of Johnson and Raveling (1987) who observed similar patterns in Cackling Geese during winter. Family break-up has been reported during autumn staging on the Alaska Peninsula for another small goose, the Black Brant *B. b. nigricans* (Jones and Jones 1965), suggesting that the benefits of social bonds may not outweigh the costs of reduced feeding due to time spent in maintenance of such bonds.

Despite the importance of the autumn staging and migration period to their annual energy budget, we still have a relatively poor understanding of the biology of Cackling Geese during this period. Some energy must be stored by geese on the Alaska Peninsula but we do not know how much weight is gained prior to departure from the Yukon-Kuskokwim Delta, nor do we know whether Cackling Geese can completely compensate for low lipid stores upon arrival on the Alaska Peninsula in years when they depart the Delta early. Furthermore, we do not understand the energetic implications of variable weather conditions during departure of geese from the Alaska Peninsula. Do geese depart the Alaska Peninsula in some years without the benefit of favourable winds, and if so, how does this affect the energetic cost of migration? Answers to these questions are important for the effective management of Cackling Geese.

The population of Cackling Geese is presently at about 15% of historic levels (O'Neill 1979; Raveling 1984). It is apparent that Ugashik Bay and Cinder River are especially important to Cackling Geese, particularly those in younger age classes. These two areas have only minimal protection and are unique along the Alaska Peninsula (R. Gill pers. comm.). Given the precarious condition of the population and the very restricted nature of its autumn staging area, steps should be taken to ensure that these areas receive sufficient protection while biologists are gaining a better understanding of their importance.

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Summary

Cackling Canada Geese *Branta canadensis minima* undergo a long (2,800 km) migration between their autumn staging areas on the Alaska Peninsula and wintering areas in Oregon and California. Adults and young lost an average of 543 g during this migratory flight. Weight gains between fledging and autumn migration are essential for the successful completion of the flight. Autumn staging is important for the acquisition or maintenance of energy stores, particularly for young of the year, as evidenced by the intense feeding of this age class at Ugashik Bay. Factors associated with the arrival and departure of Cackling Geese at Ugashik Bay are presently unknown.

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THE CENTRAL, IMPERIAL, AND COACHELLA VALLEYS OF CALIFORNIA

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Wetlands in California historically have hosted one of the largest concentrations of wintering waterfowl in the world. In the mid-1800s, an estimated 2 million ha of wetlands were present in California, and early explorers reported vast concentrations of waterfowl and other marsh and shore birds (California Department of Fish and Game 1983). As recently as the 1970s, an estimated 10-12 million ducks, geese, and swans wintered in, or migrated through, California (U.S. Fish and Wildlife Service 1978).

Wetlands in California occurred primarily in the Central Valley (Fig. 1), as did most waterfowl. Other significant waterfowl habitat was present in the Modoc Plateau, Klamath Basin, Big Valley, Honey Lake, Surprise Valley, coastal salt marshes (particularly Humboldt and San Francisco Bays), Owens Valley, Colorado River drainage, and the Imperial and Coachella valleys.

More than 95% of the historic wetland area in California has been destroyed or modified (Gilmer et al. 1982). Of the 115,000 ha of wetlands that remain in the Central Valley (U.S. Fish and Wildlife Service 1987*a*; Fig. 1), two-thirds are privately owned and managed for duck hunting; the remaining one-third is divided between state and federal ownership and managed by the California Department of Fish and Game (CDFG) as wildlife management areas (WMA) or by the U.S. Fish and Wildlife Service (USFWS) as national wildlife refuges (NWR) (Gilmer et al. 1982). Most of these wetlands are intensively managed; the cost for management may exceed that for any other wetland area in North America.

The purpose of this paper is to review existing information on the management of wetlands for waterfowl within the Central, Imperial, and Coachella valleys of California. These areas contain the majority of wetlands and wintering waterfowl in California. We describe historical and present wetlands; the evolution of management goals and strategies; current management goals relative to the nutritional and social requirements of waterfowl; and economic, political, and physical problems impeding management. Finally, we suggest needs for future research and information.

HABITAT CHARACTERISTICS

The Central Valley of California averages 64 km wide by 644 km long and is comprised of 2 lesser valleys (Sacramento in the north, San Joaquin in the south) and a delta where the two drainages meet (the Sacramento-San Joaquin River Delta [referred to as the Delta], Fig. 1). The Imperial and Coachella valleys adjoin the Salton Sea in southern California on the south and north, respectively (Fig. 1). The Central, Imperial, and Coachella valleys stretch over 7 degrees latitude and encompass a great diversity of geology, physiognomy, and climate. Because of this diversity, hydrology and plant com-

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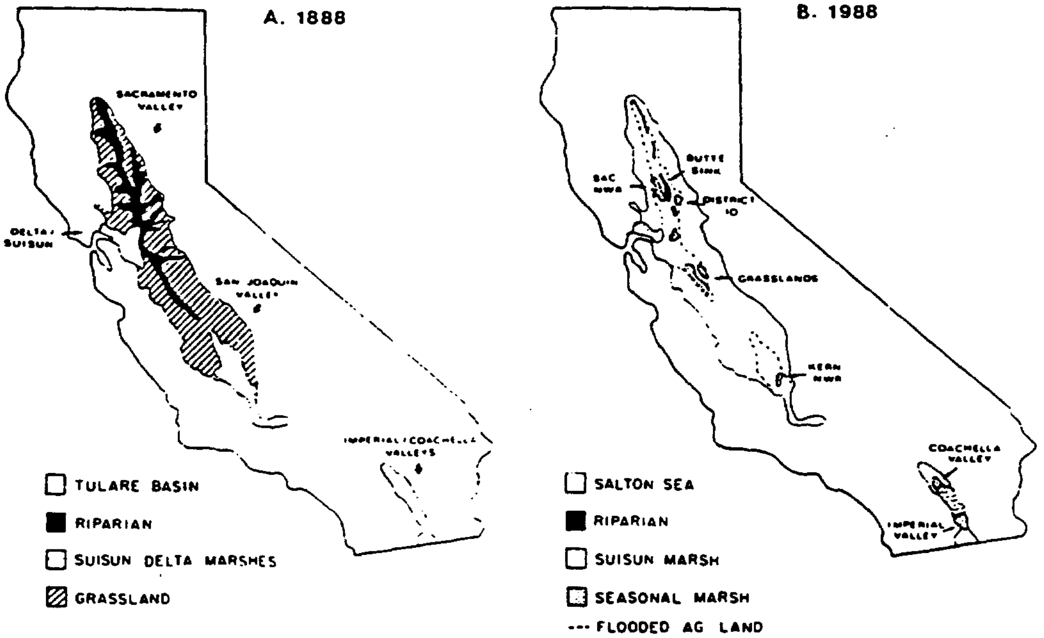

Fig. 1. Valleys of California and the distribution of historic (A) and current (B) wetlands and grasslands. Adapted from Roberts et al. (1977), U.S. Fish and Wildlife Service (1978), Madrone Associates (1980), and Barry (1981).

munities vary regionally and impose different constraints on wetland management. Hence, this paper describes characteristics of, and discusses management activities within, each region separately (i.e., Sacramento Valley, San Joaquin Valley, Sacramento-San Joaquin River Delta and Suisun Marsh, Imperial and Coachella valleys).

Sacramento Valley

The climate of the Sacramento Valley is typically mediterranean with cool, wet winters and hot, dry summers. Average annual rainfall is 50.8 cm, falling mostly between November and February (U.S. Department of Commerce 1986). Temperatures average 5 C in January and 23 C in July, the coldest and hottest months, respectively. Annually, there are <15 days of below-freezing temperatures.

The Sacramento Valley is drained by the Sacramento River and its tributaries and is bounded by the Klamath Mountain Range to the north, the Sierra Nevada to the east, and the Coast Range to the west. Peak runoff and discharges down the Sacramento River occur in March (Kahrl 1979). With the exception of the lower reaches of the Mississippi River and certain areas of the Columbia and Ohio rivers, flood waters of the Sacramento River are greater than any other river in the United States (U.S.) (Scott and Marquiss 1984).

Historically, many small creeks and sloughs were braided throughout the Sacramento Valley floor. Some creeks ended in lower depressed "sinks" and did not join the main network of the Sacramento River except during floods (Thompson 1961, Scott and Marquiss 1984). Sedimentation and scouring associated with frequent flooding created mosaics of natural levees, abandoned channels, sinks, lowland swamps, and hummocks over the otherwise relatively flat floodplains (Lapham et al. 1909, Keller 1977, Scott and Marquiss 1984). The extent of these floodplains varied

Table 1. Area (ha) of wetland habitat (percentage of wetland area in parentheses) managed for permanently flooded-summer water (PSW), seasonally flooded-tule (SF-T), seasonally flooded moist soil (SF-MS), watergrass (*Echinochloa* spp.) (WG), riparian (RIP), and upland (UP) habitat types on private duck clubs and public waterfowl areas in California during 1986-87.

Habitat type	Sacramento[a] Valley		San Joaquin[b] Valley		Imperial and Coachella valleys[c]		Delta and Suisun Marsh[d]	
	Private	Public	Private	Public	Private	Public	Private	Public
PSW	1,296 (5.4)	725 (9.3)	2,512 (12.9)	209 (4.4)	553 (28.8)	324 (18.4)	4,212 (24.5)	1,843 (34.1)[e]
SF-T	11,077 (45.8)	3,931 (50.5)	5,470 (28.2)	1,306 (27.3)	526 (27.4)	381 (21.6)	4,900 (28.5)	1,620 (30.0)
SF-MS	8,505 (35.1)	2,204 (28.3)	11,321 (58.2)	2,618 (54.6)	810 (42.1)	389 (22.1)	7,006 (40.8)	1,742 (32.2)
WG	2,268 (9.4)	908 (11.7)	122 (0.6)	243 (5.1)	34 (1.8)	666 (37.8)	101 (0.6)	61 (1.1)
RIP	1,053 (4.4)	16 (0.2)	20 (0.1)	415 8.7)	2,005[f]	111[f]	972 (5.7)	134 (2.5)
UP	1,822	2,754	7,554	2,779	526	676	2,714	1,215

[a] Data adapted from Sacramento Valley Waterfowl Habitat Management Committee 1984; Sacramento NWR Complex unpublished reports; Heitmeyer, unpublished data.

[b] Only west grasslands. Data adapted from 1979 Soil Conservation Service wetland vegetative survey; unpublished California Dep. Fish and Game (CDFG) reports provided by J. Beam; and U.S. Fish and Wildlife Service (USFWS) records supplied by G. Zahm.

[c] Data adapted from Fredrickson (1980); CDFG aerial survey estimates, Oct-Mar 1984-87; USFWS records supplied by G. Kramer; CDFG estimates provided by B. Henry; and Imperial Irrigation District estimates provided by C. Holmes.

[d] Combined Delta Suisun area. Data for the Suisun Marsh from Miller et al. (1975) with adjustments provided by F. Wernett. Data for the Delta provided by F. Wernett.

[e] Primarily on Sherman Island WMA.

[f] Mostly salt cedar tamarisk (*Tamarix pentandra*).

from a few hundred meters to several kilometers wide (Thompson 1961, Katibah 1984).

The extent of wetlands in the Sacramento Valley in the mid-1800s is not entirely known, but probably exceeded 600,000 ha (Fig. 1). Riparian forests and semipermanently flooded tule marshes composed >75% of these wetlands (Thompson 1961, Katibah 1984). At present only 32,000 ha of wetlands remain; these are dominated by semipermanently flooded tule marshes (Table 1). Most wetlands have been drained for agriculture or have been altered by land leveling and construction of levees, removal of riparian forests, and controlled water regimes. Approximately 65%, 26%, and 9% of remaining wetlands are in private, federal, and state ownership, respectively.

Riparian forests formerly were present adjacent to rivers and creeks. Sloughs, oxbows, and meander scars were interspersed within riparian forests. Riparian forests were flooded by river overflow waters during periods of increased precipitation and runoff in winter, and from snowmelt runoff from surrounding mountains in spring. Floods also occasionally occurred in fall (U.S. Department of Commerce 1986). As high water receded in late spring and summer, water drained from riparian forests but became trapped in low depressions behind natural levees and created permanently or semipermanently flooded marshes.

Plant communities in permanently and semipermanently flooded wetlands were dominated by dense emergents, whereas those in seasonally and ephemerally flooded wetlands were dominated by moist-soil annual and perennial plants (Table 2). Grassland communities were located on alkaline soils at higher elevations of seasonal wetlands and supported extensive saltgrass flats dotted with vernal pools (Crampton 1976). These grasslands often were flooded by late winter and spring rains and occasionally were flooded from river overflows in wet winters.

Presently, 162,000 ha of agricultural lands in the Sacramento Valley are subject to flooding from river overflows and local runoff during wet winters. More than 32,000 ha of harvested rice fields are intentionally flooded for waterfowl hunting during fall and winter (California Department of Fish and Game 1979). Also, 2 major flood-control bypasses adjoin the Sacramento River and flood up

Table 2. Plant species commonly occurring in wetland habitat types in the Sacramento Valley (SAC), San Joaquin Valley (SJ), Suisun Marsh (SU), and Imperial-Coachella valleys (IC)[a].

Habitat type[b] and common species	Region SAC	 SJ	 SU	 IC
Riparian Forest				
Boxelder (*Acer negundo*)	+	+		
Alder (*Alnus* spp.)	+			
Buttonwillow (*Cephalanthus occidentalis*)	+	+		
Dogwoods (*Cornus* spp.)	+			
Oregon ash (*Fraxinus latifolia*)	+			
Fremont's cottonwood (*Populus Fremontii*)	+	+		
California sycamore (*Platanus racemosa*)	+	+		
Valley oak (*Quercus lobata*)	+	+		
Poison oak (*Rhus diversiloba*)	+			
Wildrose (*Rosa californica*)	+	+		
Blackberries (*Rubus* spp.)	+	+		
Willows (*Salix* spp.)	+	+		
Elderberry (*Sambucus* spp.)	+			
Salt cedar tamarisk				+
Wild grape (*Vitis californica*)	+	+		
Permanent/summer marsh				
Water fern (*Azolla* spp.)	+	+		
Water hyssops (*Bacopa* spp.)	+	+		
Muskgrass (*Chara* spp.)		+	+	+
Marsh pennywort (*Hydrocotyle* spp.)	+			
Water primrose (*Jussiaea californica*)	+	+	+	+
Duckweeds (*Lemna* spp.)	+	+		
Frog fruit (*Lippia* spp.)	+	+		
Water-horehound (*Lycopus* spp.)	+	+		
Marsilea (*Marsilea mucronata*)	+			
Milfoils (*Myriophyllum* spp.)	+			
Water nymphs (*Najas* spp.)	+	+		
Common reed (*Phragmites communis*)			+	
Pond weeds (*Potamogeton* spp.)	+	+		+
Widgeon grass (*Ruppia maritima*)			+	+
Arrowheads (*Sagittaria* spp.)	+	+		
Tule bulrush (*Scirpus acutus*)	+	+	+	
California bulrush (*Scirpus californica*)			+	
Olney bulrush (*Scirpus olneyi*)			+	
Alkali bulrush (*Scirpus robustus*)	+	+		+
Cattails (*Typha* spp.)	+	+	+	+
Vervains (*Verbena* spp.)	+	+		
Seasonal Marsh				
Horned pondweed (*Zannichellia palustris*)		+	+	+
Iodine bush (*Allenrolfea occidentalis*)		+		
Ammania (*Ammania* spp.)	+	+		
Fathen (*Atriplex patula*)			+	
Carex sedges (*Carex* spp.)	+	+	+	+
Centromedia (*Centromedia pungens*)		+		
Brass buttons (*Cotula coronopifolia*)			+	
Pricklegrass (*Crypsis niliaca*)	+	+	+	+
Bermuda grass (*Cynodon dactylon*)	+	+	+	+
Nutgrasses (*Cyperus* spp.)	+	+	+	+
Saltgrass (*Distichilis spicata*)	+	+	+	+
Watergrass	+	+	+	+
Spikerushes (*Eleocharis* spp.)	+	+	+	+
Gumplant (*Grindelia* spp.)		+		
Swamp timothy (*Heleochloa schenoides*)	+	+	+	+
Rushes (*Juncus* spp.)	+	+	+	+
Baltic rush (*Juncus balticus*)			+	+
Smartweeds (*Polygonum* spp.)	+	+	+	+
Docks (*Rumex* spp.)	+	+	+	+
Tule bulrush	+	+	+	+
Alkali bulrush	+	+	+	+
Alkali mallow (*Sida hederacea*)	+	+		
Cattails	+	+	+	+
Cocklebur (*Xanthium* spp.)	+	+	+	+
Grasslands/vernal pools				
Allocarya (*Allocarya* spp.)	+	+		
Soft chess (*Bromus mollis*)	+	+		
Carex sedges	+	+		
Pricklegrass	+	+		
Saltgrass	+	+		
Downingia (*Downingia* spp.)	+	+		
Frankenia (*Frankenia grandifolia*)	+	+		
Swamp timothy (*Heleocloa schenoides*)	+	+		

[a] Plant nomenclature follows Mason (1957) and Munz and Keck (1975). Data are from Jepson (1893), Lapham (1909), Bryant (1914), Strahorn et al. (1911), Hoover (1935), Crampton (1959, 1976), Thompson (1961), Arkley (1962), Mall (1969), Gill and Buckman (1974), Miller et al. (1975), Conard et al. (1977), Keller (1977), MacDonald (1977), Madrone Associates (1980), Zedler et al. (1982), Josselyn (1983), and Katibah (1984).

[b] Riparian forests are habitats dominated by woody growth occurring immediately adjacent to natural water courses; permanent summer marsh are wetlands dominated by emergent vegetation and containing water for most, or all, of the year; seasonal marsh are wetlands dominated by short-stature annual and perennial vegetation and flooded from 1-8 months annually, typically from early fall through early spring; grassland/vernal pools are upland and ephemerally flooded depressions dominated by grasses or annual vegetation, typically flooded for < 2 months in late winter and early spring.

to 26,000 ha in an average of 3 of every 5 winters (Kahrl 1979). Lands within the bypasses are mostly farmed for rice and row crops, but idle lands, ditches, pasturelands, and some marshes are also present. Reservoirs constructed on the Sacramento River and its tributaries also provide some sanctuary habitat.

San Joaquin Valley

The climate of the San Joaquin Valley is arid; mean annual rainfall is <23 cm and occurs primarily from October-February (U.S. Department of Commerce 1986). Temperatures average 6 C in January and 25 C in July. Typically, there are few, if any, days with below-freezing temperatures.

The San Joaquin Valley is bounded by the Delta to the north, the Tehachapi Mountains to the south, the Sierra Nevada to the east, and the Coast Range to the west. It is divided into 2 distinct basins: the San Joaquin (northern two-thirds) and the Tulare (southern one-third). The San Joaquin River and its tributaries drain the San Joaquin Basin. The Tulare Basin, is separated from the San Joaquin Basin by an elevational uplift created by the merging alluvial fans of the Kings River and the Los Gatos Creek. Historically, waters from tributary rivers flowed into the Tulare Basin, which had no outlet to the sea. During long-term "wet cycles," Tulare Lake in the Tulare Basin filled to a depth of 27 m and diverted water from the Kings River and the Tulare Basin into the San Joaquin River.

Peak water flows and associated river overflows are lower (Fig. 2) and later in the San Joaquin Valley than in the Sacramento Valley (Kahrl 1979). Consequently, deposition of sediments and formation of natural levees and floodplains were less extensive (<81,000 ha) in the San Joaquin Valley (Strahorn et al. 1914, Arkley 1962), and riparian wetlands were generally confined to narrow strips immediately adjacent to tributaries (Katibah 1984).

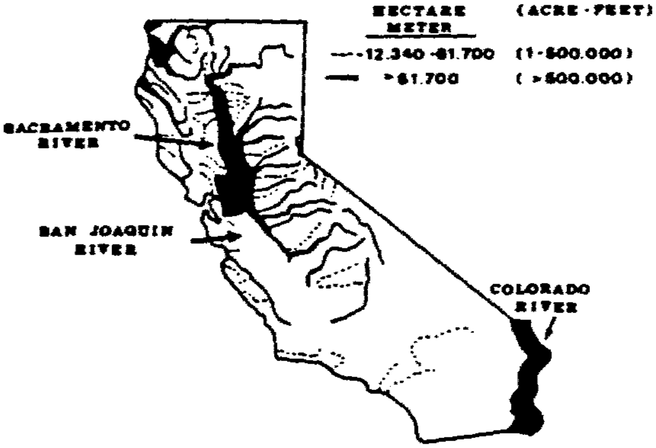

Fig. 2. Average annual streamflows in major streams and rivers in California (from Warner and Hendrix 1985).

Although water flows were low in the San Joaquin Basin, when flooding did occur, waters easily breached low natural levees and spread over extensive areas of the relatively flat valley floor. Depressions behind natural levees or in old meander scars held water until early summer and supported dense stands of cattail and tules (Table 2). Higher elevations usually became flooded only for short periods during late winter or spring, and historically supported a variety of herbaceous plants, sedges, and grasses tolerant of the highly alkaline soils (Table 1, Wester 1981). Vernal pools were also common at higher elevations and were usually inundated from December-February (Crampton 1959, Holland and Griggs 1976). The historical extent of wetlands in the San Joaquin Basin probably exceeded 400,000 ha, most of which was seasonally flooded grasslands (Fig. 1).

Wetlands within the Tulare Basin were historically confined to Tulare, Kern, Goose, and Buena Vista lakes, which covered 253,000 ha and were flooded for most of the year, except during extreme drought (U.S. Fish and Wildlife Service 1978). These lakes received most of their annual water input in spring from snowmelt from the Sierra Nevada. Following winters with heavy snows, the basins of all of these lakes were connected by sloughs. Derby (in Dasmann 1966:154-55) described these lakes in 1849-50 as large bodies of shallow open water surrounded by wide bands of dense tule marsh, sometimes up to 16 km wide. Seasonally flooded grasslands were also present on the south side of Tulare Lake.

At present, <51,000 ha of wetlands remain in the San Joaquin Valley (Table 1); most of these are seasonally flooded ponds in the San Joaquin Basin (Grassland Water District 1987). In late spring and summer, evapotranspiration can be as high as 1.5 cm per day. Where a wetland is supplied with water during summer, the transition zone between marsh and desert is usually only a few meters.

The majority of the once vast marshes of the Tulare Basin have been drained and converted to agricultural croplands (U.S. Fish and Wildlife Service 1978). Crops, especially barley, in the Tulare Basin often are flooded for a few weeks following harvest and prior to planting another crop (referred to as preirrigation); this shallow flooding provides some habitat for ducks in early fall (Jones and Stokes Associates 1988). Ponds used for evaporation of irrigation drain water are also present. Lakes on tributaries of the San Joaquin River provide some waterfowl habitat, mostly used as loafing areas. Ownership of San Joaquin Valley wetlands is 63% private, 25% federal, and 13% state.

Sacramento-San Joaquin River Delta and Suisun Marsh

Temperatures in the Delta and Suisun Marsh average 8 C in January and 22 C in July. Mean precipitation is 20 cm and occurs mostly between November and March (U.S. Department of Commerce 1986).

Delta.— The delta is an inland 284,000-ha network of sloughs and islands that formed at the confluence of the Sacramento, San Joaquin, Mokelumne, and Consumnes rivers. Historically, the delta was comprised of nearly 100 islands separated by a labyrinth of sloughs and channels. Tidal freshwater marshes covered most of the islands (Thompson 1957, Atwater 1979, Madrone Associates 1980). These marshes ranged from dense tule marshes immediately behind alluvial levees to riparian forests at higher inland elevations (Madrone Associates 1980). Most lands in the delta were close to mean sea level (MSL), with highest points only 4.5 m above MSL. When flood and runoff waters reached the delta from December-May, the entire area was inundated (Basye 1981).

Of the original 284,000 ha of wetlands in the delta, only 7,290 ha remain (Fig. 1). Beginning as early as 1852, levees were constructed, wetlands drained, and lands farmed on delta islands (Thompson 1957). Currently, all islands except Frank's Tract and portions of Mildrid and Sherman islands are protected by large levees; the elevation of many of the islands is >4.5 m below MSL. Lands in the delta are farmed for corn, wheat, rice, safflower, and milo (Smith 1979). About 8,100 ha of these croplands are flooded each winter for waterfowl hunting, or to leach soil salts, and to provide some seasonal wetland habitat (California Department of Fish and Game 1979). Levee breaks and floods also have inundated some islands in recent years and created additional temporary wetland habitat.

Suisun Marsh.—The Suisun Marsh is an estuarine wetland created 6,000-7,000 BP when sea levels rose and expanded into San Pablo and Suisun bays (Atwater et al. 1977, Josselyn 1983). The Suisun Marsh was then comprised of 12 tidally flooded islands and inland areas, interwoven by numerous sloughs and the Sacramento River.

Historically, most of the Suisun Marsh was brackish (Josselyn 1983). A gradient of tidal influence, salinities, elevations, and marsh vegetation existed from Suisun Bay inland to the surrounding hills. Below mean low-tide level, vegetation was dominated by California bulrush.

Between the mean low-tide and mean high-water levels, a mixture of cattails, California bulrush, tule bulrush, Olney bulrush, and alkali bulrush was present. Above the high-water level, a varied group of halophytes occurred. Where salinities were high, pickleweed, saltgrass, fathen, and gumplant were found. In areas where salinity was lower, brass buttons and baltic rush were common.

Currently, tide gates and levees protect most of the Suisun Marsh from flooding. Salinities have gradually increased in the marsh as waters have been diverted from the Sacramento and San Joaquin rivers (Mall 1969). Attempts to farm many of the diked lands in the Suisun Marsh were made in the 1920s-50s; however, high soil and water salinities precluded most crop production, and lands now are maintained as wetlands and managed as duck clubs. Vegetation in the Suisun Marsh is presently dominated by relatively salt-tolerant robust emergents (Table 2). Pickleweed, brass buttons, and fathen occur near high tide level, and saltgrass, baltic rush, and common reed occur above the high tide level.

The current wetland area in the Suisun Marsh (22,000 ha) is only slightly reduced from the historic area (24,300 ha) (U.S. Fish and Wildlife Service 1978). Urban expansion and agricultural development destroyed some marsh lands, but creation of private duck clubs has been primarily responsible for saving these wetlands. The Suisun Marsh Protection Act of 1977 and the 1987 "Suisun Marsh Preservation Agreement" currently provide adequate water quality in tidal sloughs. This water quality is maintained by large salinity control gates at the east end of Montezuma Slough—the principal water course into the marsh. Ownership of Suisun Marsh wetlands is 84% private and 16% state.

Imperial and Coachella Valleys

The climate of the Imperial and Coachella valleys is arid. Average annual rainfall is <5 cm and temperatures average 10 C in January and 32 C in July.

The Imperial and Coachella valleys and the Cahuilla Basin (the present Salton Sea) were created along the San Andreas fault and represented an extension of the Gulf of California (Carpelan 1961). During the Pleistocene, the Colorado River created a fanlike delta separating the valleys from the ocean, and as the river flowed over the almost flat delta, it sometimes flowed southward into the Gulf of California and at other times northward into the Imperial and Coachella valleys. When northward flows occurred, a large, inland freshwater lake (the Salton Sink) was created. At other times, the extremely arid climate of the region dried existing wetlands and maintained a desert ecosystem.

The last known historical flow of the Colorado River into the Imperial and Coachella valleys occurred in 1891 and created a lake of 40,000 ha (Carpelan 1961). When this lake water evaporated, a short-lived inland salt marsh was created. It subsequently dried, leaving behind huge salt deposits. In 1901, Colorado River water was diverted into the Imperial Valley through an old river channel to supply irrigation water. In 1905, this diversion faltered and water from the Colorado River flowed into the Imperial Valley, creating the present Salton Sea.

Since 1907, waters of the Colorado River that enter Salton Sea have been controlled by an elaborate irrigation system originating near Yuma, Arizona. In the early 1900s, the permanent water in the Salton Sea and scattered wetlands on the Colorado River Delta attracted migrating and wintering waterfowl to the Imperial and Coachella valleys for longer periods than in previous years (Fredrickson 1980). This increased waterfowl population subsequently encouraged private groups to flood lands and create freshwater ponds for waterfowl hunting. These artificial marshes, which total 3,683 ha at present (Table 1), created "new" wetlands in an otherwise dry, desert environment. Private duck clubs compose 52%, and public lands compose 48%, of these wetlands. Vegetation present in these "new" wetlands consists mostly of saltgrass, alkali bulrush, swamp timothy, bermuda grass, smartweeds, and dock (Table 2). In areas where water is fresher and more permanent, cattail and common reed occur. Levees are often overgrown with salt cedar tamarisk and arrow-weed (*Pluchea sericea*).

HABITAT IMPORTANCE RELATIVE TO WATERFOWL REQUIREMENTS

Abundance, Chronology, and Distribution of Waterfowl

Some waterfowl are present in the Central, Imperial, and Coachella valleys year-round. Mallards (*Anas platyrhynchos*) are the most common breeding waterfowl. Other species that commonly nest in California include Great Basin Canada geese (*Branta canadensis moffitti*), cinnamon teal (*A. cyanoptera*), gadwall (*A. strepera*), northern shoveler (*A. clypeata*), wood duck (*Aix sponsa*), redhead (*Aythya americana*), ruddy duck (*Oxyura jamaicensis*) and, in some locations, northern pintail (*A. acuta*) and American wigeon (*A. americana*). Postbreeding dispersals of breeding adults and young concentrate several hundred thousand ducks, especially mallards, in the Klamath Basin and Sacramento Valley in late summer and early fall.

Waterfowl concentrations are greatest in California during fall and winter when migrants from northern latitudes join locally breeding or produced birds (Kozlik 1975, Bellrose 1980). The Central, Imperial, and Coachella valleys wintered 3.5 million ducks, and 0.5 million geese and swans, annually during 1978-87 (Table 3). This represents >60% of all waterfowl (excluding sea ducks) wintering in the Pacific Flyway, and about 20% of those wintering in the entire U.S. Of special importance, California wintered >20% of all mallards, wigeon, green-winged teal, shovelers, canvasbacks, and ruddy ducks; >30% of all lesser snow geese and tundra swans; >50% of all pintails, white-fronted geese, and Ross' geese; >80% of all cackling and Great Basin Canada geese; and 100% of the Aleutian Canada and tule geese in the U.S.

Migrants begin arriving in the Central Valley in early August (Bellrose 1980). Early migrants are mainly adult male pintails and most concentrate in the Sacramento Valley (also, formerly in the Tulare Basin) (Miller 1985). By October, large numbers of female and young pintails, and all sexes and ages of wigeon, shovelers, gadwalls, green-winged teal, and ruddy ducks have arrived. In contrast, most locally nesting cinnamon teal have migrated south into the Imperial and Coachella valleys and Mexico by mid-October. Tundra swans and most geese arrive in the Sacramento Valley by mid-November; however, many may remain in the Klamath Basin in some years. White-fronted geese arrive earlier than other geese and swans. Smaller numbers of ring-necked ducks, buffleheads, redheads, and canvasbacks also arrive in November. Peak numbers of most species occur in mid-December.

Most mallards, tule geese, snow geese, large Canada geese, wood ducks, and wigeons winter in the Sacramento Valley; but most shovelers, green-winged teal, and gadwalls winter in the San Joaquin Valley (Table 3). Ross' geese, cackling Canada geese, Aleutian Canada geese, tundra swans, and white-fronted geese traditionally begin the winter in the Sacramento Valley, but by late winter, most have moved to the Delta or the San Joaquin Valley (Rienecker 1965, McLandress 1979, Woolington et al. 1979). Dabbling ducks, especially pintails, move

Table 3. Mean number of waterfowl counted in the Central, Imperial, and Coachella valleys of California during U.S. Fish and Wildlife Service mid-winter inventories, 1978-87.

	Region					% of Pacific Flyway 1977-86 Ave
Species	Sacramento Valley	San Joaquin Valley	Suisun Marsh	Delta	Imperial Coachella valleys	
Mallard	314.712	30.438	15.221	4.667	389	24
Gadwall	11.698	23.137	602	25	465	83
American wigeon	403.038	10.913	9.318	847	5.623	64
Green-winged teal (*Anas crecca*)	16.336	90.479	6.913	961	3.092	89
Cinnamon teal	131	2.541	42	2	242	74
Northern shoveler	122.557	209.142	28.456	3.022	12.670	77
Northern pintail	1.429.698	238.191	60.347	141.190	14.091	79
Wood duck	1.062	15				76
Redhead	84	87	81		336	3
Canvasback (*Aythya valisineria*)	11.735	2.036	3.446	7.065	1.691	39
Scaup (*A. affinis* and *A. marila*)	217	368	1.711	960	1.760	4
Ring-necked Duck (*A. collaris*)	3.896	717	404	85	110	56
Bufflehead (*Bucephala albeola*)	99	173	54	81	49	1
Ruddy Duck	16.361	15.985	2.558	2.184	16.269	49
Canada geese[a]	3.807	4.802	586	448	3.296	[b]
White-fronted geese (*Anser albifrons*)	20.092	4.884	6.491	20.768		83
Snow and Ross' geese (*Chen caerulscens* and *C. rossii*)	304.310	35.397	82	19.278	16.835	86
Cackling Canada geese (*Branta canadensis minima*)	10.792	4.128	2.520	830		80
Aleutian Canada geese (*B. c. leucopareia*)	360	1.035	72	59		100
Tundra swan (*Cygnus columbianus*)	21.283	357	4	19.999		66

[a] Mostly Great Basin Canada geese.

[b] Percentages of Pacific Flyway totals are not calculated because of varying populations present.

among valley areas during winter (Rienecker 1976, 1987); movements are erratic depending on disturbance, food availability, and wetland conditions.

Shifts in the winter distribution of many species have probably occurred since the late-1800s in response to habitat and land-use changes. For example, market hunting records indicate that large numbers of snow and Ross' geese were present in wetlands surrounding San Francisco Bay in the late 1800s (Stine 1980). With the large increase in small-grain production in the Sacramento Valley and major losses of coastal wetlands, snow geese are now nearly absent from San Francisco Bay and Suisun marshes, but abundant in the Sacramento Valley. The abundance of small grains, and habitat loss in other areas, have probably also attracted and held larger numbers of pintails, mallards, green-winged teal, wigeons, and small Canada geese in the Sacramento Valley in recent years.

Pintails are the first ducks to begin migrating out of the Central Valley in spring; major movements northward begin in mid-February (Bellrose 1980). By March, most pintails have left, and large numbers of wigeons and geese have migrated northward into the Klamath Basin, the Modoc Plateau, and the Willamette Valley of Oregon. By mid-April, most shovelers, gadwalls, ruddy ducks, green-winged teal, and buffleheads have migrated northward, whereas cinnamon teal have returned to the Central Valley.

Resource Requirements and Availability

Waterfowl undergo several biologically important and nutritionally costly processes throughout the year (e.g., molt, migration, pairing, nesting, and brood rearing). These physiologic and behavioral events require different quantities and qualities of nutrients, and impose different social and behavioral constraints on individuals (e.g., Weller 1975, Raveling 1979, Heitmeyer 1985, McKinney 1986, Fredrickson and Heitmeyer 1988). Species meet these requirements by varying habitat use, food consumption, flocking structures, and daily activities mediated by morphological and behavioral adaptations. The chronology and number of annual events that occur in California vary among species, and within species by sex and age, and in relation to habitat and climatic conditions (Heitmeyer 1985, 1987, Miller 1986).

Although most waterfowl have similar requirements during each annual event (e.g., all species have increased protein requirements during egg laying and molt), strategies exhibited by species to meet these requirements are different. Historically, the abundance and wide diversity of wetland habitat types present in California provided large quantities of foods and habitats necessary to support large numbers of waterfowl throughout the year.

The resources needed by waterfowl during annual events in California are provided in different habitat types (Table 4). Permanently and semipermanently flooded habitats such as tule marshes and backwater sloughs provide tubers from plants such as arrowheads, abundant floating and submergent plants, aquatic insects and their larvae, snails, and zooplankton (Usinger 1956, Josselyn 1983, Reid 1985, Murkin and Kadlec 1986). Permanently flooded habitats provide dense emergent cover used for protection by wintering birds from winds, rains, and predators. These habitats also provide nest sites for over-water nesters such as redheads, and escape cover for broods and flightless adults.

Seasonally flooded marshes range from those that support an interspersion of scattered cattails and tules (referred to as tule mix habitats) to those that primarily support annual plants such as watergrass, swamp timothy, pricklegrass, alkali bulrush, and smartweeds (collectively referred to as moist-soil habitats). Seasonally flooded habitats usually provide abundant seeds, tubers, and aquatic insects and their larvae (Table 4). Terrestrial invertebrates also are available when wetlands are first inundated. Abundance, biomass, and types of invertebrates in seasonal marshes depend on plant species composition, length of flooding, detrital material, and decomposition rates of dominant plants (Grodhaus 1980, Murkin et al. 1982, Nelson and Kadlec 1984, Reid 1985, Murkin and Kadlec 1986). Stems and leaves of sedges, bulrushes, and grasses provide forage for geese and wigeons. Dense stands of annual wetland plants also provide nest sites to ducks during drawdown stages (McLandress and Yarris 1987, McLandress et al. 1987).

Uplands, sedge meadows, and vernal pools provide forage for geese and wigeons, and when flooded, these uplands and vernal pools also provide seeds, terrestrial insects, earthworms, and spiders (Alexander 1976, Holland and Jain 1977). Uplands also provide nest sites for many waterfowl, especially where spring vegetation is dense (McLandress and Yarris 1987).

Riparian forests provide acorns, samaras, berries, moist-soil seeds, benthic crustaceans, and fingernail clams (*Pisidium* spp.) (Table 4, Batema et al. 1985, White 1985, Fredrickson and Heitmeyer 1988). Riparian forests also supply nesting and roost sites to wood ducks (Parr et al. 1979, Bellrose 1980), and courtship and pairing habitat for mallards and wood ducks (Armbruster 1982, Heitmeyer 1985).

Croplands supply residual and waste grains that are especially attractive to

Table 4. Resources provided in various wetland habitat types present in California. Number of plus signs denotes relative quantities of available resources.

Habitat[a]	Small grains	Moist-soil seeds	Acorns	Tubers	Graze	Aquatic plants	Invertebrates	Thermal cover	Nest sites
PSW				+	+	+++	++	+++	+[b]
Seasonal									
Tule mix		++		++	+	+	++	+++	+[b]
Watergrass		+++		+			+	++	
Moist-soil		+++		++	+	+	+++	+	+[c]
Alkali bulrush		++		++	+		+	++	+[c]
Pickleweed		+			+		++		
Uplands		+[d]		+	+++		+		+++
Riparian		+	+++	+		+	+++	++	+[c]
Cropland	+++	+			+		+		+

[a] PSW = permanently flooded and summer water; Seasonal = seasonally flooded and dominated by cattails and tules (Tule Mix), watergrass, moist-soil plants, alkali bulrush, and pickleweed.

[b] For species that nest over water.

[c] If water is not present.

[d] When flooded.

dabbling ducks when shallowly flooded. Some moist-soil "weeds" (e.g., watergrass) also commonly grow in croplands, especially in rice. Common invertebrates in rice fields include adult and larval insects (especially Chironomidae) and spiders (Araneae) (Darby 1962). Flooded rice fields are used by adult mallards during prelaying and laying periods, and by newly hatched broods. In early spring, crops such as winter wheat, barley, and alfalfa (*Medicago sativa*) provide forage for geese and wigeons, and, later in spring, they provide nesting sites to locally nesting ducks.

The existence requirements of waterfowl wintering in the Central, Imperial, and Coachella valleys of California can be estimated and compared to estimates of food provided in existing wetlands. An average of 75 million use-days by geese and swans and 500 million use-days by ducks occurs from September through March in the Central, Imperial, and Coachella valleys (calculated from chronology and survey data in Table 3, Bellrose 1980). The basal metabolic energy requirements (BMR) (calculated using the equation of Aschoff and Pohl 1970) of these waterfowl are 35.6×10^9 kcal for geese and swans and 100×10^9 kcal for ducks. If natural foods have an apparent metabolizable energy of 2.5-3.5 kcal/g (Miller 1987), then an average of 237 kg of available food/ha must be provided on the 120,000 ha of wetlands (excluding rice areas) remaining in the valleys of California just to satisfy requirements. Productive processes such as molt, migration, and reproduction of waterfowl are usually several times the cost of BMR, however, and when daily flight time is also considered, the food production on wetlands necessary to support current wintering and local breeding populations is estimated at 700-950 kg/ha. We emphasize that waterfowl numbers were much greater in years previous to the last 10; therefore, food requirements were also greater during these earlier years.

Impacts of Habitat Alteration

Several examples illustrate the impact of habitat loss or alteration on waterfowl in California. First, the large reduction of permanently flooded freshwater wetlands has reduced the amount of habitat available for nesting sites for over-water nesters such as ruddy ducks and redheads. The reduction of these wetlands also has reduced cover and food for broods of all species that nest locally, and aquatic plant foods needed by breeding and wintering canvasbacks, redheads, wigeon, and gadwalls. Loss of permanent wetlands has reduced nesting attempts and local production by all waterfowl.

Second, the destruction of >95% of riparian wetlands in California has reduced habitats needed by wood ducks throughout the year and by mallards and tule geese in winter. Wood duck and tule goose numbers presently are low in California. Mallards have adapted to the loss of riparian habitats by switching to waste grains to supply high-energy foods in midwinter. Protein is available to mallards from the invertebrates found in remnant riparian areas, in seasonally flooded marshes, and in rice fields. As mallards have switched to modified habitats to acquire resources, they must compete with many other species of dabbling ducks for invertebrates in marshes, be exposed to unknown biomagnification of pesticides from invertebrates consumed in rice fields, and face possible nutrient deficiencies because small grains lack adequate protein, minerals, and vitamins. The Butte Sink (Fig. 3), which contains the largest remaining area of riparian habitat in the Central Valley, supports large numbers of mallards and wood ducks in winter. Further reduction of this habitat in the Butte Sink could be devastating for these species.

Finally, changes in water quality from increased contaminants or salinity have changed plant and invertebrate communities, and thus have directly affected waterfowl populations in several areas of California. Increases in salinity in the Suisun Marsh have resulted in lower seed production of waterfowl food plants and caused a shift in plant species composition toward more salt-tolerant species (Mall 1969). Similarly, increased contamination by natural salts has occurred in the San Joaquin, Imperial, and Coachella valleys (Fredrickson 1980, Grasslands Water District 1987). Selenium contamination in the San Joaquin Valley has reduced or contaminated invertebrates and seeds needed by wintering and breeding waterfowl and created mutational deformities in embryos (Ohlendorf et al. 1986*a*, Zahm 1986). These changes in food resources may have been partly responsible for reduced waterfowl populations in the Suisun Marsh, San Joaquin, Imperial, and Coachella valleys in recent years.

HABITAT MANAGEMENT

Historical Development

The management of wetlands for waterfowl in California has a long and varied history. We consider this management as occurring in 4 eras: (1) 1880-1935: early decline of waterfowl populations, mosquito abatement, establishment of duck clubs; (2) 1936-1960: crop depredations, establishment of refuges; (3) 1960-1980: stabilized duck populations, enhancement of food production; (4) 1980-present: decline of waterfowl populations, management of marsh complexes, enhancement of breeding efforts.

1880-1935.—Sport hunting of waterfowl first became a common activity in California in the 1840s and 1850s (DeWitt 1910, Exley 1931, Stine 1980). The first duck club in California was established in 1879 in the Suisun Marsh (McAllister 1930, Stoner 1937). Market and some sport hunting were also common in the Delta (Stine 1980), Sacramento Valley (McGowan 1961), and San Joaquin Valley (Exley 1931) in the late 1800s and early 1900s, but establishment of duck clubs and eventual management of wetlands in these areas were later than in south San Francisco Bay, Napa, and Suisun marshes.

Reductions in waterfowl numbers (apparently because of market hunting and decreased wetland habitats) were noted throughout California as early as the 1870s. One of the first game laws in California outlawed shooting of wood ducks (Grinnell and Bryant 1914), and Lake Merritt in Oakland was established

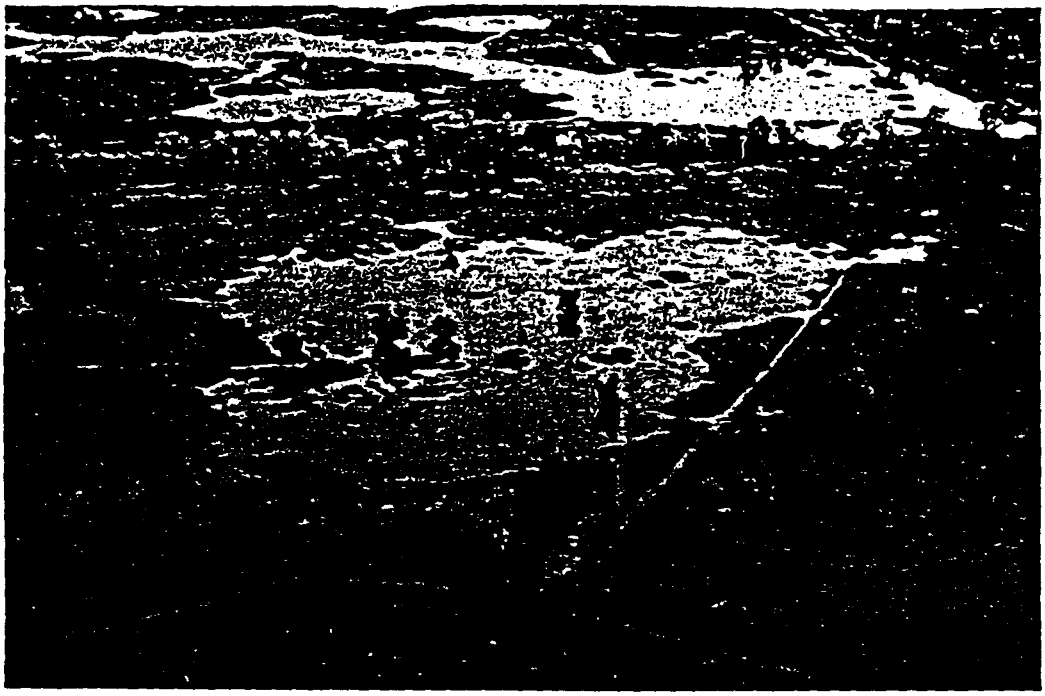

Fig. 3. Seasonally flooded emergent wetland typical on private duck clubs in the Butte Sink of the Sacramento Valley. Emergent vegetation is primarily cattail and tules; trees are mostly black willow (*Salix nigra*). Water is generally present from September through May or June.

as the first state waterfowl refuge in 1870 (Richards 1916). In 1913, the California legislature passed the Flint-Cary Law outlawing market hunting. This law was overturned in 1914, and it was not until the 1918 enactment of the Migratory Bird Treaty Act and the 1923 passage of legislation by the California legislature that it became illegal to sell wild waterfowl.

Drought in the Canadian prairies further reduced duck numbers in North America during the late 1920s and early 1930s (Farrington 1945). Wetlands continued to be drained in the 1920s, and by 1926, much of the remaining wetland habitat was in duck clubs (California Department of Fish and Game 1983). Because of concern over the lack of wetlands and sanctuaries, 4 state waterfowl refuges were purchased from 1929-31 (Table 5).

In the 1910s and 1920s, mosquitos and the diseases they carried became a concern for growing urban populations, many of which were located near historic wetlands (Elbright et al. 1916). Mosquito abatement districts became established and enforced regulations prohibiting the fluctuation of water levels in wetlands from spring through fall. Additionally, ditches were constructed to drain many wetland areas, and pesticides such as DDT were commonly used to control mosquitos.

1936-1960.— In the late 1930s and early 1940s, Canadian prairies became wet again, and waterfowl populations increased dramatically (Farrington 1945). As many as 50 million ducks and geese may have wintered in California in the 1940s (Arend 1967); however, wetland area in California had been reduced to <400,000 ha by that time. By 1945, 97,200 ha of rice were grown in California. The combination of increased waterfowl populations, decreased wetland area, shortage of ammunition during World War II, and wet weather that delayed crop harvesting

Table 5. Chronology of waterfowl habitat acquisition[a] by the U.S. Fish and Wildlife Service (NWR) and the California Department of Fish and Game (WMA) in California.

Area	Year established	Additions	Total area (ha)	Wetland area (ha)
Sacramento Valley				
Gray Lodge WMA	1931	1952-71	3.483	1.822
Sacramento NWR	1937	1971	4.371	2.491
Sutter NWR	1941	1953-56	1.049	1.011
Colusa NWR	1945	1949-53	1.636	1.040
Delevan NWR	1962		2.281	1.258
Butte Sink NWR	1980	1987	292	270
San Joaquin Valley				
Los Banos WMA	1929	1965	1.299	972
Merced NWR	1951		1.038	620
Mendota WMA	1951	1955-56	3.825	2.632
Kern NWR	1960		1.300	1.296
Volta WMA	1965		1.094	1.053
San Luis NWR	1967	1970	2.973	1.080
Kesterson NWR	1970		2.390	1.059
Imperial-Coachella Valley				
Salton Sea NWR	1930	1948	15.073	115
Imperial WMA	1931	1954	3.169	1.539
Delta-Suisun Marsh				
Joice Island WMA	1931		764	726
Grizzly Island WMA	1950		3.556	2.481
Sherman Island WMA	1965		1.256	688

[a] Ownership by fee title.

created large crop depredations by waterfowl in the Sacramento, San Joaquin, Imperial, and Coachella valleys in the 1940s. Crop damages caused by waterfowl peaked at $1.75 million during 1943 (Horn 1949, Biehn 1951). Sacramento NWR was established in 1937 to help alleviate depredations with funds from the Emergency Conservation Fund Act of 1933 and with funds from Emergency Relief Appropriations from the Department of Agriculture during 1935-38.

Waterfowl management committees recommended increased farming on refuges, leasing of farmlands in the Colusa Trough and Sutter Basin, and feeding of grains on flooded areas, especially in the Imperial and San Joaquin valleys to help alleviate crop depredations (California Department of Fish and Game 1983). Passage of the Lea Act of 1948 authorized the acquisition and development of management areas in California solely for the purpose of alleviating crop damage. Subsequently, Colusa and Sutter NWRs were purchased, and the Salton Sea NWR was enlarged. A management plan to protect waterfowl and agriculture was developed in 1950 (Gordon 1950), and shortly thereafter, the Grizzly Island and Mendota WMAs and Merced and Kern NWRs were created (Table 5).

During the 1940s, pressure to relieve crop depredations stimulated the beginning of moist-soil management for waterfowl food production. Large stands of volunteer annual plants, especially watergrass, occurred in croplands, and managers gradually managed ponds for both watergrass and grains. Management emphasis gradually switched to watergrass because its production required only half as much water as production of rice during summer when water was limited. Summer irrigations were used to increase watergrass yields, but these irrigations also encouraged cattails and tules, which often became dense within a few years. Consequently, pond management gradually incorporated rotational planting systems and burning, mowing, or disking to control dense emergents.

A consequence of large waterfowl concentrations, drainage of native marshes, and irrigation of agricultural crops was the death of several hundred thousand waterfowl caused by avian botulism (*Clostridium botulinum* Type C) in the Tulare Basin in summer and fall 1938-41 (McLean 1946). Flooding and heavy rains in 1937 and 1938 broke many levees and flooded thousands of hectares of farmland in the Tulare Basin. These flooded croplands attracted up to 4 million ducks, and as waters were pumped or receded from croplands, large expanses of mudflats and decaying vegetation occurred and facilitated botulism outbreaks. Waterfowl continued to be attracted to this area in summer and fall 1939-41, when farmers irrigated croplands following harvest in late summer, and held water on lands for up to several months. These hot, shallow conditions facilitated further botulism outbreaks, peaking with the loss of 250,000 birds in 1941. Efforts were undertaken to control these losses by CDFG, and these efforts initiated a precedent for disease control in California. Control methods included picking up dead and dying ducks, placing sick birds in pens where shade and fresh water were supplied, and giving birds potassium permanganate (Mays 1941). In 1942, new preirrigation practices were initiated in the Tulare Basin. This pre-irrigation consisted of flooding lands only until soils were saturated and then draining water to other fields. This practice decreased the attractiveness of the area to ducks and also decreased stagnation that facilitated botulism outbreaks.

In addition to crop depredation and disease problems, procurement of water to flood and manage wetlands became difficult in the 1940s and 1950s. In the Sacramento, Imperial, and Coachella valleys, irrigation waters were made available to refuges and duck clubs to help reduce crop depredation (Gordon 1950, Arend 1967). In the San Joaquin Valley, however, where water shortages were critical largely because of overdrafting of groundwater tables, water for wetland management was often limited to unpredictable surpluses (U.S. Department of the Interior 1950). Through the efforts of private duck clubs, the Grassland Water Bill (PL 674, 68 Stat. 879) authorized the Secretary of the Interior to deliver some Central Valley Project (CVP) water, mainly surpluses, to the grasslands beginning in 1953. The definition of "surplus" water was never fully reconciled; however, the delivery of 61 million m^3 of CVP water each fall was established and has since been maintained.

Breeding by many species of waterfowl in California had long been recognized (Bryant 1914), and efforts to investigate the numbers, distribution, habitat use, and success of nesting were initiated in the late 1940s and early 1950s (Hunt and Naylor 1955, Mayhew 1955, Anderson 1956, 1957, 1960, Rienecker and Anderson 1960). These studies concluded that production was greatest in northeastern California and was often limited in the Central Valley. These findings caused administrators to place primary emphasis on managing habitats in California for wintering rather than breeding waterfowl.

1960-1980.—The acquisition of wetlands in California by the USFWS and CDFG in the 1940s and 1950s, and the increased water supplied to the San Joaquin Basin each fall, alleviated much of the depredation problems. Biologists subsequently turned to developing improved techniques to maximize food production. A marsh management project was established by CDFG in 1956 and continued to some degree until 1979 (Miller and Arend 1960, George 1963, Ermacoff 1969, Connelly 1979).

Wintering waterfowl populations remained relatively stable in California from 1960 to 1980 (LeDonne 1980). Management continued to emphasize small-grain production on public lands and shallow flooding during hunting seasons on duck clubs. The high price of water, land, and levee repair frequently discouraged intensive management, and some clubs converted existing wetlands into rice fields in an effort to offset costs while providing hunting. This conversion destroyed an additional 10,000 ha of wetlands in the 1970s.

Attempts to acquire additional public wetlands in California for waterfowl management in the 1960s-70s were largely unsuccessful. High land costs, government programs that encouraged agricultural production, and the perceived lack of need because of adequate waterfowl populations precluded public acquisitions of wetlands in the 1960s and 1970s. Exceptions were the purchase of the San Luis NWR and additions to Gray Lodge and Los Banos WMAs (Table 5). Also, the U.S. Department of Agriculture established a Water Bank Program in California in the early 1970s. In California, the Water Bank Program was used to encourage private landowners to protect and improve important wetlands. The emphasis in 1988 of the Water Bank in California was to provide pair and brood habitat, and required that at least 20% of the wetland area remain flooded until 15 July each year.

1980-1988.—The laissez-faire attitude of wetland management in California during the 1960s and 1970s ended in the late 1970s. The primary stimulus for change was a decline in waterfowl numbers, particularly pintails and arctic-nesting geese (U.S. Fish and Wildlife Service 1978, Raveling 1984, U.S Fish and Wildlife Service and Canadian Wildlife Service 1986). Reduced numbers of birds made hunters less successful, especially on poorly managed or marginal properties such as reflooded rice lands. Duck clubs began seeking information on how to manage to attract more ducks, and the USFWS and CDFG intensified management for natural foods. Concern over the destruction of wetlands peaked when the relationship between winter habitat quantity and quality, and waterfowl recruitment was demonstrated (Heitmeyer and Fredrickson 1981).

Efforts to secure and protect more wetlands were accelerated in the 1980s. Important implementation programs included a conservation easement program by the USFWS under the authority of the Migratory Bird Conservation Act; recategorizing Central Valley wetlands as the top priority for waterfowl habitat preservation in the U.S. by the USFWS; and the passage by California voters of Proposition 19, a $60-million bond issue passed for wetland acquisition and management. Additionally, increased support, both financially and legislatively, from the private duck hunting sector of California, primarily through the California Waterfowl Association (CWA); increased research on wetlands and waterfowl by private, university, and government sectors; and development of wetland projects in California by Ducks Unlimited and CWA accelerated wetland protection.

Two additional developments stimulated increased interest in wetland management in California in the 1980s. First, was the "rediscovery" of large nesting populations of some waterfowl, especially mallards, in the Central Valley. Research documented that nesting success was high, local production accounted for a large portion of the mallard harvest in California, and management of upland nesting cover and freshwater wetland in spring could increase recruitment (McLandress et al. 1987). Second, was the recognition that duck hunting was better on well-managed wetlands than on flooded rice fields, and that rice lands could readily be converted back to wetland habitats. Rice lands are especially easy to convert because most exist on former wetland soils, water-control structures and delivery systems are already in place, and moist-soil seed banks are already present. The potential conversion of rice lands into wetlands is currently facilitated by the low price supports and general poor economy of rice farming, the reduced value of lands for rice production but increased values for waterfowl hunting, and current Agriculture Stabilization and Conservation Service farm programs which remove a proportion (25-35% in recent years) of existing rice lands from production.

SPECIFIC MANAGEMENT APPROACHES AND CONCERNS

Sacramento Valley

Active management of wetlands in the Sacramento Valley began during the 1920s by private managers and consisted primarily of flooding ponds immediately prior to hunting seasons, and then draining them immediately after the seasons (Sacramento Valley Waterfowl Habitat Management Committee 1984). Small areas of wetlands were naturally subject to prolonged flooding and were often left permanently flooded (Arend 1967).

At present, most wetlands are managed as permanently flooded, summer water, and seasonally flooded habitats (Table 1). In the past, these habitats have been rotated with rice production on public areas. In general, soil saturation and standing water occur for longer periods of the year in the Sacramento Valley than in other areas of the state because of greater winter precipitation and more regular river overflows. These hydrological characteristics often encourage tule bulrush and cattail growth even when water is not managed, and has led to a preponderance of these emergent habitat types (Table 1).

In permanently flooded ponds, water is held year-round at depths up to 2-3 m. Many managers drain these ponds every 5-10 years to control the dense stands of cattail or tules that develop. Burning, mowing, and disking are the methods most often used to open up dense emergent stands.

In summer water management, ponds are flooded from June through February or March. Drawdowns in March encourage some germination of moist-soil annuals; however, these summer water ponds usually develop dense stands of cattail or tules within 5 years. As with permanently flooded ponds, summer water habitats usually require control of emergent plants within 5 years.

Seasonally flooded habitats are flooded from early fall (usually just prior to waterfowl hunting seasons) through late winter or spring. Late-winter or early-spring drawdowns (January-March) encourage germination of dock, slender aster (*Aster exilis*), and smartweeds (Fig. 4). Drawdowns in April and May encourage germination of pricklegrass, swamp timothy, and watergrass. Drawdowns in May and June encourage tule and cattail growth and germination of cocklebers or alkali bulrush (Fig. 4). Seasonally flooded ponds are usually flooded 10-30 cm deep in early fall.

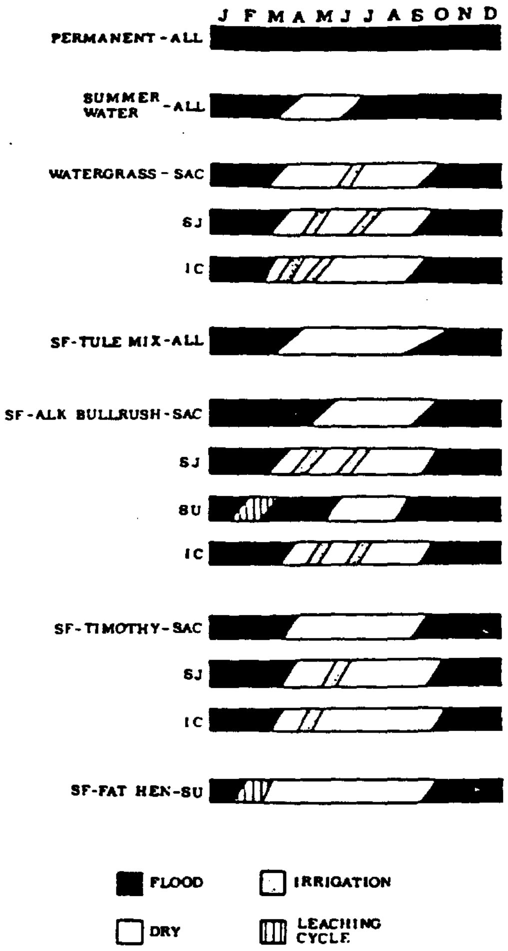

Fig. 4. Flooding and draining schedules of management for various wetland habitat types in California. Descriptions of habitat types and associated plant species are in the text. Diagonal lines represent the chronological range of flooding or drying. ALL = all valley regions. SAC = Sacramento Valley, SJ = San Joaquin Valley, SU = Suisun Marsh, IC = Imperial-Coachella valleys. SF = Seasonally Flooded. Irrigations consist of saturating soils for 1-2 weeks, leaching consists of repeatedly flooding and drying ponds with each inundation lasting up to 1 week.

Ponds managed for watergrass are typically flooded from October to mid-spring and are irrigated at least once during summer (Fig. 4). Some watergrass units are not irrigated during summer, but are flooded in early August; however, seed production is lower in unirrigated than in summer-irrigated units. Watergrass habitats on public lands were historically flooded in September or October to provide foods for early fall migrants and to deter potential depredation. Depredations have been minimal in recent years because of low waterfowl populations, presence of flooded high-energy foods on refuges, and early maturing varieties of rice. As a result, flooding of many watergrass fields on public lands has recently been delayed until November.

Although management has tended to emphasize plant production, interest in managing for invertebrates has increased (Euliss and Grodhaus 1987). Invertebrate management is still in its infancy, but flooding small ponds in late summer several weeks prior to marsh flood-up in fall may provide brood stock ponds for invertebrates and increase biomass (Euliss and Grodhaus 1987). This early flooding (i.e., September) of brood stock ponds is generally consistent with mosquito-control practices that limit water fluctuations from March through September (Garcia and Des Rochers 1985).

Providing a combination of the above habitats plus managed uplands is often a goal on public management areas. Resources in this complex of habitat types provide an abundance of moist-soil seeds, invertebrates, forage, tubers, and nesting and brood-rearing habitats (Table 4).

In contrast to public lands, most private duck clubs flood their ponds 1-2 weeks before hunting season, and drain ponds within 3 weeks following the close of hunting seasons. However, recent interest in providing pair and brood-rearing habitats to locally breeding mallards, and in providing late-winter habitat for migrants, has influenced this management. Some managers now hold water in ponds through spring. Additionally, private clubs managed under the USDA Water Bank Program are required to be flooded from 1 January through 15 July. Water to flood most private wetlands is primarily available during early fall when rice fields are drained. At other times, waters often are limited to irrigation surpluses, local runoff, and floods.

In permanently flooded wetlands, water is often circulated from August through October to avoid stagnant water conditions conducive to avian botulism (Sacramento Valley Waterfowl Habitat Management Committee 1984). When botulism outbreaks do occur, dead and dying birds are removed and water is either drained or flushed (Rosen 1965). Actions used to control avian cholera include the above methods plus hazing birds from an area and treating contaminated ponds with copper sulfate (Hunter et al. 1970, Titche 1979).

Management of uplands in the Sacramento Valley has generally been neglected. Small areas of upland habitat are, however, managed as grazing areas for geese or as dense nesting cover for ducks. Burning most commonly is used to enhance new growth of upland grasses and sedges (Sacramento Valley Waterfowl Habitat Management Committee 1984, Mensik 1986). Little direct seeding of annual grasses or legumes occurs, although winter wheat, barley, clover (*Trifolium* spp.), and alfalfa have been sown on a few areas. Uplands managed for nesting cover are sometimes seeded to tall wheatgrass (*Agropyron elongatum*), vetch (*Vicia* spp.), or ryegrass (*Lolium* spp.), but usually naturally occurring vegetation is simply allowed to grow undisturbed.

Production of rice provides considerable habitat for waterfowl. Rice fields are generally laser-leveled and diked with contour levees. Seed beds are prepared in late spring or early summer (Mar-May) by disking or plowing, applying fertilizers, herbicides, and pesticides, and by flooding fields 5-10 cm deep (Rutger and Brandon 1981). Rice seed is treated with a fungicide and applied aerially. Water is added to rice fields during summer to reduce evapotranspiration losses. Pesticides such as parathion, copper sulfate, and carbamate (and formerly, furadan) are applied to control rice water weevils (*Lissorhoptrus oryzophilus*), tadpole shrimp (*Triops longicandatus*), and crayfish (*Procambarus* spp.); and thiocarbamate and phenoxy herbicides are applied to control watergrass and sprangletop. Most currently planted rice varieties mature in 120-140 days, and water is drained from fields 20-30 days before harvest. Harvest generally is initiated when the grain has a <24% content of moisture. After harvest, most fields are burned to destroy straw that harbors the fungus *Sclerotium oryzae* that causes stem rot. Because of recent concerns with air pollution, stubble is sometimes left standing, disked, or rolled instead of being burned. Flooded rice fields provide significant habitat for breeding waterfowl and broods; however, the effects of pesticide biomagnification in food chains are not well-known. Harvested rice fields provide winter foods and habitats to waterfowl, especially if they are shallowly flooded after harvest. Some duck clubs leave fields unburned in fall and mow or disk areas around blinds; others flood burned fields only during hunting seasons.

Wild rice also is planted in California (in 1988, 10,000 ha). Methods of growing wild rice are similar to regular rice production except that fields are planted and flooded in late March. Therefore, these fields may be especially important as early brood habitat.

San Joaquin Valley

The earliest wetland management in the San Joaquin Valley occurred in the 1880s when the Miller and Lux Corporation irrigated large tracts of grassland habitat (Exley 1931). These irrigations shallowly flooded grasslands on floodplains that were normally dry during summer, and encouraged vegetation that provided abundant moist-soil seeds, forage, and invertebrates used as food by wintering ducks and geese. Early winter rains further stimulated growth of grasses and sedges and provided forage for waterfowl. In 1926, Miller and Lux sold much of its land, but retained water rights, to individuals who operated the land as shooting clubs and/or cattle ranches (U.S. Department of the Interior 1950). Miller and Lux eventually sold the water rights for this land to the U.S. Bureau of Reclamation, but the bureau had no place to sell the water from 1939 until the Friant-Kern Canal was completed in 1952. During this period, the bureau let clubs and ranchers have water at the previous low rate, and water was mostly managed by the Grasslands Mutual Water Association (U.S. Department of the Interior 1950). Since 1953, the previously mentioned Grasslands Water Bill has made provisions for supplying CVP water to San Joaquin wetlands. Most wetlands owned by duck clubs were grazed by cattle until early fall when lands were flooded for duck hunting. However, heavy grazing reduced biomass and seed production of desirable moist-soil plants. Many clubs no longer allow cattle to graze wetlands.

In the 1970s, attempts were renewed to increase food production from native marsh plants, and new techniques to grow swamp timothy and spikerush were developed (Connelly 1979). Most wetlands in the San Joaquin Valley are currently managed as seasonally flooded habitats (Table 1). Most ponds are drained in early spring to stimulate germination of swamp timothy and pricklegrass, and typically at least 1 irrigation is made in midsummer to increase seed production (Fig. 4). This irrigation is usually done when swamp timothy leaves start to show necrosis and when plants are flowering, thus preventing infertile seed heads. Some ponds are drained in late spring to enhance production of watergrass and alkali bulrush. Newly created or planted stands of watergrass and alkali bulrush usually need 2 summer irrigations to stimulate growth and seed production; however, existing stands usually require only 1 irrigation. Some wetlands also are permanently flooded to provide brood and pair habitat. These wetlands quickly become dominated with cattails and tules, however, and must be drawn down and thinned at least once every 5 years. Disking, burning, prolonged drying, grazing by sheep and cattle, and mowing are used to control undesirable cattails and tules (Ermacoff 1969).

Many duck clubs in the San Joaquin Valley manage almost exclusively for short annual vegetation such as swamp timothy or pricklegrass. This management is highly attractive to pintails and also reduces the demand for water, which is often unavailable, of poor quality, or expensive. Clubs frequently mow any emergent growth that stands above 20-30 cm, thus creating a shallow "sheet water" appearance that is desired for pintail hunting. These sheet water-timothy habitats provide abundant seeds in early fall and invertebrates in spring (Severson 1987). Disease outbreaks in the San Joaquin Valley, with the exception of major die-offs from botulism in the Tulare Basin, have not been as great as in the Sacramento Valley. When disease outbreaks occur, the disease control techniques previously described are used.

Availability of good water quantity and quality remains a problem in the San Joaquin Valley. Agricultural crops require large amounts of irrigation water; however, salts accumulate in the surface soil as a result of evaporation and must be removed by leaching. Percolation of water into aquifers and deeper soil layers is inhibited by impermeable clay layers, and soils becomes waterlogged or laden with salts, thus inhibiting plant growth. Subsurface drains have been constructed throughout much of this agricultural land to alleviate the problem (Letey et al. 1986).

The potential for using agricultural drainage water for wetland management was suggested in the 1940s and 1950s (Leach 1960, Jones and Stokes Associates 1977, Letey et al. 1986). The Grasslands Water District began accepting drainage water for flooding of wetlands with the stipulation that it contain <3,000 ppm salt, feeling that the salt could be adequately diluted with the CVP water they received each fall. This worked successfully as long as the accumulating salts were flushed from wetlands each winter. However, toxicity problems became acute in the early 1980s when reservoir ponds on the Kesterson NWR were turned into terminal evaporation sumps rather than holding or regulating reservoirs as originally intended (Letey et al. 1986, Zahm 1986). Since drain waters began flowing into Kesterson in 1978, the extreme toxicity of drain waters, particularly from naturally occurring selenium, has been recognized (Hamilton et al. 1986, Ohlendorf et al. 1986*a*, *b*). Since 1985, use of drain waters to flood private and public lands has been reduced. Litigation and proposals to dispose drain waters, prevent contamination of wetlands and ground water, and provide "good quality" alternate water sources (such as more CVP water) were pending in 1989.

Sacramento-San Joaquin River Delta and Suisun Marsh

Management of wetland habitat in the delta area is mostly restricted to the Suisun Marsh. In the delta, approximately 4,900 ha are flooded for duck hunting, but >80% of these lands are harvested corn, milo, sunflower, and rice fields. Flooding of these croplands usually occurs from October-February; little additional management occurs. Wheat is also grown in the delta and provides forage for geese and swans. The small area of marsh that exists in duck clubs in the delta is mostly managed for seasonally flooded tule habitats, but a few permanently flooded ponds exist. Water management regimes and emergent plant control are similar to those used in the Sacramento Valley.

Early (1900-1925) management of wetlands in the Suisun Marsh consisted of placing low levees around ponds and controlling water levels with tide gates (Moffitt 1938). "Overflow" lands within leveed areas were flooded from September to February; only subsoil moisture was provided in summer. This water management initially encouraged growth of desirable plants, but when this "dry" water regime management was continued over many years without adequate flushing, seasonally flooded ponds became saline and acidic, and only the most salt-tolerant plants such as saltgrass and pickleweed survived. Some duck clubs impounded freshwater that flowed into the delta during May and June, and later added this water to more saline bay waters for flooding of ponds (Moffitt 1938). Some areas were permanently flooded and equipped with gates that continually circulated water through the ponds to keep them as fresh as possible. These ponds contained abundant sago pondweed, water nymph, and widgeongrass until carp (*Cyprinus carpio*) populations became excessive. Experimentation on the Joice Island Duck Club ponds during the late 1950s proved that draining the ponds completely in February and then re-flooding them in March controlled the carp problem. Pickleweed was considered undesirable by most clubs and was discouraged by disking and flooding (Moffitt 1938). Many duck clubs allowed cattle to graze on marsh vegetation during summer. Attempts were made to farm lands within the Suisun Marsh from 1900 to 1930; however, increases in soil salinity, low pH, and 3 major floods in the early 1900s virtually eliminated the growing of crops by the early 1930s, except on Grizzly Island (Mall 1969, Miller et al. 1975).

During the 1950s and 1960s, techniques were developed within the constraints of mosquito abatement regulations to decrease soil salinity and increase production of alkali bulrush, fathen, and brass buttons (George et al. 1965, Mall 1969, Miller et al 1975, Rollins 1981). Managers were encouraged to repeatedly flood and dry marshes from the end of duck season to the first of April to leach salts. The length of these leaching cycles controlled the vegetation composition (Fig. 3, Rollins 1973). By maintaining dry conditions in pond bottoms during summer, cattail and tule growth was restricted and heavy equipment could be used to disk pond bottoms for vegetation control. Stands of saltgrass were frequently burned to prevent dense matting, which allowed it to outcompete more desirable plants such as brass buttons and fathen. Alkali bulrush was encouraged because it was tolerant of saline soils and considered to be a desirable duck food (George 1963, Mall 1969, Mall and Rollins 1972, Rollins 1981).

Managers and biologists now recognize that maintaining extremely dry soil conditions throughout summer on the cat clay soils that underlay much of the Suisun Marsh can drastically alter soil and water chemistries (Neely 1958, 1962, Lynn 1963, Crapuchettes 1987), and that alkali bulrush seeds are poorly metabolized by waterfowl (Swanson and Bartonek 1970). Interest in managing for invertebrates has also increased (e.g., Connelly and Chesemore 1980, Euliss and Harris 1987, Miller 1987), and some managers now encourage pickleweed, which was formerly considered undesirable (Moffitt 1938).

Soils and vegetation within the Suisun Marsh evolved under tidally flooded regimes and high soil moistures. Completely drying soils causes accelerated decomposition of marsh litter, subsidence, oxidation of soils, and drastically lowered pH (Neely 1958, 1962, Lynn 1963). When alkaline waters inundate these low pH soils, dissolved iron becomes suspended and eventually precipitates as ferric hydroxide (causing "red water," which is toxic to some plants and invertebrates) (Lynn 1963, Crapuchettes 1987). Red water conditions can be avoided by flooding ponds throughout the year, by rotating flooding and drying ponds in alternate summers, and by maintaining high soil moisture throughout the year by holding water at higher levels (i.e., <10 cm from the soil surface) in water delivery ditches. Maintaining high soil moisture and more permanent water regimes increases growth of alkali bulrush, tules, and cattail, and these must be controlled if undesired. Consequently, alternate yearly flooding and drying may provide the best management strategy by reducing acidity and permitting managers to control undesired vegetation during dry periods.

Mallards nest in the Suisun Marsh. Managers in 1988 provided permanently flooded wetlands for pairs and broods, maintained dense upland cover for nesting, and grew watergrass as high-energy food (McLandress et al. 1987). These habitats combined with traditional winter seasonally flooded marshes provide the complex of habitats necessary to support both breeding and wintering waterfowl.

Imperial and Coachella Valleys

Early attempts at wetland management in the Imperial and Coachella valleys consisted primarily of flooding diked ponds from October through March (Fredrickson 1980). A rise in the level of Salton Sea inundated most of Salton Sea NWR in the 1940s, and by 1950, extremely saline conditions (35 ppt) were present. Widgeongrass grew along the south shore of the Salton Sea, where dilution kept salinities at <24 ppt until 1956; however, fluctuating water levels of the Salton Sea, coupled with meandering tendencies of the New and Alamo rivers, precluded most management from 1930 to 1950, and the Salton Sea NWR became primarily an open water refuge area. Shoalgrass (*Halodule wrightii*) was introduced in the Salton Sea as early as 1957, and several truckloads of sod were transplanted from the Laguna Madre in Texas in the early 1960s. Shoalgrass persisted for a few years, but rapidly rising water and lack of tidal currents eventually eliminated it. The Imperial WMA was originally managed as a sanctuary, and no hunting was allowed. Here, water was held on ponds until early summer, and dense stands of tules and cattails developed (California Department of Fish and Game 1983).

Crop depredation problems in the Imperial and Coachella valleys in the early 1940s encouraged the USFWS and CDFG to plant crops on their own or leased lands. In 1948, the Imperial Irrigation District leased up to 9,800 ha within the Salton Sea Reserve to the USFWS and CDFG for waterfowl management, primarily for the provision of row crops (Gordon 1950). These lands were leveed to protect them from flooding by the rising water levels of the Salton Sea.

In 1947, the USFWS began placing feed on refuge lands to discourage crop depredations. This feeding program continued through 1978. In 1953, the CDFG adopted regulations to permit duck clubs to feed waterfowl on their lands during the waterfowl hunting season to help alleviate depredations. This feeding program was suspended in 1958, but was reinstituted in 1959 and continues to the present. Feeding is currently restricted to 9 southern California counties (Fredrickson 1980). The legality of the California

Feeding Program has been challenged by the USFWS since 1961, and controversies continued in 1989.

Depredation problems in the Imperial and Coachella valleys have been minimal in recent years; feeding programs have apparently done little to minimize depredations, and harvest does not seem to be affected by feeding, but rather by effective marsh management that provides abundant natural foods (Fredrickson 1980). As a result, many managers now expend more effort in managing ponds for natural plants than in the continuance of "feeding". However, the high cost of water, the salinity of soils and agricultural drain water, and evaporation rates make management costly and difficult. Club managers that have access to artesian waters in the Coachella Valley can flood and circulate water more easily and cheaply, and therefore grow more moist-soil plants than most clubs in the Imperial Valley (U.S. Fish and Wildlife Service 1987*b*).

Managers promoting moist-soil plants usually flood ponds from September to March (Fig. 4). When water is available, salinity is decreased by circulating water through ponds. This regime encourages swamp timothy, pricklegrass, dock, and sprangletop. Watergrass and Japanese millet are grown on a few clubs; however, watergrass production requires summer flooding which increases soil salinity and encourages growth of cattails, salt cedar, tules, and sesbania (*Sesbania* spp.), which are often considered undesirable. Dense emergents and salt cedar are controlled primarily by burning, disking, and mowing. Some permanently flooded ponds are present near the Salton Sea where the sea precludes drainage, but fresh water must be added periodically to maintain low salinities. Presently, the Salton Sea is much saltier than the ocean (i.e., >40 ppt).

CONCLUSION

Wetlands and agricultural lands in the Central, Imperial, and Coachella valleys of California support 20% of all (and > 50% of several species) wintering waterfowl in North America. No other area in North America is as important for wintering waterfowl, yet paradoxically, no other wintering area has experienced as great a wetland loss. The obvious question is: will the limited wetland base that remains be adequate to support current and desired future populations?

Wetlands are among the most productive (biomass/area) ecosystems in the world (Mitsch and Gosselink 1986), but food production on California's highly modified wetlands varies widely depending on location and management activities. Provision of an average of 750-950 kg/ha of food (calculated earlier as the amount necessary to support current waterfowl populations) in all wetlands in California of the seasonal quality necessary to meet requirements of waterfowl annual cycle events seems unlikely. Some intensively managed wetland complexes may exceed this theoretical need, but most do not. Hunting probably restricts waterfowl use of many private wetlands and hunting areas on public lands during hunting seasons. Because of limited wetland resources, it is apparent why the large waterfowl populations that were present prior to the 1980s readily supplemented foods obtained in wetlands with waste agricultural grains. We doubt that the large waterfowl populations wintering in California in the 1940s-1970s could have been maintained without large areas of small-grain crops. Although most waste grains are good sources of energy, many lack essential nutrients. Consequently, foods provided in wetlands that have proper complements of amino acids, fatty acids, minerals, and vitamins are crucial to survival and reproduction of waterfowl. We suspect that the availability of foods in wetlands was possibly limiting to waterfowl populations during years or seasons of drought, even as recently as the mid-1970s. The quantity and quality of foods on both wetlands and agricultural lands increase when precipitation and associated river overflows are high in winter. Correspondingly, greater availability of resources in wet winters allows birds to attain better physiological condition (Miller 1986), proceed through annual cycle events more rapidly (Heitmeyer 1985, 1987), and survive and reproduce more successfully (Raveling and Heitmeyer 1988).

Consideration of the requirements of waterfowl must not be limited to nutritional needs or to diurnal periods. Social systems vary among species (Kear 1970, McKinney 1986), and consequently, habitat use, flocking structure, and philopatric tendencies also vary. Maintenance of wintering and breeding traditions to specific areas is dependent upon the availability of refuges where waterfowl have freedom from disturbance, mortality, and predation (Raveling 1978, Cowardin et al. 1985). Waterfowl also commonly use different habitats and have different activities during the day and night (e.g., Euliss and Harris 1987). Some habitats used at night may provide food for certain species (e.g., green-winged teal), but only provide thermal cover or protection from nocturnal predators for others (e.g., wood ducks, mallards). Consequently, provision of adequate resources and habitats may often require a diversity unappreciated solely by daytime observation.

The above considerations lead us to believe that management of wetland complexes, where sanctuaries also are provided, is essential and exhibits the greatest potential for maintaining waterfowl populations in California. By managing wetland complexes where a variety of foods and habitats are available adjacent to existing private agricultural lands, the annual cycle requirements of many species can be met. The "magic" size of areas where all habitats must be present is poorly understood. If all habitats can be provided within an area, such as a large (>200 ha) duck club, we feel the response by waterfowl would be especially noticeable, biologically valuable, and financially justifiable.

Attainment of wetlands that provide adequate resources to waterfowl will require knowledge of annual cycle requirements and will require intensified management of existing private and public wetlands. Private and public lands often have different priorities and constraints, thus management should not necessarily be the same on lands of different ownership; management that complements values on adjacent lands is especially desirable. Managers of public lands often have the flexibility to provide resources that are absent or limited on private lands. Techniques and conceptual strategies for management of breeding (McLandress et al. 1987, McLandress and Yarris 1987) and wintering (Heitmeyer 1985) waterfowl in California are available, but transfer of information among managers and researchers is currently insufficient.

The diverse climate, topography, geology, and water quantity and quality available within California require different management strategies within regions. Management is often most successful when it attempts to emulate natural, hydrologic conditions. Valuable lessons were learned from attempts to manage wetlands in a way that varies considerably from natural flooding regimes (e.g., prolonged drying of Suisun Marsh soils, which increases soil acidity and reduces productivity).

For wetland management to be successful, the natural structure and function of wetlands must be maintained. Because wetlands are dynamic and complex ecosystems, management should make provisions for periodic change (such as occasional drawdowns) to alter nutrient dynamics, vegetation communities, soil and water chemistry, and associated biological productivity. Ecological studies of wetlands in California have been neglected. Integrated investigations of nutrient, plant, invertebrate, and chemical aspects of wetlands and the effects of management will be productive avenues for research.

Wetland management in California is currently reaching a new level of sophistication, but is also faced with problems. Increased urban populations in California and worldwide demands for agricultural commodities will accelerate demands on already limited water supplies. Although provisions for water to flood managed wetlands have been made in the past, litigation and compromise have been required and likely will be necessary in the future. Problems related to water quality have recently been brought to the forefront, as exemplified by selenium contamination at the Kesterson NWR. Water that is contaminated with pesticides, heavy metals, salts, or that contains extremely high nitrogen and phosphorus or low oxygen concentrations may exacerbate failures of reproduction, reduced survival, and disease outbreaks among waterfowl. Disease outbreaks and their impacts on waterfowl, and their relation to wetland management, remain poorly studied.

Reduced waterfowl populations result in poorer hunting, which discourage many hunters. As hunter numbers decline, wetland and waterfowl preservation in California likely will suffer. Without the considerable financial and political support of waterfowl hunters, it seems doubtful that wetlands of value to waterfowl will remain. On the positive side, reduced waterfowl numbers also often raise the consciousness and resolve of both private and public groups to protect and increase wetland habitats upon which waterfowl populations depend. In this light, financial and political support from the private sector and state and federal governments in California has recently increased. Recognition of biological requirements of waterfowl and the promise that this understanding offers to better management also are currently reaching an all-time high in California.

Also, the North American Waterfowl Management Plan (NAWMP) calls for action to improve, protect, and restore wetland habitats in the Central Valley of California (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986). A Central Valley Habitat Joint Venture of the NAWMP was initiated in February 1988 and adopted the following objectives: (1) protect an additional 32,400 ha of existing wetlands through fee or perpetual easement acquisition; (2) secure an incremental firm 50 million m^3 (410,050 acre-ft) of water; (3) secure CVP power for NWRs, WMAs, and the Grassland Resource Conservation District; (4) increase wetland area by 48,600 ha; (5) enhance wetland habitats on 117,450 ha of public and private lands; and 6) enhance habitat on 182,250 ha of agricultural lands.

SUMMARY

Wetlands in the Central, Imperial, and Coachella valleys of California provide resources that support the largest concentration of wintering waterfowl in North America. Despite the importance of these wetlands, only 115,000 ha remain; most are privately owned and managed for duck hunting.

Wetlands in the Sacramento Valley total 32,000 ha. These wetlands occur primarily in floodplains of the Sacramento River and its tributaries and typically flood more permanently than wetlands elsewhere in California. Management of wetlands in the Sacramento Valley has evolved from primarily flooding during waterfowl hunting seasons and attempting to discourage crop depredations in the early and mid-1900s, to providing a complex of flooding regimes and habitat types in the 1980s. Harvested rice fields in the Sacramento Valley provide waste grain to waterfowl, and 162,000 ha of farmlands are subject to flooding in winter. Additionally, 32,000 ha of rice lands are intentionally flooded for waterfowl hunting each fall.

Wetlands in the Sacramento-San Joaquin River Delta have mostly been destroyed; only 7,290 ha remain. Delta wetlands are managed similar to those in the Sacramento Valley. About 8,100 ha of croplands are flooded each winter for waterfowl hunting or to leach soil salts. The Suisun Marsh is a tidally influenced estuarine wetland complex that encompasses 22,000 ha; 84% is privately owned. Techniques have been developed in the Suisun Marsh to decrease soil salinity and increase production of alkali bulrush, fathen, and brass buttons. Repeatedly flushing wetlands in late winter and early spring created effective leaching cycles, and the timing of these flushes controls vegetation composition.

Wetlands in the San Joaquin Valley occur in the northern San Joaquin Basin (49,000 ha) and the southern Tulare Basin (2,000 ha). Most wetlands in the San Joaquin Valley are seasonally flooded, are often alkaline, and support less emergent, but more annual grassland plants than in the Sacramento Valley. This is because of the more arid (<23 cm of annual precipitation) climate in the San Joaquin Valley than in the Sacramento Valley. The arid climate has encouraged management that conserves water and encourages annual vegetation. When flooded, these wetlands have a shallow sheet water appearance that is attractive to pintails.

Wetlands in the Imperial and Coachella valleys were mostly created by man in the early 1900s after Salton Sea was created. The extremely arid (<5 cm of annual precipitation) climate and saline soils of the area often preclude marsh management, and many wetlands are simply flooded during waterfowl hunting seasons.

If numbers of wintering waterfowl in California return to mid-1970s levels, management of wetlands will have to increase production and quality of resources to meet waterfowl requirements. Breeding mallards in California also bring responsibility and the challenge to manage existing wetlands and uplands for both breeding and wintering waterfowl.

Many problems impede effective management in California; these include increased urban populations and development, inadequate quantity and quality of water, disease outbreaks and resource limitations imposed by increasing concentrations of waterfowl on reduced habitat bases, and reduced hunter numbers and incentives for privately owned wetland preservation. Despite these problems, financial and political support from the private sector remains high. The Central Valley Habitat Joint Venture of the NAWMP seeks to impact over 400,000 ha of wetlands, uplands, and agricultural lands for the benefit of waterfowl.

Future research avenues that seem most productive include identification of specific resource requirements of waterfowl species during annual cycle events, and integrated studies of nutrient, plant, invertebrate, and chemical aspects of wetlands.

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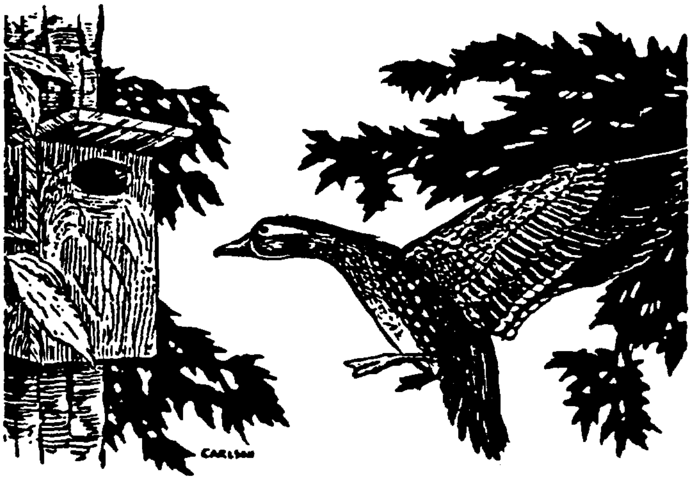
WATERFOWL MANAGEMENT HANDBOOK

13.1.3. Life History Strategies and Habitat Needs of the Northern Pintail



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Species Profile—Northern Pintail

Scientific name: *Anas acuta*
Weight in pounds (grams):
Adults—male 2.3 (1,040 g), female 1.9 (860 g)
Immatures—male 2 (910 g), female 1.8 (820 g)
Age of first breeding: 1 year
Clutch size: 8, range 3–14
Incubation period: 22–23 days
Age at fledging: 36–43 days in Alaska, 42–57 days on prairies
Nest sites: Low, sparse vegetation, often far from water
Food habits: Omnivore; primarily moist-soil seeds, as well as chufa nutlets; cultivated grains, especially rice and barley. Animal foods: aquatic insects, especially chironomids, snails, terrestrial earthworms, and spiders.

The northern pintail (hereafter pintail) is a common dabbling duck distributed throughout the Northern Hemisphere. Since 1955, the breeding population in North America has averaged 5,566,000, fluctuating between 10,124,000 (1956) and 2,471,000 (1989; Fig. 1). Pintail numbers are especially sensitive to habitat conditions that reflect the wet–dry cycle in the shortgrass prairie breeding areas of south-central Canada and the northern Great Plains of the United States. Populations of pintails also are affected by habitat conditions in key wintering areas, such as the Central Valley of California and Gulf Coast marshes. When wintering areas are fairly dry, birds have fewer resources and subsequent spring recruitment is lowered.

Through the 1970's, continental populations recovered when wetland conditions on breeding and wintering areas were good but fell when the prairies were dry and wetland conditions in wintering areas were poor. Unfortunately, habitat losses and degradation of prairie habitats caused by agricultural practices have coincided with prolonged drought since the early 1980's. This combination of detrimental factors resulted in declining pintail numbers in the past decade. The long-term downward trend in pintail numbers has focused renewed attention on this species.

This leaflet describes aspects of pintail life history that may be important for pintail management. It is not intended as a general reference on pintail biology. Readers interested in this should consult Bellrose (1980).

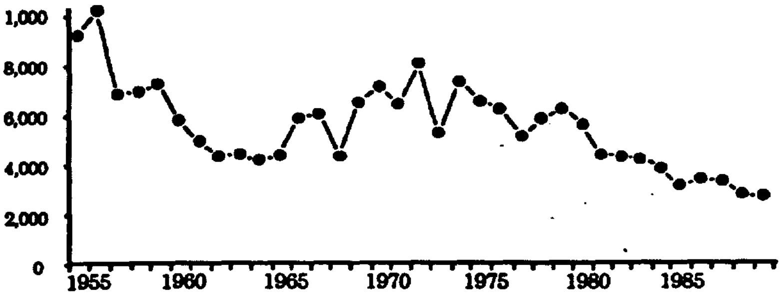

Fig. 1. Fluctuations in the continental population of northern pintails based on breeding population estimates, 1955–90.

Distribution

The northern pintail is the most widely distributed dabbling duck in the Northern Hemisphere. Although pintails regularly breed in the shortgrass prairies of the northern United States and southern Canada, their breeding distribution in North America extends from the Great Basin into the northern boreal forest and the arctic coastal plain of Alaska and Canada (Fig. 2).

In recent years, about 16% of the continental population of pintails (counted in May) occurred on the 26,000 square miles of high-latitude wetlands along the arctic coastal plain in Alaska. Pintails compose 90% of the dabbling ducks that use these habitats; thus, they are the most abundant dabbling duck in this region. Drakes account for about 32% of this total, whereas pairs account for

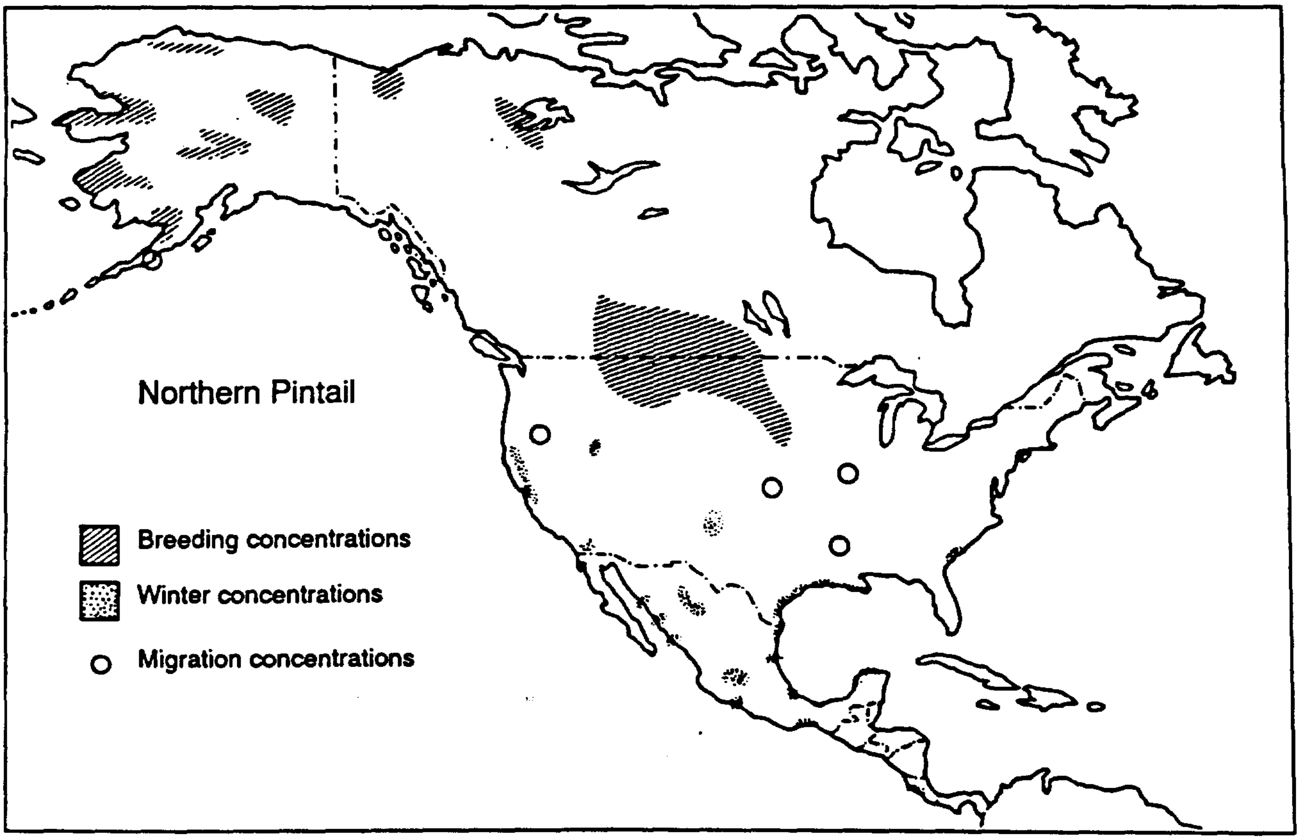

Fig. 2. Distribution of important breeding, wintering, and migration areas for northern pintails.

12% and groups about 57%. Pintails are well known for overflight into more northern wetland habitats when wetland habitat conditions on more southern habitats are poor; therefore, their numbers fluctuate erratically in Alaska.

Most pintails in the Pacific Flyway have traditionally wintered from the Central Valley of California to the west coast of Mexico, but the river deltas of the Pacific Northwest also provide important habitats. Large numbers of pintails also winter in coastal marshes and rice belt habitats in Texas, Louisiana, Arkansas, and the Atlantic Coast, especially South Carolina.

Spring Migration and Breeding

Pintails migrate early in spring and move northward as soon as wetlands become ice-free. They normally initiate nesting earlier in spring and summer than other dabblers (Fig. 3). These early-nesting females often encounter light snowfall while laying and incubating. Open habitats with sparse, low vegetation provide favored nesting sites. The shortgrass habitats of the Canadian prairie provinces have traditionally held the highest breeding populations. In the northern United States and southern Canada, first nests appear in early April during normal years, but inclement weather can delay nesting until the second week of May. Nesting activity in the more northern prairies peaks during the first 2 weeks of May. Pintails nest later in the boreal forest; the peak of first nests in Alaska's interior occurs during mid-May. Birds moving to tundra habitats on the Yukon–Kuskokwim Delta and the North Slope do not nest until late May or as late as mid-June.

Pintails lay an average clutch of 8 eggs, but clutch size ranges from 3 to 14. Incubation lasts 22 or 23 days. Pintail broods can move long distances between the nest site and rearing habitats or among different brood habitats. Recent studies suggest that pintails are well adapted to making these movements and that neither mortality nor

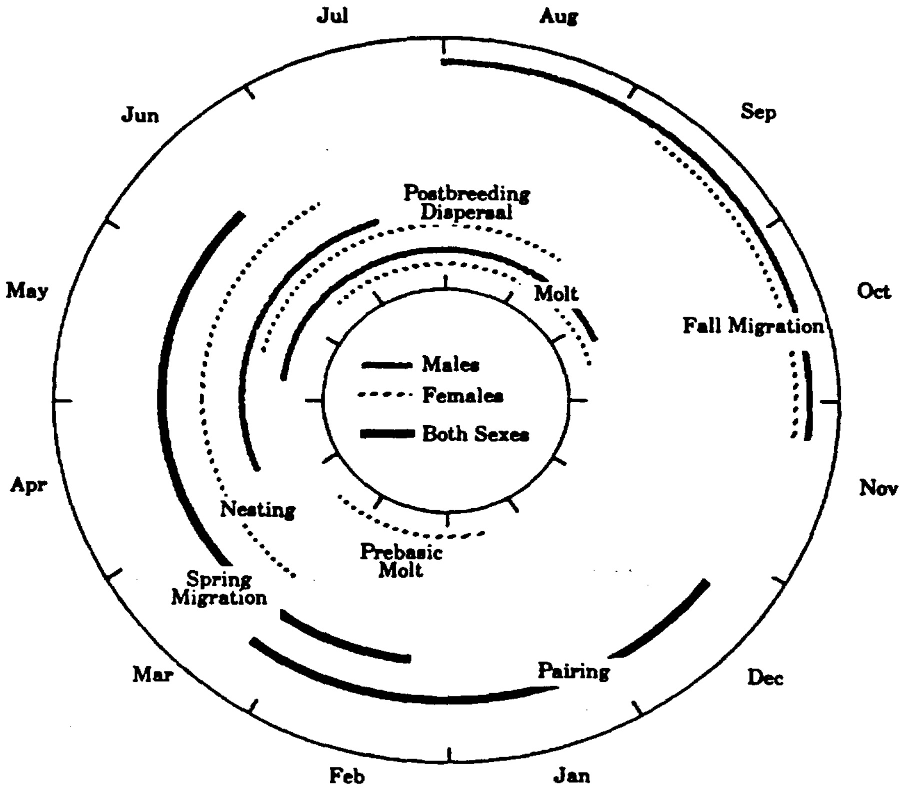

Fig. 3. The chronology of important life history events in the annual cycle of the northern pintail.

body condition of ducklings is greatly influenced by movements of less than 3 miles. Fledging time varies with latitude and is undoubtedly influenced by the length of daylight and the daily time available to forage. Females stay with the brood until the young reach flight stage. Soon after, the female initiates the summer molt and becomes flightless (Fig. 3).

Postbreeding Dispersal and Fall Migration

Males congregate in postbreeding flocks once females begin incubation (Fig. 3). Males may move to southern or northern habitats, where they often form large aggregations and begin the Prebasic molt, becoming flightless for about 3 weeks. After regaining flight in August, they often migrate south to the ultimate wintering areas. For some pintails, the fall migration is a more gradual shift south that extends over several months. Early migrant males begin to move southward in abundance in late August or early September and usually concentrate on seasonally flooded wetlands, where they select seeds from native vegetation or from agricultural crops, especially rice.

Following brood rearing, successful females form small flocks, enter the molt, become flightless, and regrow their flight feathers in rapid succession (Fig. 3). Because males generally leave the breeding area before females are flightless, the latter use habitats distinctly different than those used by males for several months. During this time, females remain on more northern habitats and feed in semipermanent marshes, where invertebrates are important in their diet (Fig. 4). Females gradually join males on migratory and winter sites in October and November. As fall progresses, the two sexes gradually intermix and pair formation begins.

Winter Behavior and Pairing

Pintails are highly social and have loosely formed pair bonds compared to mallards and most other Northern Hemisphere dabblers. Pair formation by pintails begins on the wintering

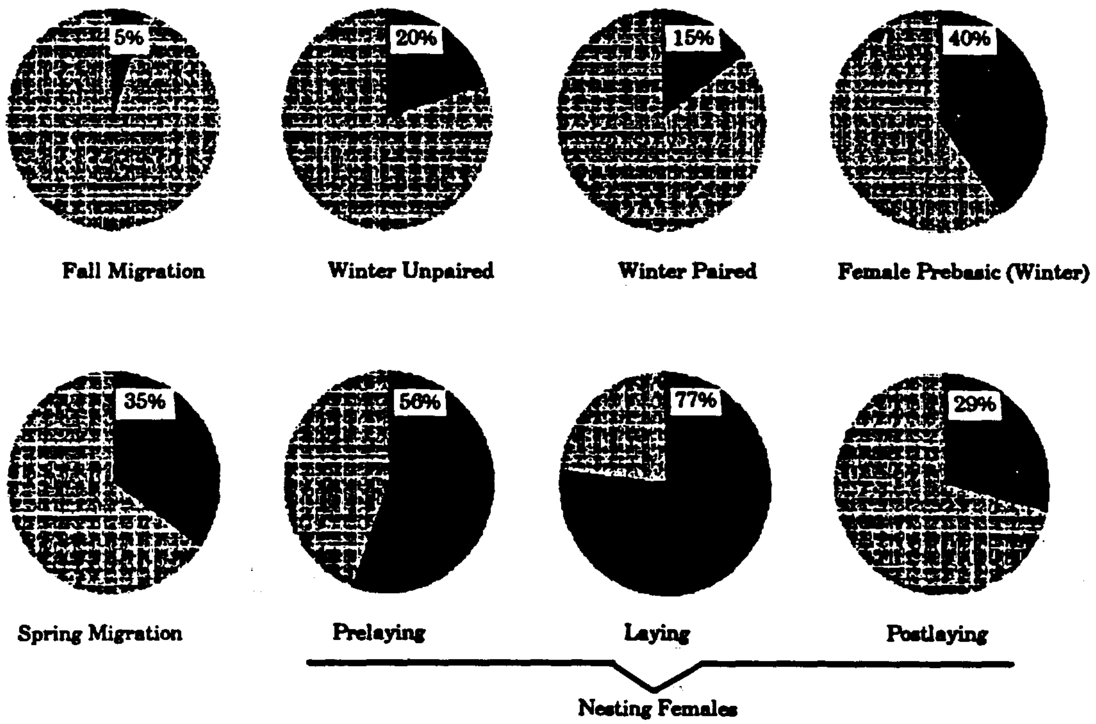

Fig. 4. Invertebrate consumption by northern pintails during selected events in the annual cycle. Includes both sexes unless indicated otherwise.

grounds, and most females are paired by January. Courtship flights often contain large numbers of males and traverse great distances, reach great heights, and last for extended periods. On the breeding grounds, these spectacular flights were once believed to distribute the nesting pairs widely among available habitats, but recent studies have not always confirmed this assumption—instead, they suggest active competition in mate selection and breeding opportunities among males in spring.

During winter, pintails undergo several important events in the annual cycle (Fig. 3). After completing the Prealternate molt, they form pairs; then, females initiate the Prebasic molt. By late winter and early spring, both sexes have accumulated large body fat reserves subsequently used in migration and for breeding. Females departing from the Central Valley of California to Tule Lake in late winter reach weights of 950 g, and of this total, 220 g is fat necessary to fuel migration and eventual reproduction.

Pintails are early migrants in spring and are especially attracted to large expanses of shallow open water where visibility is good and small seeds and invertebrates are readily available. Their preferred prairie nesting areas are short grasses where temporary ponds are abundant nearby. Nesting habitat requirements in boreal forest and tundra habitats are less well known.

Foraging Ecology

Pintails are opportunistic omnivores. They primarily consume small seeds, but underground plant parts or small tubers, such as chufa nutlets, also are important (Table 1). If available, native foods are predominant in the diet, especially those associated with moist-soil habitats, including millet, smartweed, bulrush, toothcup, panicum, and swamp timothy. Pintails also exploit seeds and tubers of aquatic pondweeds and bulrushes. Although they consume seeds of all sizes, they are particularly adept at harvesting smaller seeds such as toothcup, panicum, swamp timothy, and sprangletop. These native foods provide a well-balanced diet to meet nutritional needs (Table 2). Favored cereal grains include rice and barley; pintails are less likely to eat corn than are mallards.

Animal foods are important throughout the life cycle but particularly so during molt and egg laying (Fig. 4). Some of the more important invertebrates

Table 1. *Foods appearing in northern pintail diets during different events in the annual cycle.*

Food	Fall migration	Winter Unpaired	Winter Paired	Prebasic molt	Spring migration	Nesting	Ducklings	Summer molt	Fall staging
Plant									
Millet	++	++	++	++	++	+			+
Swamp timothy	++	++	++	++					
Smartweed	++	++	++	++	++	+			+
Sprangletop	+	++	++	++	++		+	+	
Toothcup	+	++	++	++	+	+			
Curly dock	+				+	+			
Panicum	++	++	++	++	++	+	+		+
Bulrush	++	+	+	+	++	++		++	++
Chufa	+	++	++	++					
Pondweeds	+				+	++	++	++	++
Sedges	+				++	++	+	++	++
Agricultural grains	++	++	++	+	+				++
Animal									
Chironomids	++	++	++	++	++	++	++	++	++
Snails			++	++	+	++	++	++	+
Odonates			+	+					
Ostracods				+					

consistently appearing in the diet are snails and chironomids. Chironomids, especially, are preferred by pintails and are extremely abundant on emergence from shallow wetlands immediately after ice-out. The arrival of pintails on many migration and breeding habitats tends to coincide with this period of emergence, and pintails forage voraciously on chironomids in such newly thawed wetlands.

Pintails strip seeds from the culms of native vegetation before seeds drop in fall. Once seeds have dropped onto the substrates, pintails dabble for these foods in shallow water (4 to 6 inches). As water deepens, pintails forage by upending, but this mode of feeding is restricted to waters <18 inches deep. Pintails have a tendency to avoid areas that are flooded too deeply if shallow sites also are present.

Habitat Management

Migration and Winter

Pintails are noted for their use of large expanses of shallow, open habitats. These wetlands often provide an abundance of food and good visibility for avoidance of predators and other disturbances during the day. At night, habitats with greater, robust cover are often sought. Although they forage in openings in southern hardwoods, pintails generally do not use flooded sites in the forest interior. Similarly, they are less apt to use woody riparian corridors than are mallards or wood ducks.

Many well-managed wetlands have the potential to provide an abundant supply of high-energy and nutritionally complete foods for pintails when water depths are <18 inches and preferably <6 inches. Gradual flooding and draining of impoundments at appropriate times during spring and fall migration create conditions that allow optimal foraging opportunities over extended periods. When impoundments vary in depth by more than 18 inches, gradual flooding increases the potential for pintails to consume more available seeds. Waters >18 inches can still provide important roost sites and give security from predators. Newly developed wetland areas are more easily managed for pintails if levees and other water control structures are configured to provide the maximum area in optimal foraging depths of ≤18 inches.

Table 2. *Nutritional values[a] of some important foods consumed by northern pintails.*

	Energy kcal/g		Percent				
Plant foods	Gross	Metabolized	Fat	Fiber	Ash	NFE[b]	Protein
Nodding smartweed	4.6	—	2.7	22.0	7.5	—	9.7
Big-seeded smartweed	4.3	1.1	2.6	19.1	3.8	67.3	10.6
Wild millet	3.9	—	2.4	23.1	18.0	40.5	9.1
Walter's millet	4.5	2.8	3.9	13.7	5.8	55.7	16.8
Sticktights	5.0	—	13.2	20.9	8.9	27.5	23.1
Rice cutgrass	3.9	3.0	2.0	10.6	9.3	57.8	12.0
Fall panicum	4.0	—	6.1	16.8	16.1	50.1	12.0
Hairy crabgrass	4.4	—	3.0	11.1	9.7	59.4	12.6
Redrooted sedge	5.2	—	—	—	—	—	—
Curly dock	4.3	—	1.2	20.4	6.9	—	10.4
Bulrush	3.5	0.8	3.0	23.6	4.3	59.1	7.2
Pondweed	3.9	0.4	2.1	20.6	15.0	50.6	14.0
Chufa seeds	—	—	22.0	5.6	5.1	58.9	8.4
Chufa tubers	4.3	—	10.6	7.3	3.1	57.1	7.0
Barley	—	2.9	2.1	7.1	3.1	—	20.0
Rice	—	2.3	9.3	11.4	9.7	73.5	10.8
Corn	4.4	3.7	4.0	2.3	1.5	77.4	11.6

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[a] Values are averages calculated from published information. Because of wide variation in values for some seeds and inconsistency in sample sizes for each nutrient, the sum of values may not be 100%.

[b] NFE = Nitrogen-free extract (highly digestible carbohydrates)

Because waste grains from agricultural production are of great importance to pintails, refuge or farm programs that make these grains available after harvest have special value for pintails in certain areas. Pintail use is increased by shallow flooding of any crop or by manipulating rice stubble by rolling or burning. Barley and rice usually are preferred over corn, although corn is consumed extensively in some locations such as the Sacramento–San Joaquin Delta of California. Maintaining ideal foraging conditions throughout winter and during spring migration provides required resources for molt, migration, and deposition of reserves for breeding. Stable water levels are undesirable, but gradual drawdowns have the potential to increase the vulnerability of invertebrate prey and to make seeds within mud substrates accessible. Furthermore, some good foraging sites should be protected from disturbance by hunters, bird watchers, aircraft, and boaters, as well as from management activities throughout fall and winter.

Breeding

The highest nesting densities occur in open habitats where vegetation is low and sparse. Common plants in these locations include prairie grasses, whitetop, nettle, spike rush, rushes, and buckbrush. Pintails nest in agricultural lands more frequently than other dabblers and readily use pastures, stubble fields, roadsides, hayfields, fallow fields, and the edges or margins around grain fields. In the boreal forest, nesting is concentrated on more open areas with sedge or grass meadows.

Establishment of tall, dense cover is a common practice to provide nesting sites for some dabblers. This practice is less valuable for pintails because they prefer sparser cover for nesting. Grazing programs that leave good residue ground cover but remove robust growth can enhance nesting cover for pintails. Well-conceived farm programs that protect habitats and ephemeral wetlands are especially important for breeding pintails. Because pintails regularly nest in agricultural lands, programs that provide benefits to farmers for delaying haying or for protecting nesting cover surrounding wetlands have the greatest potential to increase pintail recruitment.

Summary

Pintails offer a great challenge to waterfowl managers because they associate with many habitats that are used intensively by agricultural interests. Their preference for open areas and small, shallow wetlands in areas with little rainfall and recurring droughts puts a large part of their breeding area in jeopardy regarding consistent conditions. Developing farm programs compatible with pintail life history requirements offers the greatest opportunities for habitat enhancement, and therefore population recoveries by pintails on the prairies. Northern boreal and tundra habitats must be protected from loss or degradation.

Adequate migration and wintering habitats must be protected, restored, and enhanced. This will require continued acquisitions or other means of protection of key habitats and more effective management of public and private wetlands. One of the greatest opportunities to enhance wintering and migration habitats is to identify scenarios that will benefit rice culture and simultaneously provide needed resources for pintails. This adaptable, highly mobile species has a history of responding rapidly to good habitat conditions across the continent. By providing these habitats to pintails, we can assure their survival and abundance in the future.

Suggested Reading

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Appendix. Common and Scientific Names of Plants and Animals Named in Text.

Plants	
Toothcup *or* Ammania	*Ammania coccinea*
Sticktights	*Bidens* sp.
Sedges	*Carex* spp.
Redroot flatsedge	*Cyperus erythrorhizos*
Chufa flatsedge	*Cyperus esculentus*
Hairy crabgrass	*Digitaria sanguinalis*
Japanese millet	*Echinochloa crusgalli*
Walter's millet *or* wild millet	*Echinochloa walteri*
Spike rush	*Eleocharis* sp.
Swamp timothy	*Heleochloa schoenoides*
Barley	*Hordeum vulgare*
Rush	*Juncus* sp.
Rice cutgrass	*Leersia oryzoides*
Sprangletop	*Leptochloa* spp.
Rice (cultivated)	*Oryza sativa*
Panicum *or* panic grass	*Panicum* spp.
Nodding smartweed *or* smartweed	*Polygonum lapathifolium*
Big-seeded smartweed *or* Pennsylvania smartweed	*Polygonum pensylvanicum*
Pondweeds	*Potamogeton* spp.
Curly dock	*Rumex* spp.
Bulrush	*Scirpus* sp.
Whitetop	*Scolochloa festucacea*
Buckbrush *or* snowberry	*Symphoricarpos* spp.
Nettle	*Urtica* spp.
Corn *or* Indian corn	*Zea mays*
Birds	
Wood duck	*Aix sponsa*
Northern pintail	*Anas acuta*
Mallard	*Anas platyrhynchos*
Invertebrates (Families)	
Chironomids	Chironomidae
Earthworms	Lumbricidae

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WATERFOWL MANAGEMENT HANDBOOK

13.2.1. Waterfowl Use of Wetland Complexes

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Waterfowl are a diverse group of birds that have widely divergent requirements for survival and recruitment. Whistling-ducks, geese, and swans (Anserinae) and ducks (Anatinae) have contrasting life history requirements.

Several goose populations have expanded greatly despite extensive continental wetland losses and degradation. Most expanding populations nest in arctic areas where modifications or disturbance of nesting habitats have been minimal. These grazers often find suitable migratory and wintering habitats in terrestrial or agricultural environments. In contrast, ducks are less terrestrial and populations are influenced more by wetland characteristics, such as quality, total area of wetland basins, and size and configuration of these basins. Because many dabbling ducks nest in upland habitats surrounding wetlands, recruitment of waterfowl is closely tied to both terrestrial and wetland communities. Their primary upland and wetland nesting habitats, as well as migratory and wintering habitats, have been severely degraded or lost to agriculture.

Management for waterfowl in North America is complicated further because each of over 40 species has unique requirements that are associated with different wetland types. Likewise, the requirements for a single species are best supplied from a variety of wetland types.

In recent years, the relations between migrating and wintering habitats have been identified for mallards and arctic-nesting geese. These cross-seasonal effects emphasize the importance of habitats at different latitudes and locations. Thus, effective management requires an appreciation of the general patterns of resource requirements in the annual cycle. Recognition of the adaptations of waterfowl to changing wetland systems provides opportunities for managers to meet the diverse needs of waterfowl.

The Annual Cycle

Waterfowl experience events during a year that necessitate energy and other nutritional requirements above the maintenance level (Fig. 1). These additional requirements, associated with processes such as migration, molt, and reproduction, are obtained from a variety of habitats. Other factors that influence wetland use include sex, dominance, pairing status, flocking, and stage in the life cycle. All these processes influence the resources needed as well as access to habitats where required resources are available.

The large body sizes and high mobility of waterfowl allow them to transfer the required nutrients or energy among widely separated wetlands. The general pattern of reproduction in waterfowl is unusually costly for females at the time of egg laying because eggs (and often clutches) are large. The large egg size of waterfowl requires rapid transfer of protein and lipid stores from the female to the developing egg. In the wood duck, daily costs of egg production are high and

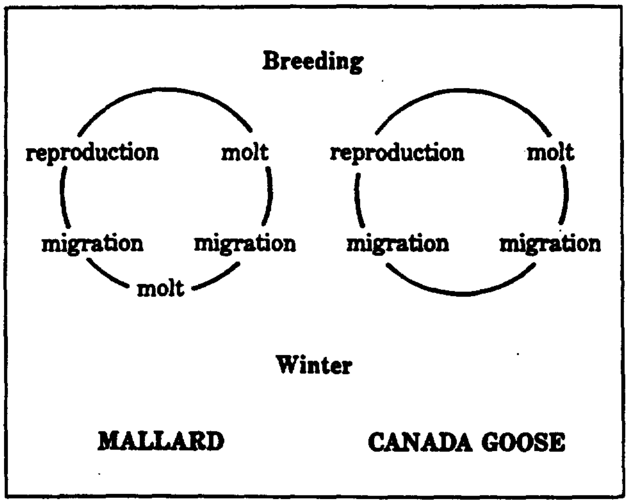


Figure 1. Major annual events in the life cycle of a mallard and a Canada goose.

Table 1. *Estimated energetic costs of some common waterfowl activities in relation to basal metabolic rate (BMR). Values represent averages from the literature.*

Activity	Estimated cost × BMR
Resting	1.3
Alert	1.5
Comfort movements	1.5
Oiling/preening	2.0
Courtship	2.0
Social interactions	3.2
Swimming	3.2
Diving	5.0
Flying	12.0–15.0
Egg laying	
Early follicular growth	16.7
Maximum during egg-laying	20+
Last egg	10.2

can exceed 210% of the basal metabolic rate (BMR) during peak demand. The daily protein requirements for egg laying are smaller than lipid requirements, but the females must meet these requirements by consuming invertebrates where they may be limiting. Parental investment after the time of hatch is small, however, compared to bird species that must brood and feed their offspring.

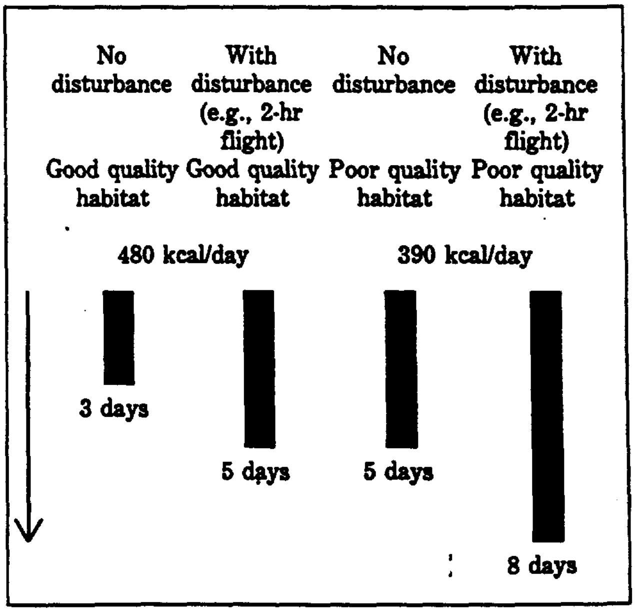
Flight is energetically expensive and is usually estimated at 12-15 × BMR (Table 1). For example, a mallard weighing 2.5 lb would require 3 days of foraging to replenish fat reserves following an 8-hr flight if caloric intake were 480 kcal/day (Fig. 2). However, if food availability were only equivalent to 390 kcal/day, then the mallard would need 5 days to replenish these reserves. If mallards must fly to reach food, the time required to replenish lost reserves is even longer. These time differences indicate the importance of well-managed areas and the need to protect waterfowl from disturbances.

The requirements for molt are poorly known or little studied, but recent information suggests the total cost of winter molt in female mallards is nearly equivalent to the energetic cost of egg laying and incubation. Not only is the loss of feathers involved, but there are thermoregulatory and foraging constraints during molt that are difficult to monitor in the field.

Waterfowl Reproductive Strategies

Each waterfowl species has a unique reproductive strategy. These strategies range from those of arctic-nesting geese, which transport large fat reserves to breeding habitats, to those of common eiders, which acquire all necessary reserves for reproduction on the breeding grounds (Fig. 3). The locations from which arctic-nesting geese acquire the different components for breeding have not been completely identified, but evidence indicates that most, if not all, of the lipid and protein

Figure 2. Time required to replenish endogenous fat reserves following an 8-hr migratory move (for a duck weighing 2.5 lb).



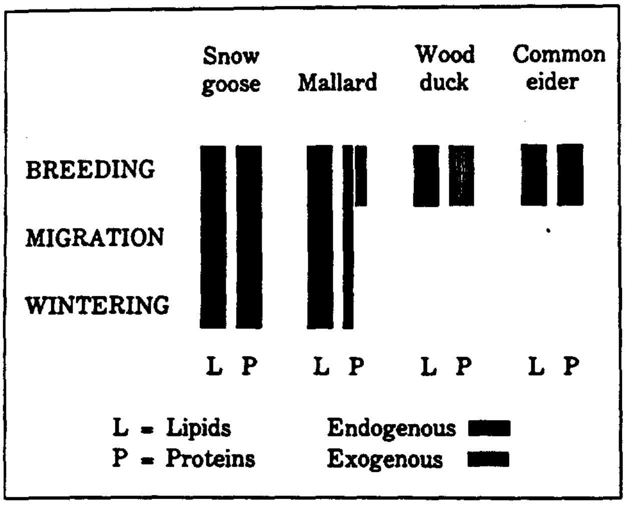


Figure 3. Reproductive strategies of four waterfowl species in relation to time in the annual cycle when the lipids and proteins for breeding are required.

resources are transported from migratory and wintering habitats as body reserves. Environmental conditions in different seasons and on widely separated habitats may have an important influence on the success of sequential activities in the annual cycle of these arctic-nesting geese.

Mallard breeding strategies differ from strategies of snow geese. Most of the lipid reserves and as much as half the protein required for reproduction in mallards are transported to the breeding grounds as body reserves. Wood ducks differ from mallards and geese because they acquire lipid and protein reserves for reproduction primarily from breeding habitats. Lipid reserves are acquired from breeding habitats before laying begins, but protein requirements are obtained solely from daily foraging. Common eiders are like wood ducks in that they acquire reserves for egg laying on the breeding grounds. But, unlike wood ducks, they acquire protein and lipid reserves for breeding and store them as reserves before laying begins.

An understanding of the range of strategies and the timing of these needs enables wetland managers at different latitudes to produce the desired resources in a timely manner.

Relation Among Habitat Variables and Waterfowl Use

Waterfowl managers have long recognized the relation among habitat structure, water depth, and water use by waterfowl. The stage in the annual cycle and the associated behavioral adaptations of waterfowl determine which resources managers must provide.

Table 2. *Water depths and vegetative characteristics at foraging sites of some North American waterfowl.*

Species	Water depth	Vegetative structure
Small Canada geese	dry, mudflat	Short herbaceous
Large Canada geese	dry, mudflat, <10 inches	Short herbaceous, rank seed-producing annuals
Northern pintail	<10 inches	Open water with short, sparse vegetation
Mallard	<10 inches	Small openings, tolerate robust vegetation
Ring-necked duck	>10 inches	Scattered, robust emergents
Lesser scaup	>10 inches	Open water, scattered submergents

Appropriate water depths should be available for effective waterfowl management. Shallow water is essential for dabblers because the optimum foraging depth is 2–10 in. (Table 2). Although diving ducks can exploit deeper water, there is little justification to provide deep waters when they can reach food resources in shallow water. Such strategies decrease costs associated with pumping or supplying water for waterfowl.

Waterfowl have various tolerances for the height and density of vegetation. Sea ducks and divers are adapted to large bodies of open water. Mallards, wood ducks, and blue-winged teal readily use habitats with dense vegetation; northern pintails prefer shallow, open habitats where visibility is good and vegetation sparse.

Little information is available on how waterfowl make decisions relating to where they feed and which foods they select. Nevertheless, geese are known for their seeming ability to select forage of high nutritional content. Complex habitat and nutritional requirements, in conjunction with recent losses and degradations of wetland habitats, require managers to consider a wide array of factors when attempting to optimize use by waterfowl (Table 3).

When conflicting factors are apparent, advanced planning is essential to optimize and maintain desired use of habitats. Such conflicts are apparent to managers facing difficult decisions

Table 3. *Important considerations to ensure optimum use of wetland complexes by waterfowl.*

1) **Life cycle event**
    - Molt
    - Reproduction
    - Migration
2) **Behavioral activities**
    - Roosting
    - Social behavior
    - Foraging
3) **Habitat structure**
4) **Water depth/regimes**
5) **Food quality/type**
6) **Wetland complex**
7) **Disease**
8) **Habitat degradations**
    - Habitat losses
    - Habitat perturbations
        - Toxicants
        - Turbidity
        - Modified hydrology
        - Modified structure
9) **Disturbance**
    - Hunting
    - Other recreation
        - Fishing
        - Water skiing
        - Bird watching
    - Aircraft—military and commercial
    - Research/management
    - Industrial/commercial

because the site may provide habitats for breeding, migratory, and wintering waterfowl. Determining a reasonable balance of the resources required to meet seasonal requirements of all populations of waterfowl using a specific refuge undoubtedly is more challenging than determining the species of plants needed to provide food and cover.

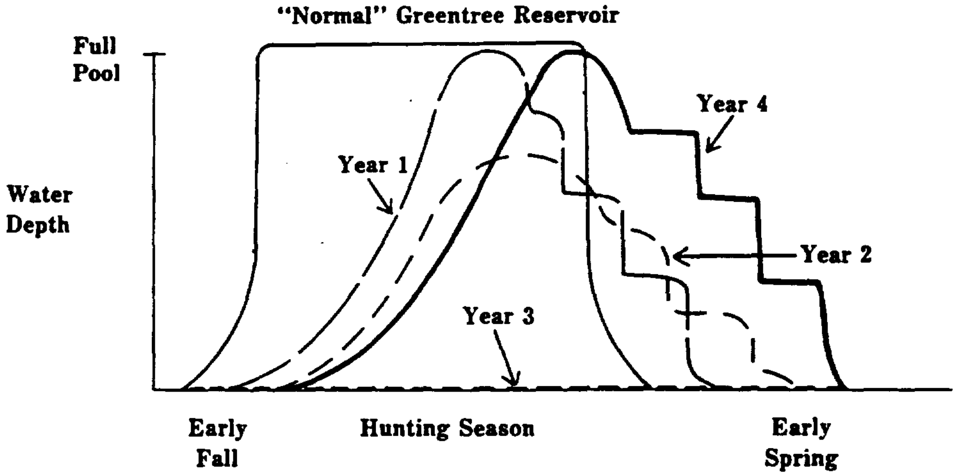
Resource Availability and Exploitation by Waterfowl

By understanding how waterfowl use resources, managers are able to attract and hold waterfowl on managed habitats. Monocultures should be avoided, whether natural plant communities (such as large expanses of dense cattail) or agricultural crops. Manipulation of soil and water to produce habitat structure or foods essential as life requisites may be a necessary part of refuge management. Production of these requisites does not ensure that waterfowl will use the resources.

Foods are only accessible if (1) appropriate water depths are maintained during critical time periods, (2) habitats are protected from disturbance, and (3) habitats that provide protein and energy are close to one another. Disturbance is particularly damaging, because it affects access to and acquisition of requirements throughout the annual cycle (Table 2, Fig. 2). The subtle effects of bird watchers, researchers, and refuge activities during critical biological events may be as detrimental to waterfowl populations as hunting or other water-related recreational activities (boating, etc.). At certain locations, predators or activities associated with barge traffic, oil exploration, or other industrial or military operations are detrimental.

Identification of the proportions of each wetland type within refuge boundaries, and of the potential for management within each wetland type, is essential. Wetlands on private or other public property within 10 miles of the refuge boundary should also be used to estimate resources within the foraging range of most waterfowl. As wetlands are lost on areas surrounding refuges, managers will be able to identify special values or needs for certain habitat types on refuges. For example, producing only row crops on refuge lands in extensive areas of agriculture may be less valuable than supplying natural vegetation and associated invertebrates to complement these high-energy agricultural foods. Furthermore, the presence of toxicants or disease may preclude use of some wetlands.

An important part of management is identification of wetlands that are productive and unmodified. These wetlands should be protected in their natural state rather than changed by development. Where man-made or modified wetlands are managed, manipulations that emulate natural wetland complexes and water regimes provide diverse habitats for a variety of waterbirds. Well-timed, gradual changes in water level are effective approaches that provide good conditions for producing foods and desirable foraging depths for game and nongame birds. In fall, many southern habitats are dry, but having pools full before waterfowl arrive and maintaining pools at capacity until after their departure may reduce access to many resources by waterfowl. By providing changing water depths in greentree reservoirs or elsewhere, managers can enhance cost-effectiveness by assuring that resources produced are also used effectively. For example, a management scenario for modifying the time and pattern of fall flooding in a greentree reservoir or a moist-soil impoundment might include four or more approaches to flooding (Figs. 4 and 5).



Rationale

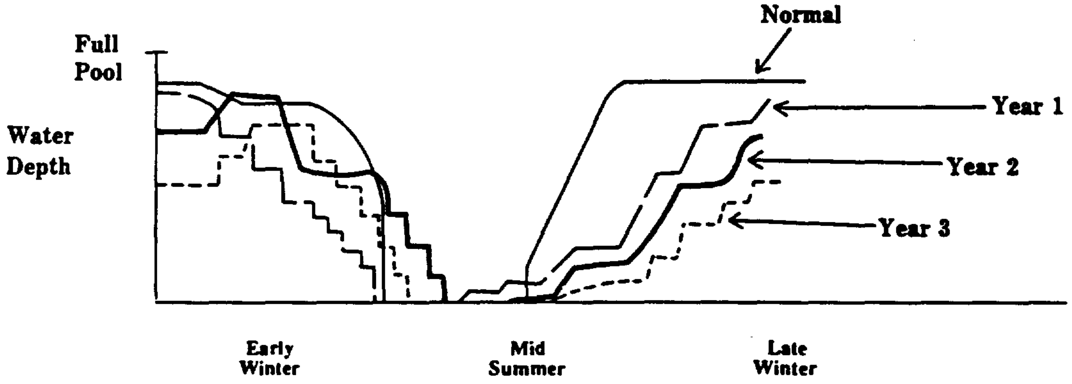
Year 1 - Gradual flooding to provide access to food resources on a continuing basis throughout the hunting season. Gradual drawdowns commence before the end of the waterfowl season.

Year 2 - Gradual flooding but water levels never reach full pool. Gradual drawdown extending into spring.

Year 3 - No flooding.

Year 4 - Similar to Year 1, but full pool not reached until end of hunting season. Gradual drawdown extending well into spring.

Figure 4. Suggested flooding regimes for southern greentree reservoirs.



Rationale

Normal - Typical midsummer drawdown to establish moist-soil vegetation. Fall and winter flooding for waterfowl.

Year 1 - Gradual drawdown to optimize use by late spring migrants. Gradual reflooding for rails and waders.

Year 2 - Gradual drawdown lasting into midsummer to optimize use by late spring, migrant waterfowl, shorebirds, and waders. Gradual reflooding in fall to optimize use of seed resources.

Year 3 - Increasing water depths in spring to make food resources available. Gradual drawdown by late spring, followed by gradual reflooding in fall to shallow depths.

Figure 5. Suggested flooding regimes for seasonally flooded wetlands of the Midwest.

By recognizing the importance of natural wetland complexes throughout the annual cycles of waterfowl, managers can provide waterfowl with required resources.

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Appendix. Common and Scientific Names of Animals Named in Text.

Wood duck	*Aix sponsa*
Northern pintail	*Anas acuta*
Blue-winged teal	*Anas discors*
Mallard	*Anas platyrhynchos*
Lesser scaup	*Aythya affinis*
Ring-necked duck	*Aythya collaris*
Canada goose	*Branta canadensis*
Snow goose	*Chen caerulescens*
Common eider	*Somateria mollissima*

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13.3.2. Initial Considerations for Sampling Wetland Invertebrates

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As the importance of invertebrates to waterbird nutrition and detrital processing has become increasingly evident, the need for effective and efficient invertebrate sampling has grown. Identification of invertebrate responses to management requires sampling and selection of appropriate sampling equipment. Goals must be established according to qualitative or quantitative needs, organism characteristics, and wetland types. Management objectives often can be met by sampling specific invertebrates to index the effect of management rather than through long-term studies requiring large sample sizes and intensive effort. Certain wetland and invertebrate characteristics that should be considered when initiating invertebrate sampling are described below.

Identification of Goals

The initial consideration in any collection of management data is how these data will facilitate more effective management. In most wetland management situations, the first step toward evaluating invertebrate populations is identification of dominant organisms. This can be accomplished by a qualitative approach using simple techniques and relatively few samples. In contrast, when comparisons of sites, techniques, or seasonal and annual variations are desired, quantitative methods are necessary and require more time and effort. Invertebrate communities can be measured using organism occurrence (presence or absence), density (number of organisms per area), and biomass (weight per sample or area). Species diversity, which embraces number and relative abundance of the species, is also commonly used for comparative purposes when monitoring different wetland sites.

Before a biologist can successfully assess invertebrate responses to management, the appropriate taxonomic classification for target species must be identified. The effort required to identify aquatic invertebrates to genus or species is often unnecessary for management purposes. However, grouping invertebrates above the family level may be too broad a classification to identify the functional roles of the organisms within the wetland system or their life history strategies. In general, identification to family is usually adequate for management studies, whereas identification to genus may be appropriate for research endeavors.

Organism characteristics should be considered when developing sampling regimes. Life history considerations should include type and timing of various developmental stages. Invertebrate survival generally drops rapidly during early age classes (Fig. 1). Because of this characteristic, managers should not become alarmed when observing temporal declines in total numbers within a species. Likewise, year-to-year comparisons should be conducted at approximately the same period in an annual cycle.

A good sampling design requires recognition of varying physical parameters of the wetland and water regime. Stream and lake systems usually are sampled in different ways. Extremes in water depth during the annual water regime may dictate the type of sampling gear that will be most effective (Table 1). Where benthos are sampled, substrate type influences choice of equipment. Density and structure of vegetation influence water column sampling. For example, sturdy, emergent vegetation may prevent effective sampling with a sweep net, whereas activity traps can be used effectively in these vegetated zones.

Sampling Technique

The effectiveness of common sampling apparatus in different invertebrate habitats is outlined in Table 1. Benthos samplers include dredges and core samplers. Core samplers are extremely effective and inexpensive and can be small and lightweight. Core samplers may be made from lightweight PVC pipe, and plastic or metal edges can be added to cut roots or crusted soils. Dredges are poor choices

Table 1. *The advantages and disadvantages of sampling apparatus for wetland invertebrates.*

Microhabitat	Apparatus	Advantages	Disadvantages
Benthos sediments	Ekman dredge, Ponar dredge	Good for deep water sampling from boat, where bottom sediments are soft	Ineffective in vegetation zones or rocks Difficult to carry Expensive
	Stovepipe sampler	Good for deep sediment samples in moderate water depths	Heavy, difficult to carry in field Expensive
	Core sampler	Can be used effectively in diversity of habitats Volume/depth of sampling easily modified by design Lightweight, inexpensive	Must use with SCUBA in deep water
Water column	Column sampler	Can sample both water column and sediments	May require long field time for small sample size Awkward to carry Expensive
	Sweep net	Provides area-density estimate Lightweight, easy to carry in field Inexpensive	Variation between collectors Difficult to use in dense, robust vegetation
	Activity trap	Standardized procedure Reduced field time Provides samples free of plant/detrital material	Does not give area-density index Predation in traps by fish and invertebrates Passive sampler—may underestimate sedentary organisms
Aerial	Emergence traps	Quantified sample Density estimates	Requires trap construction and maintenance Expensive
	Light traps	Time index Ability to collect large qualitative samples	Not an area-density index Mainly nocturnal trap
	Aerial sweep net	Qualitative samples Inexpensive	Not an area-density index Biased sampling
Shoreline	Core samplers	Area-density for semi-aquatic/terrestrial invertebrates Inexpensive	
	Activity traps/mesh bags	Good time index for mobile invertebrates Good in leaf-based detritivore systems	Passive trap Need to continually move trap in dynamic system Expensive

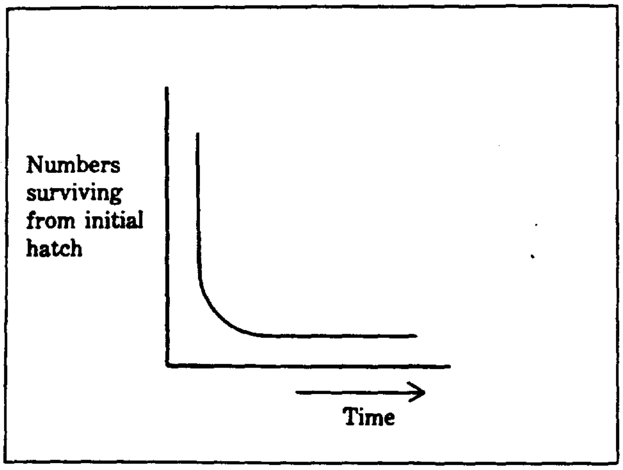

Figure 1. Type III survival curve—typical survival for most aquatic invertebrate populations.

in vegetated zones because the springs are usually activated before reaching the sediments, or the jaws will not close sufficiently to contain the entire sample. Nevertheless, in some deep-water areas they offer an acceptable approach. Stovepipe samplers have been used effectively for benthos, but they are often cumbersome for field work. Samples from all these apparatus may be washed through standard sieves to eliminate mud and roots.

Water column samplers include tubular column samplers, sweep nets, and activity traps. Column samplers are expensive and do not work well when submergent vegetation is sampled. Sweep nets are easily manipulated, and field time can be decreased if net inserts are used. Net inserts are constructed of fine netting. These inserts are secured in the larger, coarse net, removed after each sweep, placed in a plastic, zip-lock bag, and transported to the lab. Another insert is used for the next sweep. If more than one technician is available, activity traps may be used for sampling, but those traps are expensive and time-consuming to use. Aerial samples may be collected with quantifiable emergence traps, with qualitative light traps, or with sweep nets. Shoreline samples may be collected with core samples or with replicate mesh traps.

Manpower, time investment, and technical expertise must be considered when developing sampling schemes. Diversity among wetlands and their invertebrate communities may require complex sampling methods (Table 2). Field collections for quantitative sampling demand a relatively small amount of time compared to the investment required for sorting, identification, and analysis (Fig. 2).

The techniques listed here provide a framework for sampling. More specific sampling gear can be constructed for the needs of a specific study, but standardization for comparison among other regions is also desirable. Sampling of wetland invertebrates can be conducted for broad qualitative surveys, site or treatment comparisons, or as a long-term index. The needs for long-term sampling should be continually reappraised as long-term management goals are modified.

Table 2. *Examples of potential apparatus selection based on wetland type and project goal.*

Wetland habitat	Project goal	Considerations*	Potential apparatus
Seasonally flooded, annual grasses dominant	Compare general invertebrate fauna associated with dominant plant type	Need index	Sweep net/activity traps
Seasonally flooded, annual grasses dominant	Document peak hatch of midges/ mayflies for potential swallow predation	Need to capture emerging subadults	Emergence traps
Semipermanent, cattails dominant	Compare general invertebrate fauna under varying water regimes	Need index Robust vegetation	Activity traps
Seasonally flooded, pin oak forest	Compare general invertebrate fauna between two greentree reservoirs	Twig/leaf material as substrate	Activity traps/mesh bags
Lacustrine beach	Sample potential foods of a shorebird species	Sample location of feeding birds May include terrestrial environments	Core sampler and sticky traps
Deep, large river	Sample clam population in diving duck feeding area	Deep water, current, and soft substrate	Ponar/Ekman dredge

*Viable replication is a concern in each sample.

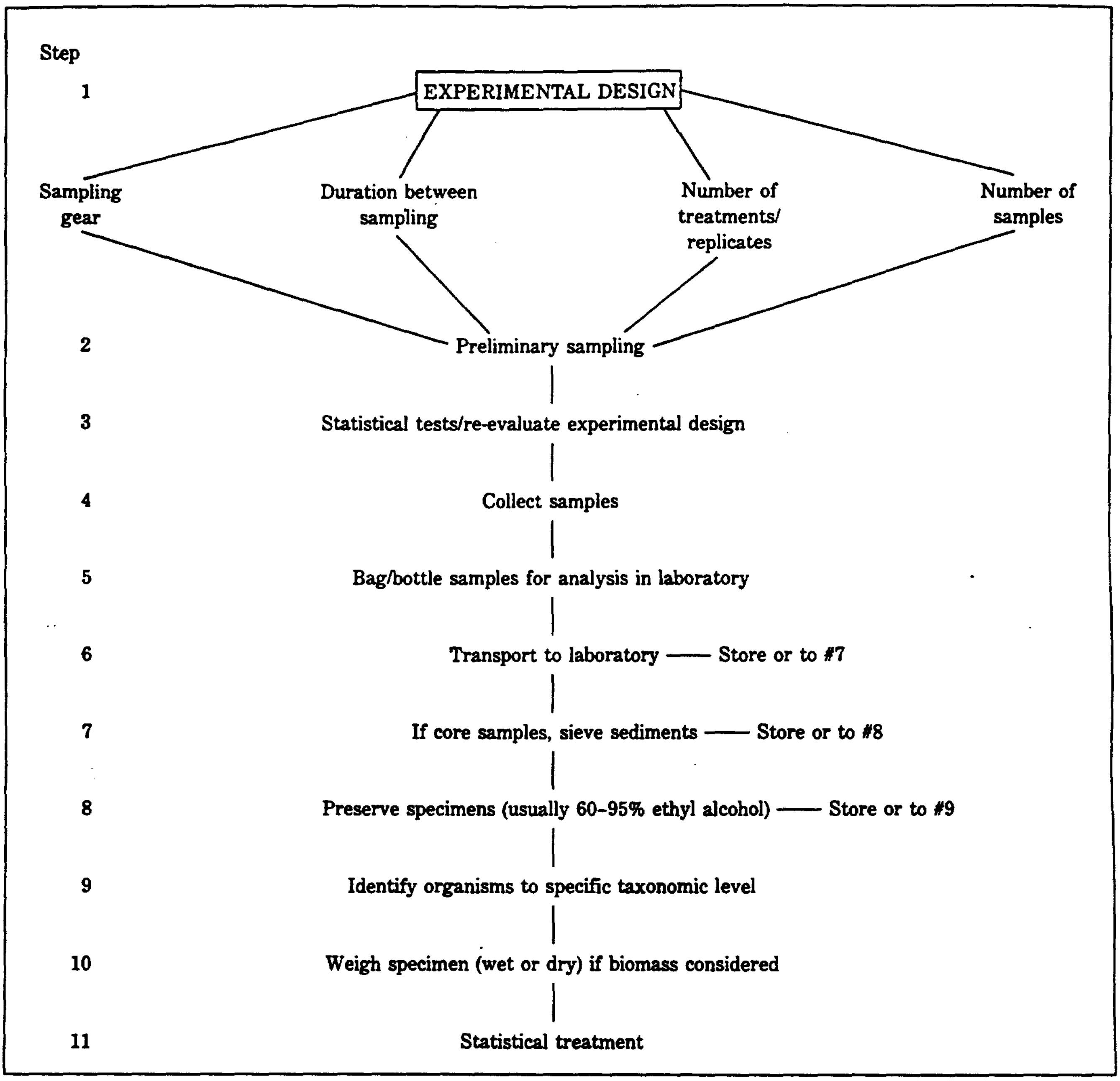

Figure 2. Chronology of steps in wetland invertebrate sampling.

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13.3.3. Aquatic Invertebrates Important for Waterfowl Production

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Aquatic invertebrates play a critical role in the diet of female ducks during the breeding season. Most waterfowl hens shift from a winter diet of seeds and plant material to a spring diet of mainly invertebrates. The purpose of this chapter is to give managers a quick reference to the important invertebrate groups that prairie-nesting ducks consume.

Waterfowl species depend differentially on the various groups of invertebrates present in prairie wetlands, but a few generalizations are possible. Snails, crustaceans, and insects are important invertebrate groups for reproducing ducks (Table). Most species of laying hens rely on calcium from snail shells for egg production. The northern shoveler and gadwall are dependent on crustaceans that swim in the water and forage on algae and fine organic matter. The northern shoveler has an enlarged bill and finely developed lamellae for sieving crustacea from the water. Early-nesting species such as northern pintails and mallards consume early-emerging midge larvae in addition to earthworms, which are often the most available food in ephemeral wetlands shortly after the snowmelt. The diving ducks consume free swimming amphipods or larger insects such as caddis fly and dragonfly larvae that tend to occur in deeper water.

The community of invertebrates present in a wetland can indicate the history of water changes in that wetland. For example, invertebrates such as leeches, earthworms, zooplankton, amphipods, isopods, and gastropods are dependent on passive dispersal (they can't leave the wetland under their own power). As a result, they have elaborate mechanisms to deal with drought and freezing. A second group that includes some beetles and most midges can withstand drought and freezing but requires water to lay eggs in spring. A third group that includes dragonflies, mosquitoes, and phantom midges lays eggs in the moist mud of drying wetlands during summer. A fourth group that includes most aquatic bugs and some beetles cannot cope with drying and freezing, so they leave shallow wetlands to overwinter in larger bodies of water. Managers can use the presence of these invertebrates to determine the effectiveness of water management regimes designed for waterfowl production.

The following descriptions of invertebrate natural history are based on Pennak (1978).

Invertebrate Natural History

OLIGOCHAETA (Aquatic and Terrestrial Earthworms)

Natural History: Earthworms mix the substrate soils and consume algae and detritus. Their distribution is usually not limited by temperature and many truly aquatic forms survive in low oxygen concentrations. Some earthworms form cysts or cocoons that are transported by birds or the wind.

Table. *Invertebrate classification. The following is a list of the taxonomy of aquatic organisms that will serve most management purposes.*

Phylum	Class	Order
Annelida	Oligochaeta (terrestrial and aquatic earthworms)	
	Hirudinea (leeches)	
Arthropoda	Crustacea	Anostraca (fairy shrimp)
		Conchostraca (clam shrimp)
		Cladocera (water fleas)
		Copepoda (copepods)
		Ostracoda (seed shrimp)
		Amphipoda (scuds and side-swimmers)
	Insecta	Ephemeroptera (mayflies)
		Odonata (dragonflies)
		Hemiptera (true bugs)
		Trichoptera (caddis flies)
		Coleoptera (beetles)
		Diptera (flies and midges)
		Lepidoptera (butterflies and moths)
Mollusca	Gastropoda (snails)	

Importance to Waterfowl: Terrestrial earthworms in temporarily flooded, ephemeral ponds early in spring are particularly important to early-nesting mallard and northern pintail hens.

HIRUDINEA (Leeches)

Natural History: Some leeches are blood sucking and forage on birds, mammals, fish, snails, insects, and earthworms. Leeches prefer warm water, and are common in protected shallows. They are primarily nocturnal and require a substrate of rocks or vegetation, so they are uncommon in wetlands that have pure mud or clay bottoms. Leeches survive winter and droughts by burrowing into the mud and becoming dormant.
Importance to Waterfowl: Leeches are not particularly important to waterfowl as food, although they are eaten by mallards in small amounts.

Crustacea

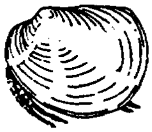
ANOSTRACA (Fairy Shrimp)

General Description: Fairy shrimp generally swim on their backs. They have 2 stalked, compound eyes, 11 pairs of swimming legs that resemble paddles, and no hard external covering.

Natural History: Fairy shrimp are common in small ephemeral and temporary ponds early in spring. They glide upside down, beating their legs in a wave-like pattern from tail to head. Their leg action draws food into the ventral groove toward the mouth. They feed on algae, bacteria, protozoa, and bits of detritus.

Fairy shrimp lay two kinds of eggs: summer eggs that hatch soon after laying, and resting eggs that sink to the bottom, where they withstand drying or freezing and hatch the next spring. Larvae develop through a series of "nauplius" instars and mature rapidly; some become adults in as few as 15 days.
Importance to Waterfowl: Because fairy shrimp are among the first invertebrates in spring, they are consumed by early laying northern pintail and mallard hens. They also occur in the diets of northern shoveler and blue-winged teal.

CONCHOSTRACA (Clam Shrimp)



General Description: This organism is enclosed in a shell-like outer carapace, and resembles a tiny swimming clam. Clam shrimp have 10–32 pairs of legs and 2 pairs of antennae.
Natural History: Clam shrimp seem to prefer brackish water and swim by moving their large biramous antennae in a rowing motion. Their natural history is similar to that of the fairy shrimp.
Importance to Waterfowl: Clam shrimp form an important part of the diet of laying gadwall hens, and also occur in the diet of mallards and northern shovelers.

CLADOCERA (Water Fleas)

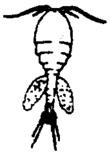
General Description: Water fleas range in size from 0.2 to 3.0 mm long. Superficially, the body appears bivalve with the abdomen and thoracic regions covered by a carapace. The head is compact with two large, compound eyes. Water fleas have large antennae with two segmented rami extending from a large base. They have five to six pairs of biramous legs that are hidden in the carapace.

Natural History: Water fleas use their antennae to swim and appear to hop uncertainly in the water. Their legs produce a current between the valves of their carapace where food collects in the median groove and streams toward the mouth. Algae, detritus, and protozoans are the major items consumed. Water fleas migrate vertically, moving upward in the evening and downward at dawn. They can exist in a variety of temperature and oxygen concentrations.

Water fleas hatch from resting eggs at first thaw. As the water warms they reproduce rapidly, often reaching a large population of 200–500 fleas per liter of water. The population wanes and by summer, few are present in the ponds. Usually they reproduce parthenogenetically; however, as conditions deteriorate later in the season, they produce eggs.

Importance to Waterfowl: Water fleas form a major part of the diet of the laying northern shoveler. Cladocera are also consumed by gadwall and mallard hens.

COPEPODA (Copepods)



General Description: Most copepods are less than 2.0 mm long. Usually they are drab in color; however, in spring, some species are bright orange, purple, and red. The head and part of the thorax are fused in a cephalothorax. The remainder of the thorax and abdomen are segmented. Copepods have large antennae and five thoracic segments that have legs that are used for swimming. They have no abdominal appendages.

Natural History: Most copepods forage on algae, plankton, and detritus. Some forage by scraping food from the pond bottom and some by filtering plankton from the water. Many swim in a smooth, slow motion that is produced by the feeding movements of the mouthparts and antennae, punctuated by jerky leg movements. The front antennae are held stiff and act as a parachute to keep the copepod from sinking.

Copepods breed throughout summer, and are tolerant of oxygen depleted water and adverse conditions such as drying and freezing. Some survive winter as resting eggs, some go into diapause on the wetland bottom and others form cysts or cocoons. Development is through a series of stages before sexual maturity. The time to maturity varies, depending on the environment and the species.

Importance to Waterfowl: Waterfowl do not depend on this group but copepods account for a small portion of the diet of laying northern shoveler and gadwall hens.

OSTRACODA (Seed Shrimp)

General Description: Superficially, ostracods resemble tiny seeds. They are usually less than 1 mm long with an opaque, bivalve shell that varies in color.

Natural History: Seed shrimp tolerate a wide range of environments, temperature, and water chemistry. Most species occur in water less than 1 m deep on varying substrates. Omnivorous scavengers, they forage on bacteria, molds, algae, and fine detritus. Eggs can suspend development in dry and freezing conditions and some live as long as 20 years in the dried condition.

Importance to Waterfowl: Seed shrimp, like copepods, do not dominate the diet of laying females; however, they are consumed in small amounts by gadwall, northern shoveler, and blue-winged teal.

AMPHIPODA (Scuds, Side-swimmers, or Freshwater Shrimp)

General Description: Most amphipods are 5–20 mm long with segmented thorax and abdomen. Their eyes are usually well developed.

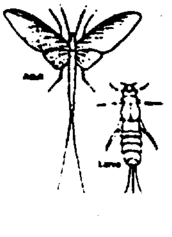
Natural History: Amphipods are primarily nocturnal. They swim rapidly just above the substrate, rolling from side to back. Omnivorous scavengers, they consume various plant and animal material. They often browse on the film covering vegetation that is composed of microscopic plants, animals, and detritus.

Amphipods are restricted to cold, shallow water, and an abundance of oxygen is essential. They are generally found in permanent wetlands where they can become abundant, and are not generally adaptable to withstanding droughts.

Importance to Waterfowl: Amphipods are very important to scaup, especially in fall, but they are not particularly important for dabbling ducks. Blue-winged teal, gadwalls, and mallards consume small amounts.

Insecta

EPHEMEROPTERA (Mayflies)

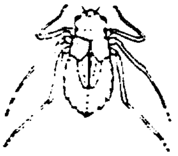


General Description: The aquatic juvenile stage of a mayfly, known as a nymph, is characterized by a long body with a large head, large eyes, and long antennae. The tracheal gills on the abdominal segments are the important feature for distinguishing the mayfly nymph from other insects.

Natural History: Mayflies occur in fresh water with a high oxygen concentration. Most are herbivores or detritivores, however, some are carnivorous and feed on midge larvae. Mayflies are nymphs most of their lives, which can extend for 1–3 years. Adults live 24 h to a few days, mate, lay eggs, and then die.

Importance to Waterfowl: Although mayfly nymphs are not an important item in the diets of waterfowl, they are commonly found in wetlands.

ODONATA (Dragonflies, Damselflies)

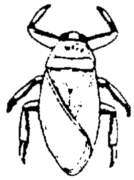


General Description: Nymph—Dragonfly nymphs according to Pennack are "... grotesque creatures, robust or elongated and gray, greenish or somber-colored." The body may be smooth or rough, bearing small spines; it is often covered with growths of filamentous algae and debris. The most striking feature of the larva is the modified mouthparts that are large and folded under the head and thorax.

Natural History: Many dragonflies and damselflies live for 1 year but the large aeschnids live for about 4 years. Odonate nymphs are carnivorous. Nymphs emerge from the water in the morning.

Importance to Waterfowl: Dragonfly nymphs are more important to diving ducks than to dabbling ducks.

HEMIPTERA (True Bugs)



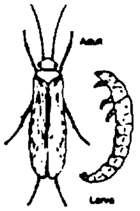
General Description: True bugs have mouthparts that form a piercing beak. Their wings are leathery at the base and membranous at the tip. Their size and shape varies.

Natural History: Aquatic bugs are predaceous, primarily foraging on other insects. They grasp their prey with specialized front legs and suck body fluids with their beak. They winter as adults hidden in the mud and vegetation.

Importance to Waterfowl: Hemiptera occur in small amounts in the diets of gadwall, blue-winged teal, and northern shoveler hens.

TRICHOPTERA (Caddis Flies)

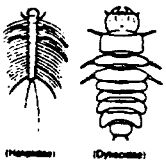
General Description: Adult—Adults are small and inconspicuous. They resemble moths with folded wings and a dodging flight pattern. Caddis fly larvae are aquatic and most build portable cases of debris.



Natural History: Caddis flies occur in a variety of wetland types that have sufficient oxygen concentrations. They may have one or two generations per year and many larvae overwinter in the wetland. Most are omnivorous but there are grazers, scrapers, suspension feeders, filter feeders, and carnivores.

Importance to Waterfowl: Caddis flies are particularly important to laying canvasbacks and they also occur in the diets of mallard, gadwall, blue-winged teal, and redhead hens.

COLEOPTERA (Beetles)



General Description: Beetles are easily distinguished as adults—their forewings are modified into horny shields that cover the abdomen. Larvae are long and thin with six legs—three on a side—characteristic of insects.

Natural History: Most adult aquatic beetles are dependent on air. Adults and larvae occur in shallow water near shore, particularly where there are quantities of debris and aquatic vegetation. Beetles are generally absent from wave-swept shores and deep water. Adults overwinter by burrowing into debris or mud on the bottom of the wetland. The aquatic larvae are highly variable; for example, Dytiscidae (predatory diving beetles) are adapted for a carnivorous life style, whereas Haliplidae (crawling water beetles) larvae are vegetarian, sluggish, and sticklike in appearance. Aquatic beetles often have terrestrial pupae.

Importance to Waterfowl: Aquatic beetles occur in small amounts in the diets of gadwall, mallard, northern pintail, blue-winged teal, northern shoveler, redhead, and canvasback hens.

DIPTERA (Flies and Midges)

General Description: This order includes all two-winged flies such as horseflies, mosquitoes, crane flies, midges, houseflies, hover flies, and bot flies. Aquatic diptera larvae are highly variable; most are wormlike and lack eyes or jointed thoracic legs. Their bodies are usually soft and flexible. Some larvae such as midges (Chironomidae) have short, stumpy forelegs.

Natural History: Midges are especially important to waterfowl. They occur throughout aquatic vegetation and on the bottom of all types of wetlands. Many hide in fragile tubes they construct of algae and silt. The most abundant type, known as "bloodworms," are bright red in color. Midge larvae are chiefly herbivorous and feed on algae, higher plants, and detritus.
Importance to Waterfowl: Aquatic Diptera are of major importance to blue-winged teal, northern pintail, mallard, gadwall, and redhead hens.

LEPIDOPTERA (Butterflies and Moths)

General Description: Only one family of Lepidoptera have larvae that are truly aquatic. These larvae resemble terrestrial caterpillars—adults are small and inconspicuous.
Natural History: The aquatic moth larvae are found in ponds that are densely overgrown with aquatic vegetation. Larvae often construct cases with two leaves and crawl around with the case. Species winter as immature larvae.
Importance to Waterfowl: Moth larvae are only of minor importance to mallard hens.

GASTROPODA (Snails)

General Description: Most snails are readily identified because of their coiled shell.
Natural History: Most snails are vegetarian. They consume the film of algae that coats submerged surfaces. Many are hermaphroditic and may be self-fertilized or cross-fertilized. Eggs are often deposited in a gelatinous mass in spring, and early development takes place before hatch. When a snail leaves the egg mass, it has taken on the morphological characteristics of the adult. Most snails live 9 to 15 months. In warmer climates, snails may have two to three generations per year. They overwinter by burrowing into the mud and hibernating.

Snails are most common in shallow water, less than 3 m deep. Most species occur in greatest abundance in slightly alkaline conditions. They need calcium carbonate for shell production. They also need water that is clean and has high levels of dissolved oxygen.
Importance to Waterfowl: Snails are very important as a source of calcium for most laying ducks.

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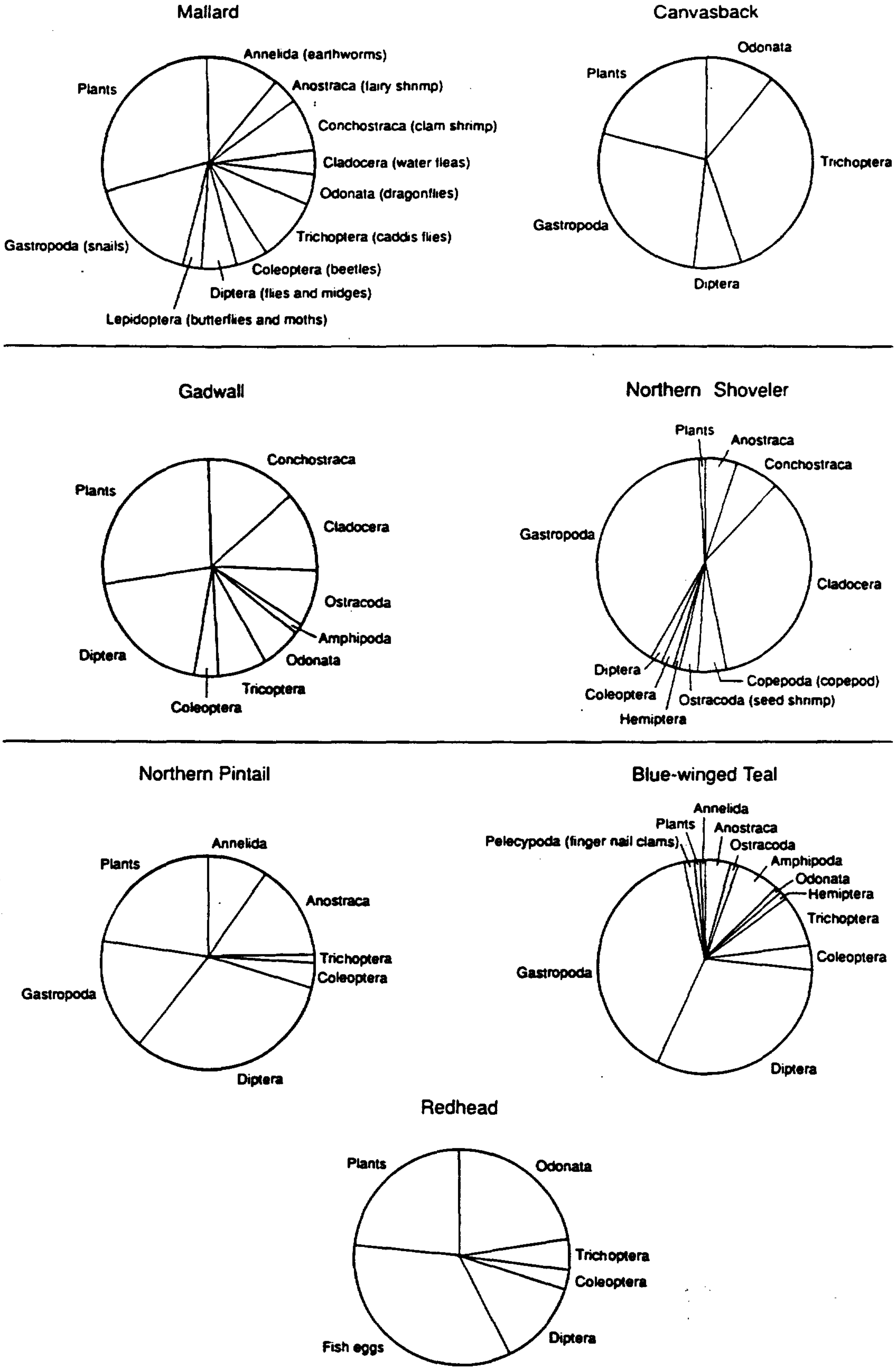

Dietary preferences by laying females of 7 duck species.

1436

Alaska Goose Populations: Past, Present and Future

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Many people think Alaska remains a pristine wilderness and that wildlife populations are still at prehistoric levels. This very likely is not true for the 11 species and subspecies of geese that nest in Alaska. Large, widely dispersed populations of geese were observed near the turn of the century. Even in the early 1970s, it was estimated that Alaskan habitats were used by 915,000 nesting and 100,000 additional migrating geese each year (King and Lensink 1971). Since then the Alaskan populations of most of these species have declined, some to dramatically low levels (Raveling 1984), even though habitats within the state have remained largely unaltered by man.

The U.S. has treaties with Canada, Mexico, Japan and the Soviet Union to protect geese and other shared migratory birds, confirming international concern for the welfare of this resource. Cooperative research on Alaskan geese during the past several decades has given understanding of their migration corridors, staging and wintering habitats, and the principal places where they are hunted, thereby providing information needed to develop effective management plans. The only attempt to reintroduce geese in Alaska has been in the Aleutian Islands. Other opportunities exist.

It is our intent here to: (1) review the historic and current status and important habitats of geese that occur in Alaska; (2) identify existing and potential threats to these populations; and (3) offer alternative management approaches for geese in Alaska.

Distribution of Alaska Goose Habitats

Six biogeographic regions (Kessel and Gibson 1978, Armstrong 1980) characterize distribution of geese in Alaska (Figure 1). The three southern regions have marine climates that permit geese and other water birds to over-winter. By contrast, the three northern areas are very cold from mid-October to mid-April, thus geese from those areas are forced to migrate. Eastern regions of Alaska are forested, while the western and northern regions are essentially treeless. All regions are mountainous, with geese using alluvial outwash plains, deltas, river valleys and, occasionally, hillsides below the 2,000-foot (610 m) contour. The highest densities of nesting geese occur in the western region. The three southern regions are part of the northern temperate zone, have the longest ice-free period and provide important staging areas where geese build fat reserves during spring and fall migrations. High tidal fluctuations on the north Pacific and southern Bering Sea coasts, often 20 feet (6.1 m) or more, result in one of the richest and most-extensive intertidal habitats of the world. The river system of the central region, which reach peak flows during snow melt, have a shallow gradient, and portions of their floodplains drain slowly. This precludes growth of shrubs; but allows sedges and grasses that provide goose forage to develop in midsummer. The main stem of the Yukon River has thousands of eroding and accreting islands dominated by early successional plants favored by geese.

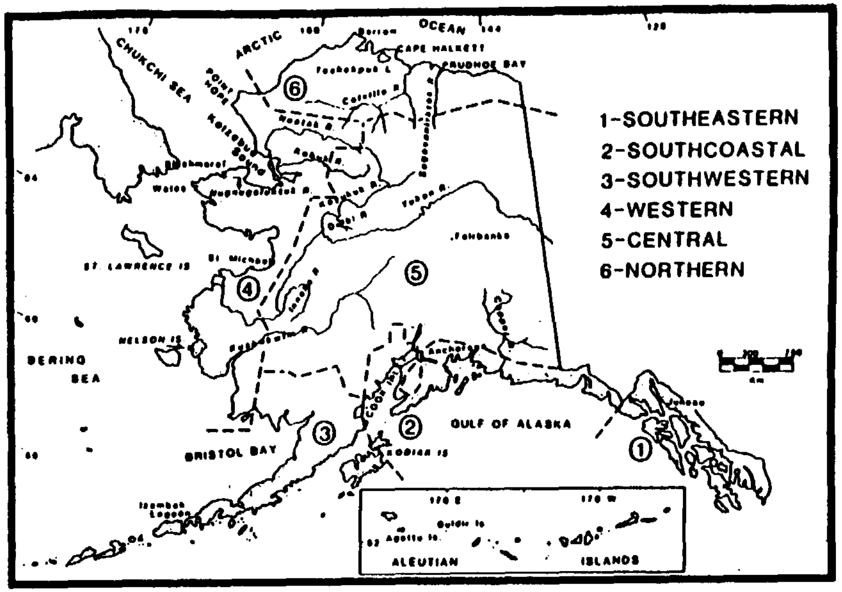

Figure 1. Biogeographic regions of Alaska (adapted from Kessel and Gibson 1978, Armstrong 1980).

Status of Alaska Goose Populations

Ornithologists have described the status of Alaskan goose populations over the past century (Nelson 1887, Bailey, 1948, Gabrielson and Lincoln 1959, Palmer 1976, Bellrose 1980). These accounts, plus our knowledge of the requirements of geese, provide insight about the decline and potential for expansion of these populations. This paper does not address whether there are resources and habitat to support more wintering geese outside Alaska, but Raveling (1984) stated that available areas and food supplies used by greater white-fronted geese (*Anser albifrons frontalis*) and cackling Canada geese (*Branta canadensis minima*) are more than adequate to sustain much larger populations.

Greater White-fronted Goose

The greater white-fronted goose is circumpolar in distribution and nests in Alaska in the central, western and northern regions. Virtually all Yukon Delta whitefronts migrate to the Pacific Flyway (Bellrose 1980, Lensink personal communication), while less-dense populations from the forested interior and the coast north of the Yukon River winter in the Central Flyway. Nesting densities vary from scattered pairs to moderate concentrations of up to 10 pairs per square mile (3.9/km^2) (King and Dau 1981, Ely and Raveling 1984).

Dall and Bannister (1869) and Nelson (1887) reported nesting whitefronts at St. Michael and Dall (1870) found their eggs all along the Yukon River to Fort Yukon. Nelson (1887) also described the whitefront as "the most widely distributed and abundant goose throughout northern Alaska." Whitefronts no longer nest in the marshes near St. Michael. Studies for the Rampart Canyon Dam in the early 1960s disclosed no nesting whitefronts along the Yukon River, although they still nest from the edge of the Flats into the hills along Beaver Creek, Birch Creek, Black River and other tributaries (USDI 1964). Sidney Huntington (personal communication) of Galena informed us that whitefronts on the Dulbi River have increased in recent years, ever since hunting molting birds there has ceased. Reports from wintering areas indicate a steady decline in Yukon Delta nesting whitefronts (O'Neill 1979, Timm and Dau 1979, Raveling 1984).

Because of their wide distribution, white-fronted geese have survived over most of Alaska, but they are reduced in number in some areas from the levels early explorers found. Hunting, egging and molting drives may have eliminated them from the smaller deltas of western Alaska, such as at St. Michael, and reduced them greatly on the Yukon Delta. Shooting and egg gathering associated with heavy boat traffic in the early part of the century may have eliminated nesting whitefronts along the major navigable rivers particularly the Yukon (Dall 1870). Excessive kill in Alaska—see Klein (1966) and Copp and Roy (1986) for harvest data—and during fall and winter outside Alaska (Timm and Dau 1979) probably reduced Pacific Flyway whitefronts in recent years. If summer hunting is eliminated, as at the Dulbi River, and winter harvest is not too intense, whitefronts should re-occupy former nesting habitats throughout western Alaska and increase their numbers.

Tule Goose

The tule goose (*Anser albifrons gambelli*) is a large, dark whitefront that was first described by Hartlaub (1852). However, it was 1980 before the nesting habitat of tule geese was located at Redoubt Bay in Cook Inlet, Alaska. Banding confirmed that they winter in central California. Breeding ground estimates of 1,500 tule geese in Cook Inlet (Timm et al. 1982) do not correspond with counts of about 5,000 birds estimated on their wintering grounds in California (Wege 1984). Timm et al. (1982) suggested that habitats near Redoubt Bay could harbor the remainder of this population. Tule geese are not subject to hunting on the nesting grounds. They were probably more widespread and abundant when first described in California in 1917 (Bauer 1979). Hunting restrictions in California have enabled this population to expand in recent years (Bauer 1979, Wege 1984). There appears to be adequate habitat for a larger nesting population in Cook Inlet. Potential threats to nesting (Timm et al. 1982) and wintering (Gilmer et al. 1982) habitats should be monitored to avoid a reversal in this trend.

Lesser Snow Goose

Lesser snow geese (*Chen caerulescens caerulescens*) nest in the Artic, from eastern Siberia to eastern Canada, and winter primarily in central California and along the Gulf of Mexico. Wintering populations in the U.S. averaged 1,277,000 birds during 1955 to 1974 (Bellrose 1980). Snow geese stage on river deltas, floodplains and uplands in all regions, but are considered rare nesters in Alaska. There are isolated nesting records from the Yukon Delta (Gabrielson and Lincoln 1959), and there have been a few broods east of Point Barrow near Smith Bay and Cape Halkett (King 1970, Derksen et al. 1981). In recent years, a small colony of 50–100 breeding pairs has become established on Howe Island in the Sagavanirktok River delta near the Prudhoe Bay oilfield (Johnson 1983, Johnson et al. 1985). Hansen (1957) reported 1,300 nonbreeding birds near Cape Halkett in 1957, but intermittent counts since 1977 have disclosed less than 300 molting snow geese there. Gabrielson and Lincoln (1959) suggested that lesser snow geese nested more abundantly east of Barrow in the early 1900s and were possibly extirpated by reindeer and their herdsmen. It seems clear that coastal Alaska habitats could support additional nesting snow geese.

We are not aware of a successful man-induced snow goose colony, but it may be possible to establish colonies in Siberia and in Alaska on the Yukon-Kuskokwim Delta, the Seward Peninsula and the North Slope. Since the Yukon Delta is used by staging Wrangel Island snow geese in spring and fall, there is potential for resource competition between this population and a new colony. If successful, an expanding colony might short-stop Siberian birds in a pattern that seems to have occurred in several places in Canada (Bellrose 1980). Alternatively, birds produced on the Yukon-Kuskokwim Delta might follow the main migration to Wrangel Island in subsequent years, as may be the case with the few snow geese that presently nest there.

Emperor Goose

Emperor geese (*Chen canagica*) have a restricted distribution—they nest on the shores of the Bering and Chukchi seas, and winter from Kodiak through the Aleutian and Commander islands to the Kamchatka Peninsula. Nelson (1887) thought they nested most abundantly along the coast between the Yukon and Kuskokwim rivers. Other observers reported that their primary nesting areas were on the east side of Kuskokwim Bay, the south side of Kotzebue Sound and on St. Lawrence Island. Emperors were also found nesting at Port Clarence and St. Michael (Gabrielson and Lincoln 1959). Some emperors nest on the northern coast of Siberia where Dement'ev and Gladkov (1952) described their numbers as "low" and "extremely depleted," and suggested the need for a ban on shooting "which locally threatens to annihilate this form completely."

The Alaska fall population of emperors was estimated to be about 150,000 in 1971 (King and Lensink 1971). More-recent surveys indicate there has been a decline to about 100,000 birds in fall 1982 (Petersen and Gill 1982), and 58,800 in spring 1985 (Dau and King 1985). Bailey (1948) listed the emperor as a common nester from Wales east along the north side of the Seward Peninsula in 1921. Thayer (1951) found nine emperor nests on the Serpentine River near Shishmaref. King (1982) could only find 133 emperors on the entire Peninsula during an air search in June 1982. Fay (1961) reported 10,000–20,000 emperors molting along the southern coast of St. Lawrence Island, and up to 2,000 in the breeding population. Fay and Cade (1959) noted that molting birds were formerly captured in large numbers by hunters, but that this practice had been discontinued. King and Derksen (1986) conducted an extensive aerial survey of St. Lawrence Island in July 1984 and counted fewer than 4,000 molting emperors and only two broods.

There are vast stretches of seemingly good emperor goose nesting habitat that are unoccupied or used only by remnant populations. The legal harvest has averaged only a few thousand birds per year with 1,188 killed in 1984–85 (Campbell and Rothe 1986). In winter, they are dispersed across more than 1,500 miles (2,400 km) of remote island shores and reefs in Alaska and Siberia. Although emperors could be subjected to oil spills or other pollutants from foreign and domestic fishing fleets in western Alaska waters, there is no evidence that this has occurred. For more than 100 years, observers have reported heavy kill of emperors on the nesting grounds and during the molt (Dall 1870, Turner 1886, Nelson 1887, Nelson 1914, Gillham 1941, Jenness 1970). Fall harvests have been at low levels for some time, while spring and summer kills on the Yukon Delta have been greater. Although it appears that hunting has been a major factor contributing to the decline of these geese, the effects of other mortality factors are poorly understood.

Black Brant

Black brant (*Branta bernicla nigricans*) nest near the coast of the western and northern regions of Alaska (Figure 1) and Arctic Siberia and Canada. Spencer et al. (1951) described brant nesting on the Yukon Delta in a large colony extending 100 miles (160.9 km) from the northern side of Nelson Island to the Askinuk Mountains and a smaller colony on the southern side of Nelson Island. Much of the original nesting habitat is now unoccupied, and the remaining brant are largely confined to three remnant colonies. The Tutakoke River colony has recently experienced additional significant losses, from an estimated 14,000 pairs in 1981 (Byrd et al. 1982) to 1,100 pairs in 1985 (Sedinger et al. 1985). Banding has shown association between Alaskan, Canadian and Siberian brant (Uspenski 1965, King and Hodges 1979). Virtually the entire world population feeds on protein-rich eelgrass (*Zostera marina*) at Izembek Lagoon in fall, and stores reserves for transoceanic flight (Hanson and Nelson 1957) to wintering areas from British Columbia to western Mexico. In the past 10 years (1975–85) winter population counts in Mexico have fluctuated between 105,000 and 182,000 (Conant and Eldridge 1985).

We are unaware of any brant colonies along the shores of Norton Sound or Kotzebue Sound, except at a few islets near the Nugnugaluktuk River. Thayer (1951) found 24 brant nests at Shishmaref Lagoon, but brant seem to have ceased using this area for nesting in recent years. There is little habitat available at the Nugnugaluktuk and it is probably saturated with some 400 pairs (King and Conant 1983). The Serpentine River on Shishmaref Lagoon has more-extensive habitat and should be able to support a substantial nesting colony of brant. The principal difference between these two areas, besides size, is that the Serpentine is occupied throughout the spring and summer by hunters and fishermen, whereas the Nugnugaluktuk is far from any village and probably seldom visited by man. Other small western Alaska deltas north of the Yukon River appear suitable for brant colonies but are not now used. Small colonies and scattered pairs nest on the Arctic slope in Alaska, and up to 22 percent of the entire brant population molt near Teshekpuk Lake in July (King and Hodges 1979). Protection on the Cape Halkett/Teshekpuk Lake area from development is advisable because of the unique combination of large, isolated lakes that afford security to molting geese, and abundance of nutrient-rich foods (Derksen et al. 1979, Derksen et al. 1982).

Vancouver Canada Goose

The Vancouver (*Branta canadensis fulva*) is a large, dark goose that nests secretively within the coastal rain forest (Lebeda and Ratti 1983) of northern British Columbia and southeastern Alaska (Van Horn et al. 1979). It is unclear what limiting factors preclude this subspecies from inhabiting contiguous, similar habitat in southern British Columbia. Vancouvers winter on the tidal flats near nesting areas. There is a small population of Canadas that nest on the islands in Prince William Sound and winter in nearby estuaries that might be of this subspecies (Islieb and Kessel 1973). Although Vancouvers are hunted in fall, the kill appears to be low. The Vancouver may be the last Canada goose in North America that is limited primarily by natural causes, and whose summer and winter habitat is still mostly unaltered by man.

Since the Vancouver winters almost exclusively on vegetated tidal flats—a limited and specialized habitat—we are concerned about other uses of these areas. Log rafting and deposition of logging debris at the high tide line has covered extensive areas of goose-foraging habitat in some locations. The Mendenhall tideflats in Juneau, now a State Game Refuge, support a winter population of about 600 Vancouvers that are easily visible along the main highway to Juneau. Saving this urban flock may be a major conservation test, as habitat is threatened by highway crossings, gravel mines and airport expansion. The town of Hoonah also has a tidal flat airport that destroyed a Vancouver feeding area. Substantial numbers of Vancouvers make a molt migration to glacial or other open coastal areas in July, and protection of these sites is needed (Lebeda and Ratti 1983).

Most of the present Vancouver Canada goose range was ice-covered during the most-recent glaciation, and Ploeger (1968) suggested that these geese occupied habitats south of the ice. They continue to pioneer northwestward as retreating glaciers expose habitat along the Gulf of Alaska, as at Glacier Bay. Kodiak and Afognak islands have no nesting or wintering Canada geese, although the climate and habitat seem similar to southeastern Alaska. Thirteen Vancouvers were released on Kodiak in 1973 to determine whether this subspecies would become established, and recent observations of a few large Canadas at Uyak Bay indicate that there is potential for further successful translocations. It is not clear why Canada geese have not occupied Kodiak Island since the last glaciation, but perhaps additional introductions of Vancouvers from southeastern Alaska could accelerate use of these habitats. There has been some objection to establishing a new population of Vancouvers separated from the parent stock by a population of duskies at the Copper River and a splinter population of lessers at Cook Inlet. This is less of a problem to those who accept Palmer's (1976) classification that combines Vancouvers with duskies.

Dusky Canada Goose

Dusky Canada geese (*Branta canadensis occidentalis*) nest within a 125-square mile (324 km^2) area on the Copper River Delta, and winter in the Willamette Valley of Oregon. Once overharvested in Oregon, they responded to the creation of refuges that provided winter protection, and the population more than doubled to about 26,000 in 1975 (Timm et al. 1979). Recent counts indicate the dusky population declined from 23,000 in winter 1981 to about 13,000 in summer 1985. The Copper

River Delta was uplifted about 6 feet (1.9 m) during the 1964 earthquake, causing drainage of many waterways (Timm et al. 1979), which may have reduced protection of duskies from terrestrial predators. Studies are in progress to assess the impact of predation and examine the response of nesting pairs to artificial nest platforms and islands (Pollard 1984).

Duskies nesting at Egg Island off the mouth of the Copper River have 30–50 percent higher success than those using the mainland (B. Campbell personal communication). Other nearby islands appear suitable for nesting, and perhaps duskies will or could be induced to nest on these areas. Several unvegetated islands are subject to storm tides and unsuitable for nesting geese. It may be possible to create goose habitat in these areas by stabilizing sand dunes and introducing grasses and sedges.

Lesser Canada Goose

The lesser Canada goose (*Branta canadensis parvipes*) is widely scattered throughout forested valleys of the central region and to the coast only at the head of Cook Inlet. Pairs and small flocks occur in marshlands and along river courses in summer. Several hundreds molt on the islands in the mid–Yukon River and along the Innoko River. Dall and Bannister (1869) listed them as abundant breeders on Yukon River islands from the Delta to Fort Yukon. Biologists working on the Rampart Canyon Dam study found lessers nesting near large lakes but not on the Yukon River, and estimated a breeding population of 8,000 for the Yukon Flats (USDI 1964). In recent years, lessers have nested on Yukon River Flats islands where 19 broods were seen in 1985 (S. McLean personal communication). Some lessers have a molt migration to the Artic slope, where nonbreeders mix with Taverner's Canada geese (*Branta canadensis taverneri*) (King and Hodges 1979).

Timm (1978) estimated 2,000 lesser Canada geese in Upper Cook Inlet. This expanding population (Timm et al. 1979) apparently did not exist prior to 1964. A few pairs nest at the Potter Point State Game Refuge in the city of Anchorage, where a marsh was created by a railroad embankment. Ten lesser Canada goose families were observed at the Lake Hood seaplane base in 1985. Increasing agricultural development and deforestation for pastures and small grain fields have provided additional new foraging areas for lessers near Anchorage. Banding has shown that some of the lessers nesting near Anchorage winter in the Willamette Valley in Oregon where they flock with duskies (Timm 1978).

The presence of a goose flock in Anchorage suggests that lessers can adapt to a close association with man and enhance the urban environment. There are opportunities in the Anchorage area to improve habitat and increase goose production (Bader 1983). Ducks Unlimited completed an enhancement project in the Palmer Hay Flats State Game Refuge near Anchorage, where dikes, ponds and islands were developed on a tideflat.

In the interior, a State Game Refuge in the center of Fairbanks attracts migrant lesser Canada geese in spring, and it may be possible to establish a nesting flock there. Elsewhere throughout their nesting range, lesser Canadas are so widely distributed that habitat enhancement and other management opportunities are limited. If the kill is maintained at reasonable levels on their winter range, lesser Canada geese will probably continue to succeed.

Taverner's Canada Goose

The Taverner's Canada goose is similar in size, appearance and habits to the lesser, except that it occupies tundra nesting sites often far from the coast in the northern and western regions, from Bristol Bay to Canada. This subspecies is not recognized by Palmer (1976), who includes it with lesser Canada geese. The Taverner's geese nest on the Yukon Delta, where their range meets that of the cackling Canada goose. Taverner's Canada geese stage on the north side of the Alaska Peninsula in fall, and more than 73,000 have been tallied at Izembek Lagoon in October (Timm et al. 1979). Banding at Izembek and also near Cape Halkett on the North Slope has shown they are widely scattered in winter from Washington through central California (Johnson et al. 1979, King and Hodges 1979).

The Taverner's Canada goose population appears to be stable, although no precise techniques have been developed to identify this subspecies in surveys. Nests are widely dispersed throughout their range, making mass depredations unlikely. About 100 pairs nest within the Prudhoe Bay oilfield, where hunting is prohibited. They are seen occasionally during migration on the deltas of Kotzebue Sound (King 1982) and possibly once nested on the Kobuk, Noatak, Buckland and other deltas. The Taverner, like the lesser Canada and the whitefront, may be capable of reoccupying former nesting range if summer harvests are regulated carefully. As with the lesser Canada and the whitefront, Taverner numbers could be adjusted by manipulation of recreational hunting regulations in the Pacific Flyway.

Aleutian Canada Goose

The Aleutian Canada goose (*Branta canadensis leucopareia*), recently thought to be in danger of extinction, was once abundant throughout the Aleutian, Commander and Kuril islands, but was eliminated from most of its range when Arctic foxes (*Alopex lagopus*) were introduced to nesting islands (Springer et al. 1978). Fox farming failed prior to World War II and the stock was abandoned on the uninhabited islands where introduced. Fewer than 800 Aleutian geese were counted in the mid–1970s. Banding on Buldir Island (Figure 1) revealed harvest locations in California and Oregon, and hunting closures in these areas have enabled the population to increase to about 4,000 (Hofmann et al. 1986). Removal of foxes and an intensive program of releasing captive–reared birds with relocated wild birds from Buldir Island have resulted in the reestablishment of nesting geese on Agattu Island. There is evidence that the abandoned foxes have disappeared from some islands where foods have been exhausted or rabies outbreaks have occurred (E. Bailey personal communication). Small populations of Aleutian–like Canada geese were recently discovered in the Semidi Islands (Hatch and Hatch 1983) and in the eastern Aleutians on Chagulak Island (Bailey and Trapp 1984). Mitochondrial DNA sequence analysis of tissues from these geese confirmed their taxonomic status as *B. c. leucopareia* (Shields 1985). Continued efforts to eliminate foxes and protect geese from fall hunting offer hope that the Aleutian Canada goose population can be restored.

Although reintroduction of hand–raised Aleutian geese failed and progress toward recovery has been more costly and time–consuming than expected, several lessons have been learned. California responded with season closures on all migration and wintering areas where Aleutians mix with other geese. Traditional migration behavior was maintained despite the problem of "teaching" migration corridors to relocated

Agattu Island birds. Propagation, handling, holding and releasing techniques in a remote area have been enhanced. In short, Americans have demonstrated the will and commitment to restore a wild goose population.

Cackling Canada Goose

Early explorers described the cackler as the most-abundant nesting goose along the shores of western Alaska (Nelson 1887, Gabrielson and Lincoln 1959). Gabrielson and Lincoln (1959) cited nesting records from Point Hope to the head of Bristol Bay prior to 1930. Cacklers were most numerous from Kuskokwim Bay to the head of Kotzebue Sound. Oddly, there was a gap on the Seward Peninsula where this species was not regularly recorded. Nelson (1887) reported *B. c. minima* abundant at St. Michael, and cited others who found them nesting on the lower reaches of the Noatak and Kobuk rivers. In 1946, on a flight along the Bering Sea coast from Bethel to St. Michael, Gabrielson and Lincoln (1959) reported that cacklers outnumbered all other geese combined, including emperors, whitefronts and brant. Recently, cackling geese have been confined to a more-limited area between the Kuskokwim and Yukon rivers. Fall migrants stage in large flocks on about 30 square miles (77.7 km^2) near Ugashik Bay on the Alaska Peninsula to build reserves for flights to winter habitats. In 1985, an estimated 39,000 cacklers (R. E. Gill, Jr. personal communication) used this area for about three weeks in September/October (Bollinger and Sedinger 1985). Canada goose hunting was prohibited at this important staging area in 1985, and we recommend additional state-designated critical habitat for those areas not presently protected. Spring staging areas on the Copper River Delta and Cook Inlet estuaries provide new-growth grasses and sedges necessary to attain peak weights for reproduction (Raveling 1979). Fall and winter counts in Oregon and California show that cacklers have declined by 93 percent since the mid-1960s, from near 400,000 to less than 30,000 in 1983 (O'Neill 1979, Raveling 1984). Factors responsible for the decline are unclear, but excessive summer and winter hunting are most likely the primary causes. Restoration of the cackling goose to former abundance should be a high priority.

Goose Colonies

Geese are large, hardy birds and strong flyers that generally cope well with the dangers of their environment, but there are times in summer when they are vulnerable to predators. Incubating females, goslings and molting adults are relatively defenseless, so must use special strategies to aid survival. Solitary nesting species conceal their nests as defense against predators. All but the largest geese migrate to far northern latitudes for nesting and molting, where predators are relatively few in number and variety. Colonial nesting and communal brood rearing is advantageous to survival in areas where predators are present. Lesser snow geese and brant are considered colonial-nesting species. Arctic-nesting emperors, whitefronts and Canada geese can sometimes attain nesting densities almost as great as snow geese and brant at certain favorable sites.

There are a few places, mostly in the treeless Arctic, with abundant food and few predators, where geese nest in colonies with potential for very high production. The clipping and manuring of vegetation by grazing geese stimulates growth of food plants (Marriott 1973, Cargill and Jefferies 1984). Gulls and other predators that occur in these areas can be mobbed and put to flight (Barry 1967). Bears and canids may be attracted to goose colonies in summer and prey on peripheral nesting birds, but normally these predators are limited by winter conditions, and colony damage is sporadic (Uspenski 1965, Barry 1967). Predation by humans at goose colonies can cause significant losses or complete destruction, as has occurred on Arctic river deltas and Wrangel Island in Russia (Dement'ev and Gladkov 1952, Uspenski 1969, Portenko 1971, Owen 1980, Bousfield and Syroechkovskiy 1985).

The greatest goose-nesting concentration in the world may once have been on the 26,301-square mile (68,120 km^2) (King and Dau 1981) Yukon-Kuskokwim Delta (Spencer et al. 1951, Ogilvie 1978). We have documented the decline of four Delta-nesting species from nearly 1 million geese in the 1950s to less than half that in the 1980s (Raveling 1984). Even in the 1950s, only a portion of what appeared to be good habitat was occupied, and prehistoric populations may have been several times larger and more widespread.

The U.S. Fish and Wildlife Service (USFWS) has conducted systematic aerial waterfowl breeding pair surveys across the Yukon Delta as part of an international program since 1956. There are 65 segments, each 16 miles (25.7 km) long, including 5 that cross portions of the Delta goose-nesting concentration area, although only 1 segment is entirely within it (Figure 2). This survey was designed to enumerate ducks, which, unlike geese, normally remain on the water or shore as the plane flies over. Figure 3 shows geese counted on five transect segments in the dense nesting habitat described by Spencer et al. (1951), compared with counts from 20 segments outside the colony. The peak in 1964 reflects an influx of spring migrants that remained on the delta much longer than usual because of prolonged snow and ice cover in northern nesting areas. The trend within the concentration area has been a precipitous decline for all species (brant, white-fronted, emperor and cackling geese). Areas beyond the main concentration have supported small, stable populations of geese over the same time period (Figure 3). Nesting populations of geese have been reduced substantially. The collective impact of harvests throughout the Flyway resulted in a situation that allowed disturbance, predation and other factors to inhibit population growth.

Early explorers in western Alaska described an abundance of the same four species of geese north of the Yukon-Kuskokwim Delta along the coast of Norton and Kotzebue sounds where the geese are now scarce (Turner 1886, Nelson 1887, Bailey 1948, Gabrielson and Lincoln 1959). It seems likely that the smaller northern deltas also supported concentrations of nesting geese in precolumbian time. The Nugnugaluktuk River, remote from any villages, still supports a colony of several hundred pairs of brant and emperor geese (King and Conant 1983). Small nesting colonies of Pacific Flyway geese continue on the northern rim of the continent at the Colville, Sagavanirktok, Mackenzie, Anderson and other rivers (Bellrose 1980). No regular nesting-season hunting occurs in any of these colonies.

Management Alternatives for Yukon Delta Geese

Progress has been made with management of western Alaska geese (Pamplin 1986), but there has been relatively little discussion of long-term management alternatives and population objectives. What should we do for the next 10, 20, 50 or 100

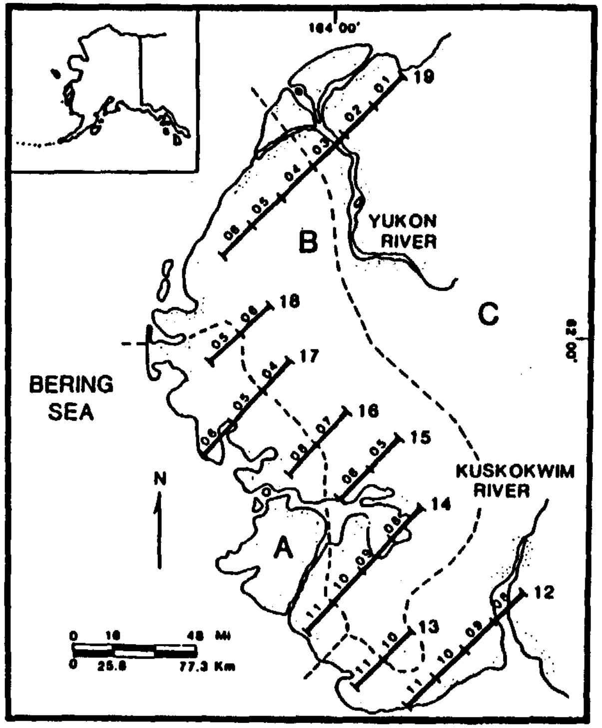

Figure 2. Yukon–Kuskokwim Delta waterfowl population survey transects. Numbered transects are subdivided into 16–mile (25.7 km) segments. A = the densest goose–nesting area surveyed from 1956–85; B = upland habitats surveyed from 1956–85; C = upland habitats surveyed from 1964–85.

years? We have identified several management options for geese that occur in the southern and central regions. However, it is the thousands of square miles of underutilized and unoccupied nesting habitat in western Alaska that represent the greatest challenge and opportunity. Should we apply management techniques that will allow these geese security to rebuild populations to some previous level of greater abundance?

As a first step in developing a management program for western Alaska, it is imperative to review the alternatives and establish goals. Alternatives include:

A. No management. This alternative would minimize the need for public funds. However, the cost would be a continued decline of geese, loss of a food resource, reduction of recreational opportunities and diminished revenues from recreational hunting activities.

B. Maintain present population. This option may not be possible on the Yukon Delta. Some nesting populations have been reduced by 50–90 percent and may continue to decline from natural causes unless intensive management is initiated.

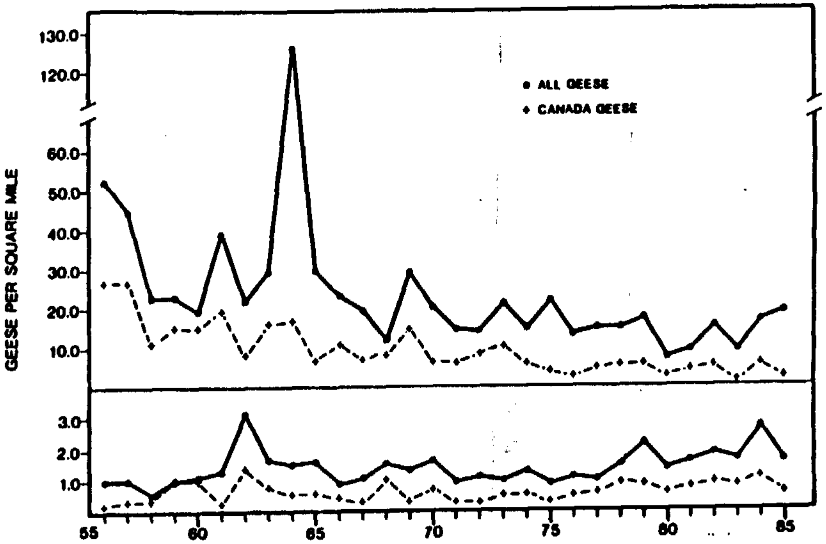

Figure 3. Population index of geese on the Yukon–Kuskokwim Delta from 1956 to 1985. Upper graph compares the status of all species (brant, white–fronted, cackling Canada and emperor geese) with Canada geese in the densest, coastal, goose–nesting habitats. Lower graph is a plot of annual counts of geese from upland habitats adjacent to the main colony.

C. Restore populations to 1950 levels. Restoring the Yukon Delta colony to about 1,000,000 birds could be accomplished by designating inviolate nesting sanctuaries in areas formerly occupied by geese. Reduction of fox, gull and jaeger predation within these areas could accelerate restoration.

D. Double the 1950 level. Building Yukon Delta geese to a population of 2,000,000 or more would require extensive control of hunting and disturbance on the Yukon Delta, additional reduction of fall and winter hunting, and perhaps some improvement or increase in winter feeding refuges.

E. Establish goose–nesting colonies. Using wild birds from the Yukon Delta or captive stock, whitefront, emperor, cackler and brant nesting populations could be established on vacant river deltas bordering Kotzebue and Norton sounds and on the arctic slope. This would require protection of nesting and wintering areas until populations became well–established. Using stock from Canada or Siberia, it might be possible to establish a major Alaskan snow goose colony.

F. Maximum goose–nesting populations. Establishing maximum goose populations on all available western and northern Alaska habitats would entail protection and restoration of nesting habitat as previously described, and probably selective protection and improvement of migration and wintering habitats. Eventually, a major increase in hunter recreation, subsistence harvest and in the hunter–support industry could be expected.

Conclusions

State and federal wildlife management agencies have the expertise and authority to increase populations of geese in Alaska. Restoration would require a commitment by the public to provide funds, and by people living near goose habitat, particularly nesting habitat, to cooperate in preventing disturbance or destruction of the breeding stock. It would not be necessary to end hunting to rebuild populations, but nesting security would be essential. If the Migratory Bird Treaty Act is amended to permit spring hunting by rural Alaskans, areas outside designated nesting sanctuaries could be managed for hunting. As goose populations increased, hunting opportunities for everyone would improve.

If the public supports restoration, are we collectively willing to accept initial sacrifices in anticipation of the benefits larger populations of geese can provide? We believe that depleted populations can be increased to any level desired.

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1984

Geese and Hunters of Alaska's Yukon Delta: Management Problems and Political Dilemmas

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The delta of the Yukon and Kuskokwin (Y-K) Rivers was described in 1951 as America's greatest goose-brant nesting area (Spencer et al. 1951). The U.S. Fish and Wildlife Service (USFWS) began systematic surveys of waterfowl on the Y-K Delta in 1956. J.G. King described his first inventory experiences as follows: "In the earlier years the air was so full of flying geese that as one cruised across at 100 feet there was fear of a strike. . . The whole scene was overwhelming" (King and Conant 1983).

By the early 1970s, E.J. O'Neill (USFWS) voiced concern about declining numbers of geese stopping at Klamath Basin National Wildlife Refuges (NWR) during autumn migration in northern California. In 1979, publications revealed an alarming decline of cackling Canada geese (*Branta canadensis minima*) and Pacific white-fronted geese (*Anser albifrons frontalis*) which nest on the Y-K Delta and winter in California (O'Neill 1979, Timm and Dau 1979). King and Conant (1983) were recording only one-tenth to one-third the numbers of geese in the 1980s compared to the late 1950s.

In 1951, Spencer et al. did not believe that hunting on the Y-K Delta had an adverse impact on total bird production, but that there was a depressing effect around villages. By the mid-1960s it was recognized that the Y-K Delta supported the largest concentration of Eskimo people in the world and that their annual rate of increase was one of the most rapid in the world (Klein 1966). Estimated harvest of geese by these people was about 83,000 (of 5 species) including as much as 15 percent of the spring populations of cackling and white-fronted geese (Klein 1966). Timm and Dau (1979) concluded that the year-around kill of white-fronted geese far exceeded that necessary for a stable population and they urged better rapport between Y-K Delta residents and management agencies. Last year, Director of the USFWS, R.A. Jantzen (1983) acknowledged that subsistence hunting by natives and a diminished population of cackling geese were major problems.

What has happened? The objectives of this paper are to: (a) summarize data on goose populations; (b) describe actions taken and their effects on goose populations; (c) explore some difficulties and misunderstandings between native hunters and sport hunters; and (d) make recommendations for data gathering, education, and decision making.

Status of Goose Populations

Geese Which Nest on the Outer Y-K Delta

The outer fringe of the Y-K Delta is the major nesting range for four populations of geese (Table 1). Nearly all cackling geese and Pacific Flyway white-fronted geese winter in California (Nelson and Hansen 1959, Miller et al. 1968, Lensink 1969, King and Lensink 1971). In the 1960s, peak numbers of white-fronted and cackling geese monitored at their major autumn concentration area in the Klamath Basin of California exceeded 450,000 and 350,000, respectively (Figure 1). Since 1979, numbers of white-fronted geese averaged 81,000 and numbers of cackling geese averaged 69,000. Cackling geese declined to 36,000 in 1982 and to 26,000 in 1983 (Appendix).

Up to 50 percent of the black brant (*Branta bernicla nigricans*) which winter along the Pacific Coast of North America (nearly all in Mexico) originate from the outer Y-K Delta (Tech. Comm. Pacific Flyway Council 1978). J.G. King (in Bellrose 1976:173) estimated the late summer population of brant on the Y-K Delta in 1968 at approximately 150,000. The Technical Committee of the Pacific Flyway Council (1978) management plan for brant proposed that hunting seasons be closed if the 3-year moving average winter population size falls below 120,000 geese. The current 3-year (1982–84) average is 121,000 and has declined steadily from the 1979–1981 average of 157,000.

King and Lensink (1971) estimated the autumn population of emperor geese at about 150,000 in the 1960s. Inventories along the Alaska peninsula suggest a decline of emperor geese by as much or more than 34 percent between the 1960s and 1981 (Petersen and Gill 1982).

Geese Which Nest Elsewhere in Alaska

Two small populations of geese nest away from the Y-K Delta and winter in California (Table 1). The Aleutian Canada goose (*B. c. leucopareia*) was almost extirpated by

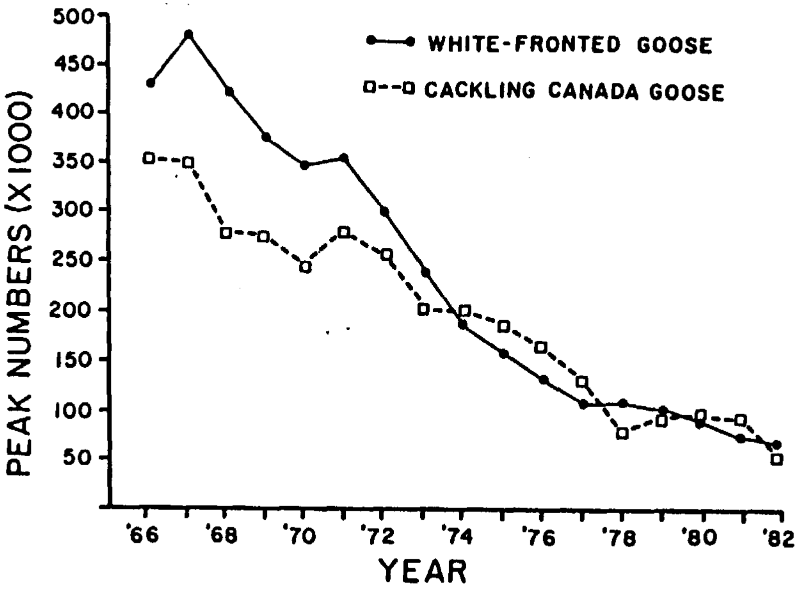

Figure 1 Peak numbers of white-fronted and cackling Canada geese recorded during aerial inventories in autumn at Tulelake and Lower Klamath National Wildlife Refuges. Data are expressed as three-year moving averages which smooth out year-to-year fluctuations caused by a variety of factors (e.g., poor weather conditions during surveys). Some values expressed in O'Neill (1979) from the same area were peak numbers from each refuge from different dates. As geese readily move between these two refuges, some of O'Neill's figures are probably overestimates. The annual peak estimates used for this figure are listed in the appendix.

Table 1. Status of most goose populations nesting in Alaska.

Population	Primary Nesting Range[a]	Primary Winter Range[a]	Recent Status[a]
Cackling Canada goose	Outer Y-K Delta	California	Declining, >85%
Pacific Flyway white-fronted goose	Outer Y-K Delta	California	Declining, >85%
Black brant	Outer Y-K Delta	Mexico	Declining[b]
Emperor goose	Outer Y-K Delta	Aleutian Islands, Alaska	Declining, ≥34%
Aleutian Canada goose	Aleutian Islands, Alaska	California	Increasing >240%
Tule white-fronted goose	Cook Inlet, AK	California	Increasing >150%
Taverner's and lesser Canada geese	Inner Y-K Delta, Interior and Northern Alaska	Washington and Oregon	Increasing (47% in Oregon)
Mid-continent white-fronted goose	Interior and Northern Alaska; Western Canadian Arctic	Texas and Mexico	Increasing (ca. 380%)

[a] See Bellrose 1976 for summary, and references in text.
[b] See text.

introduction of arctic foxes (*Alopex lagopus*) (Jones 1963, Springer et al. 1978). Numbers of these geese have increased 240 percent, from 790 in spring 1975 to 2,700 in spring 1982 (Springer et al. 1978, Woolington et al. 1979, Pomeroy and Springer 1982). The tule white-fronted goose (*Anser albifrons elgasi*, following the taxonomy of Delacour and Ripley 1975), is a distinct race (Krogman 1979) which nests in a restricted range in Cook Inlet, Alaska (Timm et al. 1982) and winters in central California (Bauer 1979, Timm et al. 1982). Numbers of tule geese inventoried in California increased from about 2,000 to 5,000 between 1978–79 and 1981–82 (Wege 1984).

Canada geese which nest in interior and northern Alaska [Taverner's Canada goose (*B. c. taverneri*) and lesser's (*B. c. parvipes*) (e.g., see Johnson et al. 1979)] comprise a significant portion of all Canada geese which winter in Washington and Oregon (Timm 1974, King and Hodges 1979, Parker and McCaughran 1979, Simpson and Jarvis 1979). Numbers of Canada geese in Washington have not varied in a systematic manner between 1970–74 and 1975–81 [averaging 61,300±7,900 (S.E.) during 1970–1981, calculated from data in Pacific Flyway Representative (PRF) 1983]. In Oregon, average numbers of Canada geese rose 47 percent from 71,400±7,600 (S.E.) during 1970–74 to 104,800±5,700 (S.E.) during 1975–82 (t=3.553, P<0.01) calculated from data in PFR 1983).

White-fronted geese (*A. a. frontalis*) which nest to the interior and north of the outer Y-K Delta in Alaska and in the western Canadian arctic migrate through the Central Flyway to Texas and Mexico and are classified as the western segment of the mid-continent population (Miller et al. 1968, Lensink 1969). Their numbers have increased over at least the past 15 years and the spring population now exceeds 240,000 compared to 40,000–60,000 during the 1960s (Central Flyway Representative 1982, Benning 1983).

Harvest and Management Actions in Relation to Population Status

I will report here only on those geese which nest on the Y-K Delta as they are the populations experiencing declines.

Black Brant and Emperor Geese

Annual sport harvest of brant from Alaska through California has averaged 5,570±1,290 (S.E.) (range 2,250–15,230) (1971–72 through 1981–82) which was 4 percent of the average winter population inventoried during the same time span (calculated from data in PFR 1983). Total harvest of brant in Mexico is unknown, but most brant in Mexico are in relatively inaccessible locations. The only readily accessible population is in San Quintin Bay where hunters killed between 1,740 and 6,500 brant during the 1974–75 and 1975–76 hunting seasons, respectively (Kramer et al. 1979). I conclude that sport harvest alone could not be responsible for the recent decline of the entire Pacific population of brant.

Washington and Oregon closed their brant seasons for 1983. California closed parts of two bay estuaries to hunting in 1981 and, for 1983, reduced its bag limit to three and changed the dates of its hunting season to reduce harvest pressure and shift harvest from adults to immatures. Beginning in 1980, Mexico reduced bag limits on brant and limited hunting to three days a week.

Annual sport harvest of emperor geese in Alaska averaged 1,495±325 (S.E.) (range 307–3,862) during the 1970–82 hunt seasons (calculated from USFWS annual reports on harvest and hunter activity—also see Timm 1974). This harvest is less than 2 percent of the population and could not be responsible for its decline.

White-fronted and Cackling Geese

Approximately 86 percent of the sport harvest of Pacific white-fronted geese (Timm and Dau 1979) and 75–89 percent of the sport harvest of cackling geese [Nelson and Hansen 1959, Calif. Dept. of Fish and Game (CDFG), unpubl. data] occurs in California. Therefore, I will detail here only the data pertaining to California.

From 1975 to the present, the CDFG has closed three large areas to hunting of Canada geese: two counties on the northwest coast for the entire season, parts of the Sacramento Valley (SV) from the opening of the season in late October or early November until December 15, and parts of the San Joaquin Valley (SJV) after December 15. These closures were originally intended to benefit the Aleutian Canada goose (see Springer et al. 1978), but these actions should have also substantially reduced harvest on cackling geese. Closures in the SV reduced the season length to 30–35 days in an area from which 28–47 percent of band recoveries occurred (Nelson and Hansen 1959, CDFG, unpubl. data). When Aleutian Canada geese remained in the SV beyond December 15, the hunting closure was extended. In 1982–83, e.g., the hunting season for Canada geese in the SV special zone was only 9 days long. As cackling geese do not arrive in the SJV until mid-December, closures in this area, which had accounted for 9–16 percent of band recoveries (Nelson and Hansen 1959, CDFG, unpubl. data) were tantamount to a cessation of hunting of cackling geese.

Further restrictions on bag limits and seasons for hunting Canada and white-fronted geese in the Klamath Basin (KB) and Central Valley (CV) were instituted in 1979 and have been in place in various forms to the present (Table 2). The KB was the location of 16–38 percent of band recoveries of cackling geese (Nelson and Hansen 1959, CDFG, unpubl. data). During 1979 and 1980, hunting of white-fronted geese was not allowed in the areas closed for hunting of Canada geese described above.

The impact of these restrictions can be assessed partially by examination of harvest estimates provided by the USFWS and CDFG. Hunters are asked how many geese they killed, but they are not asked to identify species. Lesser snow geese (*Anser caerulescens caerulescens*) and Ross' geese (*Anser rossii*) are both abundant in California (O'Neill 1979, McLandress 1979) and make up large portions of the goose harvest. Therefore, total harvest in relation to restrictions described (Table 3) above provides only an index of the impact of these regulations. Note that estimates of the absolute numbers of geese killed by hunters differ substantially between USFWS and CDFG surveys, but that *proportionate declines* in kill *were nearly indentical* in each survey. Harvest of geese in California was greatly reduced (67 percent lower in 1979–82 than in 1970–74) and, although numbers of hunters also declined greatly, the kill per hunter was reduced.

Since different subspecies of Canada geese are not identified in USFWS species composition surveys, estimates of harvest of Canada geese cannot be applied to cackling geese. However, subspecies of Canada geese are identified at hunter-check stations on federal and state managed areas in the KB and CV. Harvest of cackling geese was reduced 78 percent in the CV after 1975 and reduced 51 percent in the KB after 1979 (Table 4).

The impact of changing hunting restrictions in California on total harvest of cackling geese can be estimated by applying the data of Table 4 to the distribution of harvest in the state based on recoveries of geese banded in Alaska which were nearly equally divided

Table 2. Daily bag and possession limits for dark geese (whitefronts and Canada geese singly or in combination) in California.

Year	Area of state[a]	Season length	Daily bag	Possession limit
Before 1978	Northeastern[b]	Mid Oct.–mid Jan.	3	6
	Balance of state[c]	3rd weekend of Oct. thru 3rd weekend of Jan.	3	6
1979	Northeastern[b]	Oct. 27–Jan. 13	2	4
	Balance of state[c]	Oct. 20–Jan. 20	1	1
1980–83	Northeastern[c]	Mid Oct.–mid Jan.	1	2
			for first 14 days	
			2	2
			for balance of season	
	Balance of state[c]	1st week of Nov.–3rd week of Jan.	2	4
			in 1980	
			2	2
			in 1981–83	

[a] Large portions of state closed to hunting of Canada geese–see text.
[b] Primary concentration area is the Klamath Basin.
[c] For this report, refers to other locations in which cackling and white-fronted geese concentrate.

Table 3. Estimates of harvest of geese (all species) and numbers of hunters in California (× 1000).

	Harvest estimates[a]			Kill per hunter[c]	
Time Period	State	Federal	No. of hunters[b]	State	Federal
1970–1974	349.1±14.5[d] (296.7–3.77.7)[e]	240.5±26.7 (173.3–331.2)	161.8±8.4 (144.6–188.9)	2.17±0.09 (1.95–2.42)	1.48±0.66 (1.16–1.75)
1975–1978	243.0±24.7 (188.6–297.0)	173.7±25.2 (112.9–235.4)	132.8±4.2 (124.1–143.3)	1.82±0.15 (1.52–2.20)	1.30±0.17 (0.91–1.74)
1979–1982	115.6±8.0 (100.2–137.8)	80.6±11.4 (53.2–108.8)	113.3±3.6 (107.2–122.8)	1.02±0.08 (0.93–1.27)	0.71±0.10 (0.50–1.00)
			1970–74 vs. 1975–78		
Statistical testing	$t=3.90, P<0.01$	$t=1.78, P=0.12$	$t=2.85, P=0.05$	$t=2.12, P=0.07$	$t=0.89, P<0.4$
			1975–78 vs. 1979–82		
	$t=4.90, P<0.01$	$t=3.37, P<0.002$	$t=3.53, P<0.02$	$t=4.78, P<0.001$	$T_i=2.94, P<0.05$
			Magnitude of Changes Among Time Periods		
1970–74 vs. 1975–78	−30%	−28%	−18%	−16%	−12%
1975–78 vs. 1979–82	−52%	−54%	−15%	−44%	−45%
1970–74 vs. 1975–82	−67%	−67%	−30%	−53%	−52%

[a] State from Calif. Dep. Fish and Game (1983); federal from U.S. Fish and Wildl. Serv. annual reports on waterfowl harvest and hunter activity.
[b] From sales of migratory bird hunting and conservation stamps.
[c] Harvest ÷ no. of hunters.
[d] Mean ± standard error of mean.
[e] Range.

Table 4. Harvest of cackling Canada geese on state and federal waterfowl management areas in California[a].

Time period	Location	Kill[b]	Statistic	Change
1970–1974	Central Valley	2038±276 (1507–3076)		
1975–1982	Central Valley	456±121 (148–1183)	$t=6.02$, $P<0.001$	−78%
1970–1978	Klamath Basin	2596±330 (1580–3250)		
1979–1982	Klamath Basin	1280±199 (960–1790)	$t=2.65$, $P<0.05$	−51%

[a] From data compiled by Pacific Flyway Representative (1983).
[b] $\bar{x}\pm$S.E. (Range).

between the KB and CV (Nelson and Hansen 1959). Total harvest of cackling geese in California was reduced by 39 percent due to area closures in the CV and 65 percent when these closures were combined with bag limit restrictions in the KB and CV (Table 5). These estimates assume that compliance of hunters on private areas was the same as on agency managed hunting grounds.

Kill of white-fronted geese in California can be calculated using the USFWS species composition survey data (estimates in PFR 1983). Harvest during 1970–78 averaged 42,700±4,160 (S.E.) and was reduced 59 percent during 1979–82 to an average of 17,500±3,090 (S.E.) $t=2.32$, $P<0.05$). Reduction of harvest on managed areas was also greatly reduced (Table 6) and these data can be used to approximate the reduction of harvest in the state (Table 7) using the procedure defined above for cackling geese. The close agreement between the estimated reduction in harvest from kill and species composition surveys (59 percent) and that provided by use of data from managed areas in conjunction with distribution data from band recoveries (Table 7, 57 percent) suggests that hunters on private lands behaved as those on managed areas.

Table 5. Estimated reduction of harvest of cackling geese in California in response to hunt season restrictions.

	Proportionate harvest in:			
Time period	Klamath Basin	Central Valley	Total harvest	Change
1970–74[a]	50[b]	50[b]	100	
1975–78[c]	50	11[c]	61	−39%
1979–82[d]	24[d]	11[d]	35	−65%

[a] Before restrictions of recent years.
[b] Distribution of harvest based on band recoveries (Nelson and Hansen 1959).
[c] Area closures in Central Valley reduced harvest by 78 percent (from Table 3; 50×0.78=39; 50−39=11).
[d] Restrictions in Klamath Basin reduced harvest by 51 percent (from Table 3; 50×0.51=25.5; 50−25.5=24.

Table 6. Harvest of white-fronted geese on state and federal waterfowl management areas in California[a].

Time period	Location	Kill[b]	Statistic	Change
1970–1978[c]	Klamath Basin	9,804±856 (7,270–14,930)		
1979–82[d]	Klamath Basin	3,350±497 (2,190–4,520)	$t=4.867$, $P<0.0001$	−66%
1970–78[c]	Central Valley	1,306±160 (543–2,005)		
1979–82	Central Valley	622±110 (311–793)	$t=2.673$ $P<0.05$	−52%

[a] From data compiled by Pacific Flyway Representative (1983).
[b] $\bar{x}\pm$S.E. (Range).
[c] Before restrictions of recent years.
[d] Area closures in 1979–80 and 1980–81 and bag limit and season length restrictions (see text and Table 2).

Table 7. Estimated reduction of harvest of white-fronted geese in California in response to hunt season restrictions.

	Proportionate harvest in:			
Time period	Klamath Basin	Balance of state	Total harvest	Change
1970–78[a]	35[b]	65[b]	100	
1979–82	12[c]	31[d]	43	−57%

[a] Before recent restrictions.
[b] Distribution of harvest based on recoveries of geese banded in Alaska (data in Pacific Flyway Representative 1983). White-fronted geese were included in the Central Valley area closures of hunting for Canada geese in 1979 and 1980 but not in other years.
[c] Restrictions in Klamath Basin reduced harvest by 66 percent (from Table 5; 35×0.66=23; 35−23=12).
[d] Restrictions in the rest of the state away from the Klamath Basin reduced harvest by 52 percent based on data from Central Valley management areas (from Table 5; 65×0.52=34; 65−34=31.

Other Research on White-fronted and Cackling Geese

Research has not indicated that factors other than harvest were instrumental in the decline of cackling and white-fronted geese. Over 1,600 whitefronts were marked with neck-bands between 1979–1981 and over 1,400 cackling geese were neck-banded during 1982–83 to allow for more intensive study of the timing of their migrations, distribution during winter and mortality (Ely and Raveling 1980, 1981, 1982, Johnson and Raveling 1983). While analyses are yet incomplete, these studies have not revealed that changes in migration pattern could account for declines of the magnitude observed. Levels of contamination with toxic materials are far below that presently known to be deleterious (Anderson et al. 1984). Age-ratios of geese trapped or observed at KB in autumn (CDFG, USFWS, unpubl. data) do not indicate problems with production of young. No known die-offs due to disease or starvation have occurred with the consistency or magnitude necessary to account for the long-term population declines. While loss of wetland habitat and changes in agricultural patterns and intensity continue in California, it is my judgement that available areas and food supplies used by the geese are more than adequate to sustain much larger populations.

Discussion and Conclusions

The clear implication is that harvests of geese on the Y-K Delta are excessive for all geese and alarmingly so when combined with harvest in California. This is correlated with a 42 percent increase in the human population of coastal Y-K Delta villages between 1960 and 1980 (Copp and Smith 1981)[1] and rapid advances in availability of modern technology. In the 1950s many people on the Y-K Delta still lived in sod houses and used kayaks and even a one h.p. motor was a luxury (Peterson and Fisher 1955:372, 378, 380). Dog teams were a major means of travel for the spring goose hunt in the 1960s (Klein 1966). By 1972, about 2,000 boxes of shotgun shells were sold in one village of about 550–600 people (D. Eisenhauer in Timm and Dau 1979:288). Boats now commonly have motors of 25–75+ h.p. (often twin engines). Most families now have a snowmachine whereas they were a relative scarce luxury in the mid-1970s (personal observation). This technology enables even short-term hunts to commonly exceed 20 miles (32 km) in distance from villages (Copp and Garrett 1983).

This is not to suggest that the dramatic declines of white-fronted and cackling geese were due solely to harvest by native peoples. The large-scale reductions in harvest in California are less than the reductions in the size of the populations. Therefore, even this reduced harvest in California may be more adversely affecting these populations than a few years ago because of the greatly diminished numbers of these geese. However, the fact that brant and emperor geese have also declined suggests that harvest by natives themselves is excessive, and when combined with harvest in California is near catastrophic.

This situation has created frustration for managers because: (a) useful data on kill of geese by natives are meagre so that judgements on impact are inferential and biologists cannot make meaningful analyses of harvest in relation to population size; (b) cultural differences between native and non-native groups contribute to misunderstandings and lack of action or agreement on courses of action; (c) California hunters feel they have made sacrifices without corresponding efforts by other users; and (d) resource agencies in Alaska have not provided needed information and are widely perceived as not having vigorously tried to do so.

Harvest by Natives

Harvest of geese by northern natives is an important, traditional activity. Kills of 40–60 geese (up to 130+) per hunter are common (Klein 1966, Boyd 1977, Prevett et al. 1983). Biologists studying geese on the Y-K Delta have witnessed large-scale shooting when geese arrive in spring, flushing geese on nests with snow-machines in order to drive them to hunters, shooting geese on nests, taking of eggs, and shooting or capture of geese with broods. If one contemplates a direct relationship, however small, between the increased human population of the Y-K Delta and their greater mobility and technology in recent years with harvest levels reported by Klein (1966) for the early 1960s, one has no trouble in predicting disaster for the geese. However, we do not have comparable data. Direct observations reveal that harvest continues. For example, Eisenhauer (1977) observed one party of hunters who collected 657 eggs and 51 geese in a 10 hour period; hunters were frequently encountered when geese were molting and 10 hunters had killed 215 flightless brant; 7.7 percent of the 207 newly banded goslings were killed within 10 days and 4 km from the time and location at which they were originally captured. How wide-spread are these activities and what is their impact on population levels? Why do we not know the answers to these questions?

Pacific Flyway Council Actions. Minutes of the Technical Committee and Council meetings of the Pacific Flyway reveal that concern over goose populations has long been expressed, but that major declines occurred before formal actions were recommended (Table 8; compare to Figure 1). The issue of spring harvest had a long incubation period from concern (1974) to formal Technical Section recommendations (1978) to endorsement by Council (1983). But, Flyway representatives can only recommend; only the Alaska Department of Fish and Game (ADFG), USFWS, and native hunters can take direct action to provide information and limit harvest.

Table 8. Consideration of problems and recommendations of the Technical Committee and Council of the Pacific Flyway with respect to white-fronted and cackling geese.

Year	Actions by Pacific Flyway Technical Committee (TC) and Council (C)
1974	TC—AK thought harvest of white-fronted geese (WFG) excessive.
1976	TC—AK recommended additional research on WFG.
1977	TC—AK reported on policies with respect to spring hunting of waterfowl.
1978	TC—recommended resolution to request USFWS and AK seek cooperation of Y-K Delta residents to refrain from taking snow, cackling (CG), WFG geese and brant (B) in recognition of their diminished numbers and actions by states to decrease harvest on these geese; C—deferred action.
1979	TC—briefing on protocol with Canada with respect to subsistence hunting; C—opposed regulations which would legalize subsistence harvest of waterfowl in excess of current levels until impacts are determined; TC—proposed additional restrictions for hunting, additional aerial inventories and recommended work with AK to reduce harvest of B, CG, and WFG on Y-K Delta; C—accepted recommendations for sport hunting restrictions and discussed, but did not act on, subsistence issue.
1980	TC—recommended yet additional coordinated inventories of geese over a broader area and further discussed subsistence issue; C—accepted inventory recommendation.
1981	TC—formed a C/WFG subcommittee and recommended 6 additional research programs including measurement of harvest on Y-K Delta; C—adopted recommendations.
1982	TC—recommended additional research on CG; C—action not required.
1983	TC—recommended specific research and management programs and two resolutions: (a) an urgent effort to evaluate the USFWS subsistence survey and to use expertise of social scientists to assure effective data gathering; (b) hunters of the Y-K Delta, the USFWS and AK take actions necessary to significantly reduce take of CG and WFG; C—adopted both resolutions.

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[1] Data are from: Kwigillinok, Kipnuk, Chefornak, Nightmiute, Tununak, Newtok, Hooper Bay, Chevak, Scammon Bay, Sheldon's Point, Alakanuk, Emmonak, Kotlik, Stebbins, St. Michael (1960 population = 3,500; 1980 populations = 4,985; the human population of the entire Delta increased 67 percent from ca. 9,000 to > 15,000; geese are also killed in other villages and by people who travel to the coast from more interior locations, especially Bethel).

Alaska Fish and Game Actions. Despite the facts that ADFG created a special Division of Subsistence in recognition of the importance of this activity for rural residents (Kelso 1982) and that some of their own biologists called attention to problems with geese (cf. Timm and Dau 1979, Table 8), I am not aware of any direct effort by ADFG to assess harvest of geese by natives. This issue is complicated by political divisions of responsibility and land holdings in Alaska. Ultimate responsibility for migratory birds rests with the USFWS and, as part of the Alaska National Interest Lands Conservation Act (ANILCA) of 1980, 20 million acres (810,000 ha) of the Y-K Delta were made into a National Wildlife Refuge. The apparent view that geese are "federal animals" has not done the geese any good—nor the people who use them. I conclude that ADFG has been remiss in fulfilling its responsibilities when faced with knowledge of the rapid disappearance of geese important to their constituency.

USFWS Actions. In ANILCA, Congress explicitly declared its policy was to support continuation of subsistence uses of fish and wildlife on public lands of Alaska *consistent with sound management principles and conservation of healthy populations of fish and wildlife.* The law also mandated the Secretary of the Interior to undertake *research* on fish and wildlife and subsistence uses.

The USFWS initiated a study of waterfowl harvest by Y-K Delta natives in 1980. Responsibility for design and conduct of the program was assigned to staff of the Yukon Delta NWR (YKNWR). The study involved interview of consenting native hunters in a sample of villages on numbers and kinds of waterfowl taken between April 1—June 30. The USFWS contracted with the University of California, Davis (UCD) in 1981 to provide assistance in organization and analysis of data already collected and to make recommendations. This analysis revealed many weaknesses in selection and training of interviewers and sampling procedures (Copp and Smith 1981). The program continued with few changes in 1982 and 1983 and the most recent analysis (Copp and Garrett 1983) revealed the same problems remained, a deterioration in quality of data, differences between harvest observed and reported, and problems with identification or reporting of subspecies of Canada geese. Copp and Garrett (1983) concluded that this program is unlikely to meet its objective, and they provided several specific recommendations for improvement.

To assist education and communication between native peoples and agencies, the YKNWR employs a Delta resident as Native Liason Officer. His efforts were vital to explaining refuge programs and facilitating cooperation (cf. Copp and Smith 1981). The refuge also employs native people in both permanent and temporary staff positions. In 1982, an information officer joined the staff at the refuge. The USFWS has sponsored visits by native representatives to California and invited them to meetings.

Gathering of biological data on geese of the Y-K Delta has followed an erratic course. Studies in place through 1979 were ended for 1980 and new proposals were denied or discouraged. Expansion of refuge programs began in 1981 and a contract was made with UCD to provide assistance and recommendations (e.g., Anonymous 1981, Aldrich and Byrd 1981, Aldrich et al. 1981). An expanded refuge biological program was carried out in 1982 and 1983 and has provided a great deal of new information on the status and biology of geese (e.g., Byrd et al. 1982, Butler 1983, Garrett 1983). This program is heavily dependent on temporary staff and volunteers. The role of research staff of USFWS has been limited to one field study of the status and biology of emperor geese in 1982 and 1983 (Petersen 1982, 1983) with additional support for the UCD field study in 1983.

Refuge programs have been severely hampered by instability in staff tenure and lack of continuity. Since 1976, YKNWR has had significant portions of time in at least two years without a manager, three different managers, and a fourth will be assuming duties in 1984. Similar instability occurred with assistant managers and biologists. This is a deplorable situation for a 20-million-acre (810,000 ha) refuge encompassing the most valuable nesting grounds of geese in the U.S.

Minutes of Pacific Flyway meetings reveal a difference between desires and reality of USFWS programs with respect to subsistence harvest. In March 1979, the USFWS suggested that the *problem may be solved* with the U.S.-Soviet Treaty recognizing the need for regulated subsistence hunting and the protocol agreement between the U.S. and Canada. In 1980, the USFWS reported that they were giving the subsistence hunting issue *high priority* and launcing a *major effort* to educate natives to the problems and to reduce take of geese on the Y-K Delta.

Persons of good intentions may disagree on interpretation. I submit the USFWS effort was neither major nor of high priority. I believe the geese would agree with me.

Native Actions. The people of the Y-K Delta are aware and concerned that there are many fewer geese. The Pacific Flyway Council was assured at 1979 and 1980 meetings that natives would reduce their harvest. Natives reported to the Flyway in 1981 that they undertook efforts to urge voluntary restraint of harvest on cackling and white-fronted geese. Notices were sent to villages expressing concern about brant and taking of their eggs.

Since there are no adequate baseline data, one cannot evaluate whether or not voluntary actions were effective at the village level. As with California, even if harvest by natives was reduced substantially, the populations are so low that impacts of reduced harvest may be more harmful than in the recent past. Despite assurances provided the Flyway Council, there are indications of increased harvest activity in at least some local areas (personal observations, Garrett 1983).

Sport Hunter Actions. The California Waterfowl Association (CWA) and Waterfowl Habitat Owner's Alliance (WHOA) represent the interests of organized California hunters. Their executives have been active participants at Flyway and other meetings and a CWA representative visited Alaska in 1979 where he was assured that harvest by natives would be reduced to match reductions in California. Frustrated by the lack of meaningful data on harvest in spring-summer and the continuing decline of goose populations despite large-scale reduction of hunting in California, CWA has admonished the Pacific Flyway Council and USFWS for avoiding the issue and threatened legal actions to require enforcement of the Migratory Bird Treaty. Sharing responsibility is the cornerstone of the Flyway Concept.

Recent Agreements. In recognition of problems with goose populations, the Association of Village Council Presidents (AVCP) of the Y-K Delta formed a Waterfowl Conservation Committee (WCC) in August 1983. During autumn-winter of 1983–84, a series of meetings of the WCC-AVCP with representatives of ADFG, USFWS, CDFG, CWA and WHOA resulted in agreements by the AVCP to stop hunting of cackling geese and to restrict harvest of white-fronted geese and brant to time periods before egg-laying and after resumption of flight in 1984. In exchange, sport hunting of cackling geese would be closed and regulations sought that would reduce kill of white-fronted geese and brant by about 50 percent (already accomplished in California for brant for 1983). As a result of these meetings, California enacted an emergency closure of Canada goose hunting for the last 12 days of their 1983–84 season.

These meetings represent a positive development in communication and education for all organizations. The emperor goose was, however, neglected in these negotiations. If natives direct their hunting to emperor geese to replace harvest of other geese, this species is likely to suffer dramatic declines beyond that already occurring.

Cultural Differences

A major difficulty in obtaining data on harvest in Alaska and in effective communication is a result of cultural differences between natives and sport hunters. Misunderstandings contribute to suspicion and hamper development of effective programs.

Hunting: Needs and Methods. Sport hunters have difficulty understanding the value of hunting to native peoples. Subsistence is equated to primitive, inefficient methods. Modern technology coupled with harvest of numbers of animals per hunter far in excess of what a sportsman can take conjure up images of unnecessary slaughter; the taking of eggs and killing of adults on nests or with dependent off-spring are considered not only detrimental, but immoral.

These attitudes conflict with the reality of Eskimo life, especially the view that the land and its wildlife is their "grocery store." Technology makes hunting easier, as it has for sport hunters. Although social and economic change is occurring rapidly, wildlife continues to provide essential economic and cultural benefits to natives (Kelso 1982). Traditions which allowed survival over millenia will not change quickly; e.g., people must kill animals to live and the animals know this and their death is not permanent (cf. Nelson 1980:50, 69, 100, 171). Hunting is life and identity as an Eskimo (Nelson 1973:288, 311; Nelson 1980:50, 97, 172). Taking food for granted and emotional attachment to animals are luxuries afforded only by those who do not gather their own food; as in any society, a highly successful provider gains power and respect (cf. Nelson 1980:9, 34, 52, 60). An abundant harvest is commonly shared not only with immediate family but with others (Nelson 1980:60, 141; Kelso 1982). Although waterfowl are secondary to other game, they provide important variation in diet and, at times (at least in recent memory), an essential supplement arriving at just the right time (Klein 1966, Nelson 1969:154–158). When a non-native thinks it is easy for a native to substitute foods of another culture, he should ponder how easily he could accept the natives' foods and methods of preparation (Nelson 1969:158). Appreciation of the meaning of culture may then follow.

Sensitivity to the importance of hunting, however, should not stifle recognition of dwindling resources. While the behavior of people in rural, indigenous societies is now commonly recognized as the outcome of adaptations to natural environments (Kelso 1982), it is naive and destructive to ignore the impacts of expanding human populations and technology. Sympathy with the past should not obscure realistic evaluation of changes. A decrease in knowledge of wildlife and skills in hunting and traditional survival abilities by young natives has long been obvious (cf. Nelson 1969:383). Many hunts have taken on a sport character when one considers the cost of machines and fuel and amazing waste of costly ammunition in relation to some harvests (personal observations; see also Macauley and Boag 1974). Failure to deal with these issues will result in collapse of the resource bases which form the goal of subsistence policy to maintain productivity for human use.

Some observers have cautioned against overemphasis on harvest as this may lead to misleading characterization of ecosystem dynamics (Kelso 1982) such as confusion of correlation with cause and effect and negligence in recognizing other potential causative factors (Copp and Garrett 1983). These concerns are legitimate and caution is wise as a principle. However, in this case, they have far less basis for concern than that on harvest. The fact remains that it is only the harvest that we can control in the short term.

Native hunters have difficulty understanding the value of hunting to sport hunters who are considered wealthy and do not need to hunt. Commercial exploitation is suspected, as easily witnessed by the ubiquity of goose-down clothing.

These attitudes also conflict with reality as they fail to respect intense, emotional relationships that tie sport hunters to wildlife. Native and sport hunters share many traits and rewards (Copp 1975, 1979). Native hunters need to recognize that licenses, fees, and special taxes paid by sport hunters support acquisition and management of habitat and studies of the status of waterfowl. Approximately 69 percent of the remaining wetland habitat in California is maintained by private owners to provide waterfowl hunting (Gilmer et al. 1982). Without hunting, most of that land would be converted to agricultural uses. Since 1970, the numbers of waterfowl hunters in California have declined 44 percent from 189,000 to 107,000, which represents a major loss of revenue and support for waterfowl programs. The staff of the Waterfowl Section of CDFG has dwindled from 12 to 5 at a time when we need them more than ever.

The commonly expressed concern about commercial exploitation illustrates how far we have to go in providing meaningful education in the native community. It is, of course, not true, but that fact will not help until native peoples understand that.

Legality. The fact that spring hunting violates the Migratory Bird Treaty with Canada hampers data collection and working together. The treaty is a classic example of a law made by groups remote from, and without consultation with, all people affected. Native hunters had no choice but to consider a law affecting their ability and right to gather food as an intrusion or irrelevant. Such a law is a failure because it compels illegal activity (Kelso 1982), is politically unenforceable in the north (Boyd 1977), and fails to recognize spring-summer harvest as a necessary component to rational management.

The obvious long-term solution is to proceed with modification of the Migratory Bird Treaty with Canada. There are serious concerns over wording of the treaty amendment (cf. Copp 1981) that need to be addressed, but it has been more than four years since the process began. The costs of the delay are serious; we do not have a legal foundation for acquiring data and formulating management policy. The problem is obvious. A short-term solution is needed to help goose populations long before a long-term solution can be effective.

Recommendations

Educational Needs. Native people must understand that they share responsibility with other groups for the welfare of migratory bird populations. The issues are far more complex than that of gathering and presenting data; they involve special problems in communication, beliefs, trust, and politics. Resource agency personnel generally have little or no formal training or expertise in these matters. Educational materials should be designed by experts who understand native culture, human psychology, and effective use of communication media in cooperation with native representatives.

Sport hunters need to recognize that they share responsibility for depleted goose populations and that their views of native life are often ill-informed. Agencies have been painfully slow to provide in-depth analyses of data on population and harvest statistics, reticent about suggesting that sport harvest can be a problem, and relatively inactive in communicating concerns through their own or public information channels. The seriousness of the decline of the geese warrants a greater effort.

Data Gathering. Attempts to survey harvest by natives have provided some benefits and insights, but have been a failure in terms of the major goal. The USFWS must either devote the money and expertise needed to upgrade the effort or consider alternative programs. Interview research must be designed and conducted by experts in this type of study and by those who understand the social dynamics of native peoples. Biologists and managers know what kind of information is needed but, regardless of dedication and intelligence, they are ill-prepared to conduct this type of research. Copp and Garrett (1983) provided a detailed critique of the program and recommendations for improvement that should be implemented.

Regardless of the fate of the harvest-survey study, there are many other more indirect studies that could provide needed insights and be of value in assisting understanding by natives of their impact on wildlife. Examples include the effect of human disturbance on nest success, distribution and success of geese in relation to distribution of human activity, the impact of harvest by age-sex class and time of year (eggs, goslings, adults, summer and winter), and the role of waterfowl in the present economy of natives.

The recently expanded refuge biological data gathering program represents a positive response to needs for information. These data are vital to providing the baseline upon which to measure future responses of populations to management actions. Continuity in methods and direction is vital and the program could be usefully assisted by more support, as could the involvement of the research branch.

Organizational Needs. The Pacific Flyway in general, and these geese in particular, have been relatively neglected. The complexity of the problem has exceeded the ability of agencies to deal with it as add-on responsibilities to already over-loaded personnel. Tasks have been assigned to personnel who do not have the experience, training, authority, or resources needed to effectively complete them, thus placing them in an untenable position. Team-approach and use of expertise beyond that available in-house have not been effectively employed. Methods of selection of personnel compatible with living and working conditions and needs on the Y-K Delta should receive special attention.

An individual, or committee, needs the freedom and authority to devote full-time to the total complex of problems in order to provide continuity and coordination. Redirection of personnel and money is needed. A multi-membership task force, including native representatives could provide oversight similar to that developed for endangered species recovery teams. The parallel is not made loosely; extension of population declines illustrated in Figure 1 forecast threatened or rare categorization in less time in the future than it has taken us to generally acknowledge and publicize the problem. Perhaps a National Academy of Sciences panel should be convened to make recommendations.

The alternatives to immediate, effective action are unpleasant. Legal actions could increase suspicion and hostility and promote a situation where resources are damaged even further in a power struggle. Yet, lack of effective action leaves no alternative to legal recourse. The losers are the geese—and the people who cherish them for whatever reason. An entire generation of hunters has begun to pay the price for the past lack of effective action; they will be paying a heavier price for the next 10–20 years even if we take effective action now. Such depleted populations will certainly not foster the maintenance of traditional ties with land by natives or the opportunity to renew those ties by sport hunters.

Summary

Numbers of geese nesting on the Yukon-Kuskokwin (Y-K) Delta, Alaska have declined even though harvest in winter is insignificant (brant, emperor goose) or curtailed by as much as 59–65 percent (Pacific white-fronted goose, cackling Canada goose, respectively). Autumn inventories indicate alarming decreases of 85 percent of Pacific whitefronts from 450,000 to < 100,000 and of cackling geese from 350,000 to < 50,000. Numbers of geese nesting elsewhere in Alaska have increased (Taverner's, lesser and Aleutian Canada geese, tule and mid-continent white-fronted geese). Tule white-fronted geese and Aleutian Canada geese occupy large portions of the winter range in California used by Pacific whitefronts and Cackling geese. Restrictive hunting regulations should have benefitted all these populations.

The implication is that impacts of human activity on geese of the Y-K Delta are excessive, and combined with harvest in California, are near catastrophic. This is correlated with a 42 percent increase in the coastal population of Yupic Eskimos since 1960, who now hunt more efficiently with modern means of travel.

The remoteness and size of the Y-K Delta, the fact that spring-summer hunting of waterfowl violates the Migratory Bird Treaty with Canada, and cultural differences between native and non-native groups result in great difficulty in gathering pertinent data, recognition of resource problems, and working effectively for solutions. Native hunters consider a law interfering with their right and ability to gather food as an unwelcome intrusion or not applicable. Opponents argue that such needs have been abrogated by changes in law and life-style and threaten legal action to require enforcement of the Migratory Bird Treaty. Both groups frequently exhibit a lack of understanding of the needs of each other and the necessity of working together for mutual interests.

In the long term, modification of the Migratory Bird Treaty is needed to allow for regulated, legal harvest of birds and eggs in spring. This eventuality, however, seems years away. Effective action is needed now. Agencies responsible for protection of migratory bird resources have not devoted sufficient attention to these problems. Better organization, addition and/or redirection of personnel and money is needed. Specific needs include more intensive and extensive efforts to involve native groups at every level of increased data gathering and analysis, problem recognition and solving, and education. These programs need an identifiable and responsible authority and the assistance of experts in fields outside those normally represented in resource agencies (e.g., social scientists, modelers, media consultants).

Lack of immediate, effective action will likely lead to further polarization of viewpoints via political and legal confrontation while resources continue to suffer. Such depleted populations negate the goal of maintenance of traditional ties of natives to wildlife and the opportunity to renew those ties by sport hunters.

Acknowledgments

This paper presents information collected over many years by a large number of dedicated biologists. It was my purpose here to collect in one place the results of much of their efforts. It would take several pages to mention all the individuals responsible; they know who they are and I hope this report provides some measure of reward for their toil. Specific mention is, however, due to several individuals for their efforts in drawing together the data and my thoughts: D.P. Connelly (CDFG) for excellent coordination and cooperation in compilation of California and Flyway information; J.C. Bartonek (USFWS) for summarization of data on populations and perspectives on the Pacific

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Appendix. Peak numbers of white-fronted and cackling Canada geese estimated in autumn at Tulelake and Lower Klamath National Wildlife Refuges, California.

Year	Peak numbers[a]	
	White-fronted goose	Cackling goose
1965	303,200	384,000
1966	492,900	351,000
1967	495,500	322,400
1968	457,700	376,100
1969	310,600	143,000
1970	353,500	314,000
1971	383,600	289,000
1972	320,600	234,400
1973	196,200	244,800
1974	199,600	136,300
1975	165,300	217,900
1976	112,300	212,300
1977	117,700	62,000
1978	100,700	118,300
1979	114,900	60,200
1980	97,000	123,800
1981	64,200	98,700
1982	48,000	35,500
1983	80,100	26,200

[a] Rounded to nearest 100

WATERFOWL MANAGEMENT HANDBOOK

13.1.1. Nutritional Values of Waterfowl Foods

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Over 40 species of North American waterfowl use wetland habitats throughout their annual cycles. Survival, reproduction, and growth are dependent on the availability of foods that meet nutritional requirements for recurring biological events. These requirements occur among a wide variety of environmental conditions that also influence nutritional demands. Recent work on nesting waterfowl has identified the female's general nutrient needs for egg laying and incubation. Far less is known about nutritional requirements for molt and other portions of the life cycle, particularly those during the nonbreeding season. Although information on specific requirements for amino acids and micronutrients of wild birds is meager, the available information on waterfowl requirements can be used to develop waterfowl management strategies. For example, nutrient content of foods, nutritional requirements of waterfowl, and the cues waterfowl use in locating and selecting foods are all kinds of information that managers need to encourage use of habitats by feeding waterfowl. Waterfowl nutritional needs during the annual cycle and the nutritional values of natural foods and crops will be discussed below.

Composition of Waterfowl Foods

Compared to the nutritional information on many agricultural crops, the composition of wild foods is poorly documented. Nevertheless, the available information on nutritional quality of wild foods, in conjunction with known waterfowl requirements, provides general guidelines for management. Terminology commonly used when discussing the nutritional values of foods or requirements for waterfowl include the following:

Basal metabolic rate (BMR)—The lowest level of metabolism necessary for basic body functions for an animal at rest.
Gross energy—The amount of energy (often expressed in 1000 calories = 1 kcal) produced when a food sample is ignited in a bomb calorimeter. Gross energy represents the most common nutritional information available, because techniques to determine gross energy are relatively simple and costs are minimal.
Metabolizable energy—The amount of energy that can be utilized for metabolic processes by an animal. Metabolizable energy is more complicated to determine than gross energy—animals must be fed a diet of food containing a known amount of gross energy, and the portion excreted as feces, urine, and gases must be identified and quantitifed.
Proximate analysis—A chemical process to identify the major components in foods. Samples must be handled carefully to ensure that chemical composition represents the nutritional content. The food is first ground to a fine homogenate, then dried to determine water content. Components identified by proximate analysis include the following:

- *Fats or lipids*—The most concentrated energy sources in foods. Fats occur as structural components and serve as insulation or as energy stores.

- *Ash*—Mineral content.
- *Crude Fiber*—Least digestible fraction in foods that includes cellulose, hemicellulose, or lignin. Waterfowl lack rumens; thus, little fiber is digested.
- *Nitrogen-free extract (NFE)*—Highly digestible carbohydrates.
- *Protein*—Compounds containing nitrogen that are major components of muscle tissue, animal cell membranes, and feathers; also active as enzymes, hormones, and clotting factors in blood. These serve many different functions.

More sophisticated testing provides identification of the specific composition of proteins and fats:

- *Amino acids*—Mixtures of 20 to 25 different amino acids, linked by peptide bonds, form plant and animal proteins.
- *Essential amino acids*—The 10 amino acids that must come from the diet because of the inability of an animal's metabolic pathway to produce them.
- *Fatty acids*—Components of fats with varying molecular weight and number of double bonds. Unsaturated fatty acids such as palmitoleic, oleic, and linoleic acids are important in waterfowl.

Information is generally available on the gross energy of foods (Tables 1 and 2), but metabolizable energy and outputs of proximate analyses including the amount of fat, fiber, ash, or nitrogen-free extract in these same foods are rarely identified (Table 3). Proteins supply the essential amino acids and are in high demand during egg laying and molt. Fats or lipids serve as energy reserves, as structural elements in cells, and as sterol hormones. Ash indicates the mineral content. Crude fiber is a measure of the least digestible food components, whereas NFE provides an estimate of the highly digestible carbohydrates.

Food quality is best predicted when information is available on metabolizable energy, ash, protein, fat, and NFE. Protein values are reported for about half of the foods that have energy values, but the content of fat, fiber, ash, or NFE is identified for less than one-third. Foods with a very high fiber content generally have lower levels of metabolizable or usable energy because fiber is poorly digested by waterfowl. In some cases, values from chemical analyses can be misleading. Crude protein content may be high, but the form of the protein or chemical inhibitors within the food may reduce the amount usable by the bird. For example, soybeans have a high level of crude protein, but only a small portion is available to waterfowl because of inhibitors. Waterfowl require a balance of amino acids. Some foods, such as crustaceans, usually have a better balance of amino acids than

Table 1. *Chemical composition of some common waterfowl plant foods. Values represent averages from the literature.*

Common name[a]	Gross energy (kcal/g)	Fat	Fiber	Ash	NFE	Protein
Sticktights	5.177	15.0	19.7	7.2	27.5	25.0
Schreber watershield	3.790	2.9	36.7	4.8	45.9	9.3
Pecan hickory	7.875	40.8	19.0	12.6	35.1	8.4
Chufa flatsedge (tubers)	4.256	6.9	9.0	2.5	55.4	6.7
Hairy crabgrass	4.380	3.0	11.1	9.7	59.4	12.6
Barnyardgrass	3.900	2.4	23.1	18.0	40.5	8.3
Rice cutgrass	3.982	2.0	10.6	9.5	57.8	12.0
Fall panicum	4.005	3.1	16.8	16.1	50.1	12.3
Smartweed	4.423	2.8	22.0	7.5	—	9.7
Pennsylvania smartweed	4.315	2.3	21.8	4.9	65.3	9.0
Pin oak	5.062	18.9	14.7	1.6	58.6	6.4
Willow oak	5.296	20.6	14.0	1.7	55.3	5.1
Curly dock	4.278	1.2	20.4	6.9	—	10.4
Duck potato	4.736	9.0	10.8	4.9	55.5	20.0
Milo	4.228	3.1	6.0	3.5	72.2	10.2
Corn	4.435	3.8	2.3	1.5	79.8	10.8
Common soybean	5.451	20.5	5.4	6.2	27.1	39.6
Common duckweed	4.235	3.5	11.3	10.7	49.8	25.7
River bulrush (rhizomes)	4.010	—	—	—	—	—

[a] For alternative common names and scientific names consult Appendix.

Table 2. *Chemical composition of some common waterfowl invertebrate foods.*

Invertebrate	Gross energy (kcal/g)	Protein (%)
Water boatmen	5.2	71.4
Back swimmers	5.7	64.4
Midges	4.6	61.2
Water fleas	4.0	49.7
Amphipods (*Hyallela azteca*)	4.9	47.6
Amphipods (*Gammarus* spp.)	3.8	47.0
Cladocera (unclassified)	2.7	31.8
Pond snails	1.0	16.9
Orb snails	1.0	12.2

do insects and spiders. Certain amino acids can be synthesized by waterfowl, but the essential amino acids must be acquired in the diet.

Because values for metabolizable energy are reported for individual food items rather than as combinations of foods normally consumed by wild waterfowl, nutritional information is not always accurate. Synergistic interactions among foods during digestion are more difficult to identify compared to the usable energy available from a single food item fed separately. Thus, providing a nutritionally balanced diet from wild and domestic foods, alone or in combination, continues to be a perplexing challenge facing wetland managers.

The Energetic Costs of Waterfowl Activities

Wild animals must provide for general body maintenance and for processes that require additional nutrients, such as growth, reproduction, and migration. The BMR includes the demands for energy of an animal that is at rest. Basal costs for locomotion, digestion, reproduction, or thermoregulation at extreme temperature ranges are not included. Large body sizes allow waterfowl to use their body reserves to meet the demands of maintenance and other demanding processes. For example, arctic-nesting geese transport all of their protein and energy needs for laying and incubation with them to arctic nesting grounds. Such species may lose nearly 50% of their body weight by the time their clutches hatch. Reserves for migration are particularly important in some waterfowl such as Pacific populations of brant. In their 3,000-mile journey from Alaska to Mexico, they lose one-third of their body weight (about 1.87 lb of fat) in a few days.

Waterfowl engage in a variety of activities that have high energetic costs. The locality and the environmental conditions under which these activities occur determine the energetic expenditures for each event. These are usually expressed in relation to the basal metabolic rate for an animal at rest.

Activities such as swimming, preening, foraging, or courtship are more energetically costly. Flight is the most expensive activity with estimates ranging from 12–15× BMR. Diving is less costly (i.e., 3.5× BMR). Furthermore, temperatures have important effects on energetic requirements. For example, captive mallards will increase their metabolic rate above the basal level by 2.1× at 0°C and by 2.7× at −20°C. Wild ducks and geese reduce the frequency of their feeding flights under extreme cold to conserve energy. Determining actual energetic costs of activities is difficult in the field; hence, the values for wild birds are usually based on estimates rather than actual measurements.

The general nutritional requirements for biological events in the annual cycle are known for an increasing number of waterfowl. The best estimates are those for breeding birds (Table 4), whereas far less is known about nonbreeding requirements.

Table 3. *Metabolizable energy of some common waterfowl foods.*

Taxon	Test animal	Metabolizable energy (kcal/g)
Water flea	Blue-winged teal	0.82
Amphipod (*Gammarus* spp.)	Blue-winged teal	2.32
Pond snail	Blue-winged teal	0.59
Coast barnyardgrass	Duck (male)	2.63
Coast barnyardgrass	Duck (female)	2.99
Rice cutgrass	Duck (male)	3.00
Common duckweed	Blue-winged teal	1.07
Pennsylvania smartweed	Dabbling duck (male)	1.12
Pennsylvania smartweed	Dabbling duck (female)	1.10

Table 4. *Nutritional requirements for breeding waterfowl compared to the composition of corn and common native foods.*

	Requirements breeding ducks/geese	Plant foods			
		Corn	Acorns	Barnyardgrass	Pigweed
Energy	2,900[a]	3,430[a]	5,577[b]	4,422[b]	4,623[b]
Protein (%)	19	8.7	6.0	12.5	22.0
Methionine[c]	2.0	0.18	–	–	–
Ca (%)	2.7	0.02	0.24	0.13	1.72
Mg (ppm)	350	5	–	69	35

[a] = kcal ME/kg
[b] = Gross energy (not metabolizable energy)
[c] = % of protein

Note that no single food supplies a diet that meets all energy, protein, or micronutrient needs of breeding waterfowl. Likewise, activities other than breeding have varying costs in relation to specific nutrient energy and differ greatly from reproduction, where a mix of energy, minerals, and protein are required to supply the needs of egg-laying females.

Food Quality in Relation to Deterioration and Habitat Conditions

The quality of plant foods is largely determined by heredity, but other factors, such as soil nutrients and environmental conditions during the growing season, are important. For example, seeds having a high fat content may vary greatly in energy content among seasons because of environmental conditions. The supply of minerals is closely related to the mineral concentrations in water.

One of the major problems facing waterfowl managers is deterioration of seeds during flooding, but information on rates of deterioration is only available for a few seeds. Soybeans break down rapidly; nearly 90% of the energy content is lost during 3 months of flooding, whereas corn loses only 50% during a similar period of flooding (Table 5). Breakdown of wild seeds is variable. Hard seeds such as bulrush decompose slowly, whereas softer seeds such as common barnyardgrass deteriorate 57% after 90 days under water. Such variations have important implications for the timing of flooding for waterfowl (Table 6). If some seeds are submerged for a month or more before waterfowl are present, much of the food value will be lost because of deterioration.

Supplying Nutritional Needs for Waterfowl

The large body sizes of waterfowl enable them to store nutrients as body reserves. In some cases nutrients for an upcoming stage in the life cycle are acquired at a distant wetland and transported as body reserves. The best known examples are the transport of fats, calcium, and protein by arctic-nesting geese from wintering and migrational stopovers to breeding habitats. Because waterfowl store body reserves, managers should make an effort to supply required nutrients throughout the annual cycle rather than supplying nutrients solely for events at the time they occur.

Identifying shortfalls in nutritional needs is becoming more of a reality as the requirements for free-living animals are identified. Waterfowl are

Table 5. *Deterioration of selected seeds after 90 days of flooding.*

Plant name	Decomposition (%)
Soybean	86
Barnyardgrass	57
Corn	50
Common buckwheat	45
Milo	42
Giant bristlegrass	22
Pennsylvania smartweed	21
Cultivated rice	19
Water oak (acorns)	4
Hemp sesbania	4
Horned beakrush	2
Saltmarsh bulrush	1

Table 6. *Comparison of deterioration of 100 lb of five selected seeds in relation to different flooding schedules. Estimates assume a constant daily rate of deterioration.*

	Percent remaining			
	15 September	15 October	15 November	15 December
Flooding date				
18 August				
Soybeans	71	43	14	0
Corn	83	67	50	33
Millet	81	62	43	24
Giant bristlegrass	93	85	78	71
Smartweed	93	85	79	72
Total percent remaining	84	68	53	40
15 September				
Total percent remaining		84	68	53
15 October				
Total percent remaining			84	68
15 November				
Total percent remaining				84

well adapted to the dynamics of natural wetland systems. Mobility and foraging adaptability are behavioral characteristics that enable waterfowl to acquire needed resources. Dynamic wetlands supply a variety of food resources that allow waterfowl to feed selectively and to formulate nutritionally adequate diets from a variety of sites. Although a single wetland site may not provide adequate food for all requirements, management areas with a variety of wetlands or flooding regimes usually have a mix of habitats that provide all nutritional requirements.

Because a variety of strategies exists within and among waterfowl species (wintering, migrating, or breeding), not all individuals or species require similar resources simultaneously. Thus, a diverse habitat base is a logical approach to meet the various needs of waterfowl. Furthermore, when suitable food and cover are within daily foraging range, acquisition of required resources is enhanced. A good rule of thumb is to provide many wetland types or food choices within a 10-mile radius of waterfowl concentrations. Some species such as snow geese have far greater foraging ranges, but they are the exception rather than the rule.

Appropriate management requires preservation, development, and manipulation of manmade and natural wetland complexes. Such an approach provides nutritionally balanced diets for diverse waterfowl populations. Where natural wetlands remain intact, they should be protected as unique components of the ecosystems. The protection of natural systems and the development and management of degraded systems increases choices of habitats and foods for waterfowl. Likewise, the provision of adequate refuge areas where birds are protected from disturbance is an essential ingredient to ensure that food resources are available to waterfowl and can be used efficiently.

Suggested Reading

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Appendix. Common and Scientific Names of Plants and Animals Named in Text.

Plants

Pigweed	*Amaranthus* sp.
Devils beggarticks *or* sticktights	*Bidens frondosa*
Schreber watershield	*Brasenia schreberi*
Pecan hickory	*Carya illinoensis*
Chufa flatsedge	*Cyperus esculentus*
Hairy crabgrass	*Digitaria sanguinalis*
Common barnyardgrass *or* Japanese millet	*Echinochloa crusgalli*
Coast barnyardgrass, wild millet, *or* watergrass	*Echinochloa walteri*
Common buckwheat	*Fagopyrum esculentum*
Common soybean	*Glycine max*
Rice cutgrass	*Leersia oryzoides*
Common duckweed	*Lemna minor*
Cultivated rice	*Oryza sativa*
Fall panicum *or* panic grass	*Panicum dichotomiflorum*
Curltop ladysthumb *or* smartweed	*Polygonum lapathifolium*
Pennsylvania smartweed	*Polygonum pensylvanicum*
Pin oak	*Quercus palustris*
Willow oak	*Quercus phellos*
Water oak	*Quercus nigra*
Horned beakrush	*Rhynchospora corniculata*
Curly dock	*Rumex crispus*
Common arrowhead *or* duck potato	*Sagittaria latifolia*
River bulrush *or* three-square bulrush	*Scirpus fluviatilus*
Saltmarsh bulrush *or* bulrush	*Scirpus robustus*
Hemp sesbania	*Sesbania exalta*
Giant bristlegrass *or* giant foxtail	*Setaria magna*
Common sorghum *or* milo	*Sorghum vulgare*
Indian corn *or* corn	*Zea mays*

Birds

Blue-winged teal	*Anas discors*
Mallard	*Anas platyrhynchos*
Brant	*Branta bernicla*
Snow goose	*Chen caerulescens*

Invertebrates (Families)

Midges	Chironomidae
Water boatmen	Corixidae
Water fleas	Daphnidae
Pond snails	Lymnaeidae
Back swimmers	Notonectidae
Orb snails	Planorbidae

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13.3.1. Invertebrate Response to Wetland Management

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By gaining greater understanding and appreciation of wetland environments, managers have developed creative insights for waterfowl conservation. Among the most exciting new developments in the understanding of functional wetlands has been the recognition of the important roles of invertebrates in aquatic ecosystems. These roles include trophic linkage from primary production to secondary consumers such as waterfowl, packaging of specific nutritional components such as amino acids and micronutrients for vertebrate predators, and detrital processing of wetland organic material. Although specific invertebrate responses to various management techniques are not always predictable and may differ among invertebrate species, patterns related to water regimes, water chemistry, and vegetative structure have emerged. Managers should consider the following invertebrate responses to natural and manipulated wetland complexes when managing for waterfowl.

Importance to Waterbirds

Although wetland systems are some of the most productive ecosystems in the world in terms of vegetation biomass, few duck species acquire substantial energetic or nutritional resources directly from consumption of plant material other than seeds. Much of the energy from plants is initially transferred to primary consumers, including a diverse group of invertebrate species. A variety of invertebrates are consumed by waterfowl. Ducks rely heavily on invertebrates as a major food source throughout the annual cycle. Dabbling and diving ducks use invertebrates extensively during protein-demanding periods, such as egg laying or molt (Table 1). Duck species are adapted to consumption of invertebrate prey by selection of microhabitats, structure of the bill and lamellae, and foraging strategies.

Relation to Water Regimes

Long-term hydrologic cycles have shaped the life history strategies of wetland invertebrates. These organisms have developed many adaptations that include:

- egg or pupal stages that can tolerate drought periods,
- initiation of egg development only after specific water/oxygen levels have been reached,
- marked seasonality in life cycle,
- rapid development,
- large number of offspring (high reproductive potential)
- obligate diapause (period of nondevelopment) tied to seasonal flooding, and
- parthenogenic reproduction (as in cladocera).

Invertebrates often move into deeper pools, wetland sediments within the water table, and other nearby wetlands when water levels drop or change within a specific wetland. Many species (e.g., leeches, crayfish) will burrow in sediments to avoid

Table 1. *Invertebrates consumed by laying female waterfowl collected from 1967 to 1980 in North Dakota. Data expressed as aggregate percent by volume. Modified from Swanson 1984.*

Food item	Blue-winged teal (20)	Northern shoveler (15)	Gadwall (saline) (20)	Gadwall (fresh) (35)	Mallard (37)	Northern pintail (31)
Snails	38	40	0	4	16	15
Insects	44	5	52	36	27	37
Caddis flies	7	tr	1	8	9	1
Beetles	3	2	16	4	5	3
True flies	32	2	26	18	6	3
Midges	20	1	26	17	4	20
Miscellaneous	2	1	9	6	7	0
Crustaceans	14	54	20	32	13	14
Fairy shrimps	5	6	tr	0	4	14
Clam shrimps	tr	7	0	14	6	tr
Water fleas	0	33	10	10	3	tr
Scuds	8	0	0	7	tr	tr
Miscellaneous	1	8	10	7	tr	tr
Annelids	1	0	0	tr	13	11
Miscellaneous	2	0	0	0	3	0
Total	99	99	72	72	72	77

desiccation. Adults of several insect groups may fly to other wetlands if conditions become unsuitable. Flight distances may be less than a few yards to another basin within a wetland complex or more than 50 miles to a distant wetland.

Long-term hydrologic changes shape invertebrate life history strategies. Short-term hydrologic regimes may determine the actual occurrence and abundance of invertebrates. Flooding affects wetland invertebrate occurrence, growth, survival, and reproduction. Entirely different invertebrate communities (Fig. 1) are present in wetland basins with differing hydrological regimes (timing, depth, and duration of flooding). As litter is flooded, nutrients and detrital material (as coarse particulate organic matter) are released for a host of aquatic invertebrates (Fig. 2). As material is broken down into finer particles (fine particulate organic matter), organisms that gather detritus or filter feed will take advantage of the newly available foods. Grazing organisms (Fig. 3) feed on free-floating algae or periphyton, which grows on aquatic plant surfaces. When litter material is consumed, invertebrate populations decrease rapidly. Thus, prolonged flooding (longer than 1 year) of uniform depth leads to reduced wetland invertebrate numbers and diversity. Freezing may also lower spring invertebrate populations in northern locations.

Association with Vegetation Structure

Water regimes not only directly affect invertebrate populations, but indirectly affect other fauna through modification of aquatic plant communities. Hydrological regimes influence germination, seed or tuber production and maturation, and plant structure of aquatic macrophytes. Invertebrate associations are influenced by the leaf shape, structure, and surface area of aquatic vegetation. Macrophytes with highly dissected leaves, such as smartweeds, tend to support greater invertebrate assemblages than do plants with more simple leaf structure, such as American lotus (Fig. 4). The composition of invertebrate populations is associated with plant succession.

Discing and other physical treatments are regularly used to modify less desired plant communities. Initial invertebrate response is great following shallow discing in late summer when the shredded plant material is flooded immediately. The shredding of coarse litter material by discing results in quick decomposition in fall, but invertebrate numbers are reduced the following spring. Cutting robust, emergent vegetation above the ice in winter can also result in a rapid invertebrate response, after spring thaw.

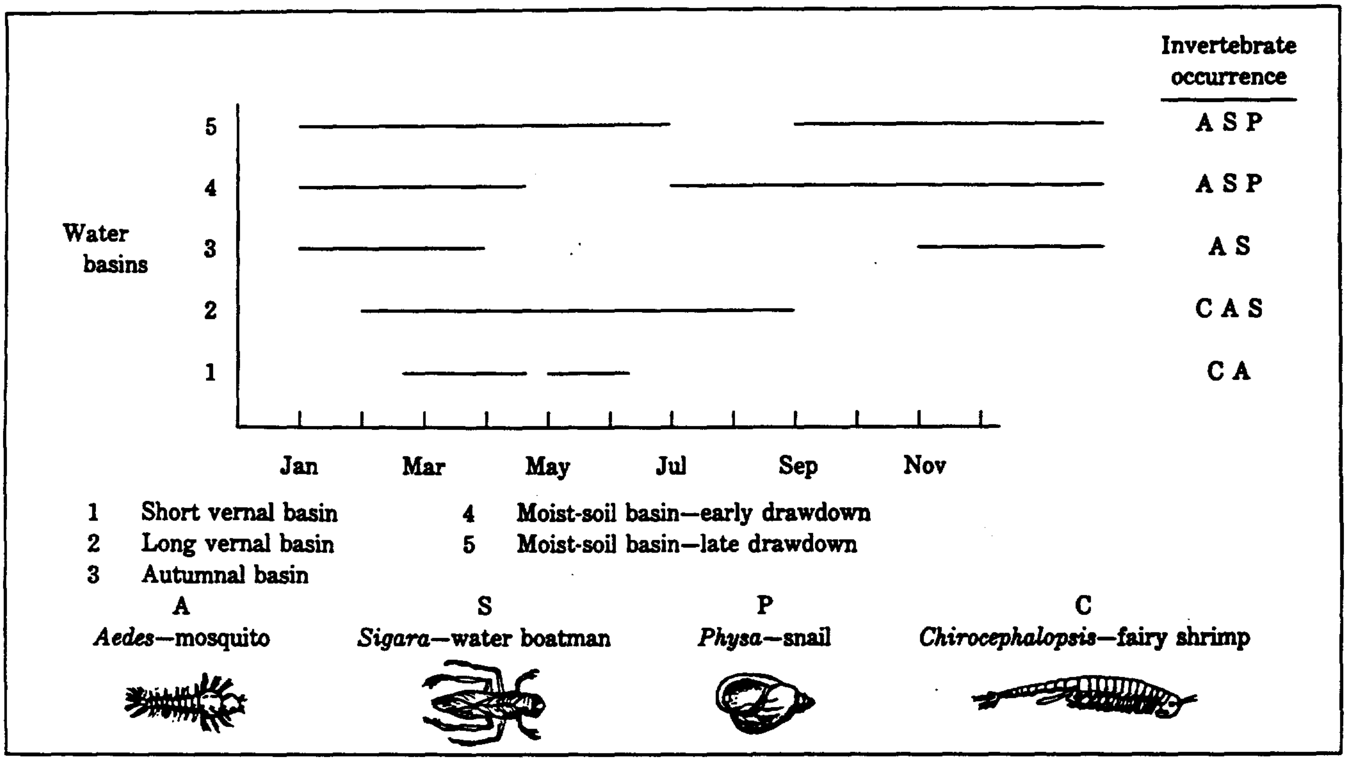

Figure 1. Occurrence of four common invertebrate genera relative to water regimes of five different seasonally flooded basins. Horizontal lines represent presence of water.

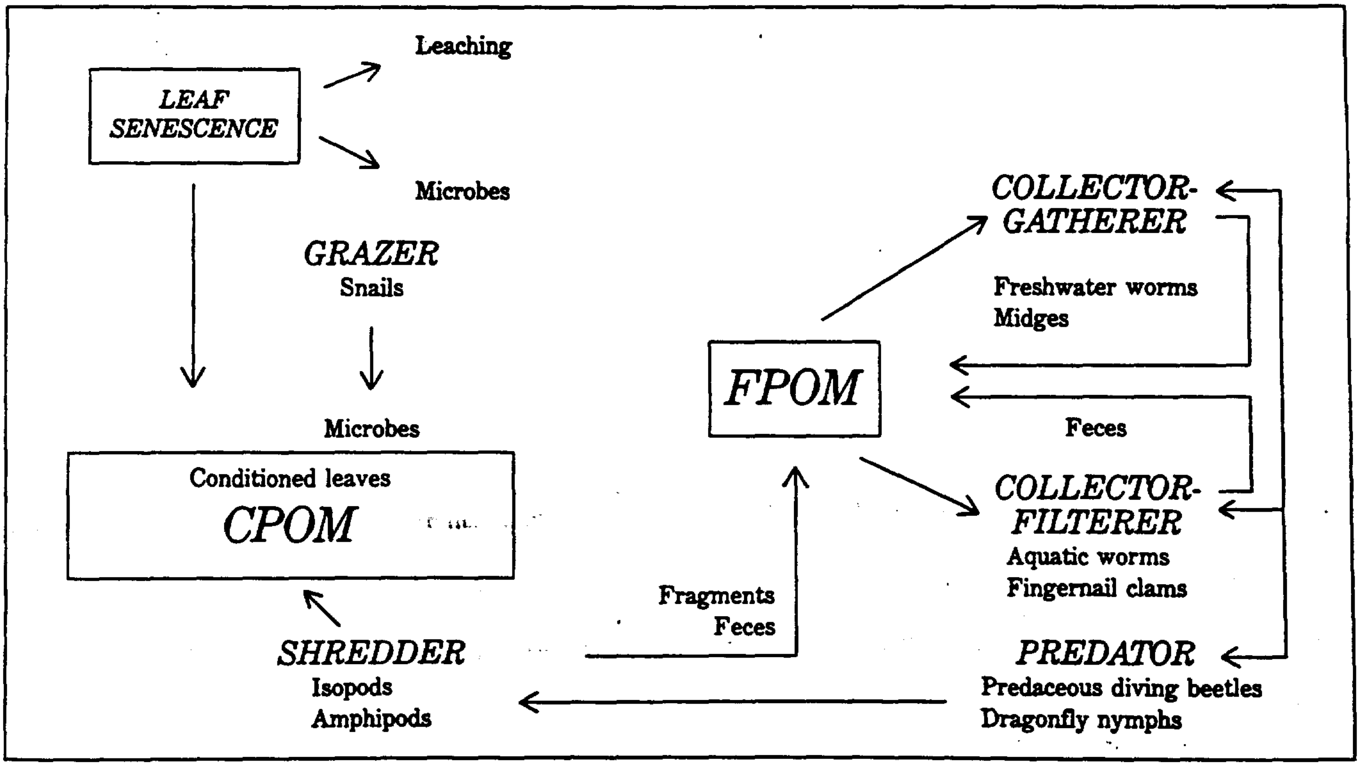

Figure 2. Invertebrate detritivore community. CPOM = Coarse particulate organic matter; FPOM = Fine particulate organic matter.

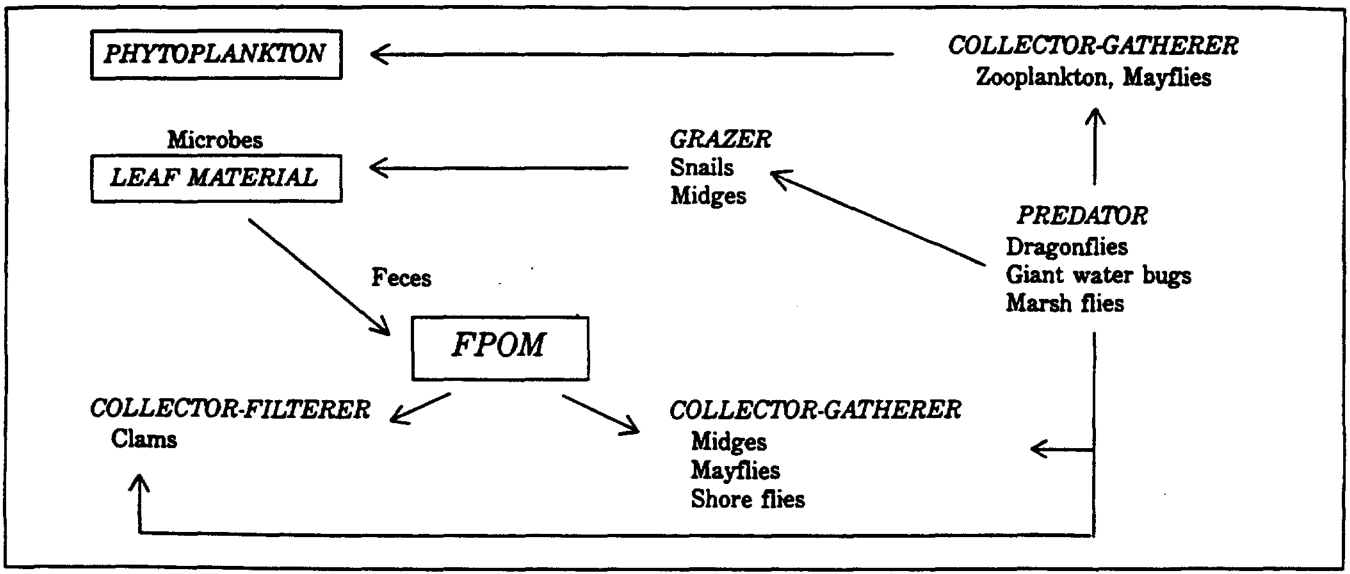

Figure 3. Invertebrate grazer community. FPOM = Fine particulate organic matter.

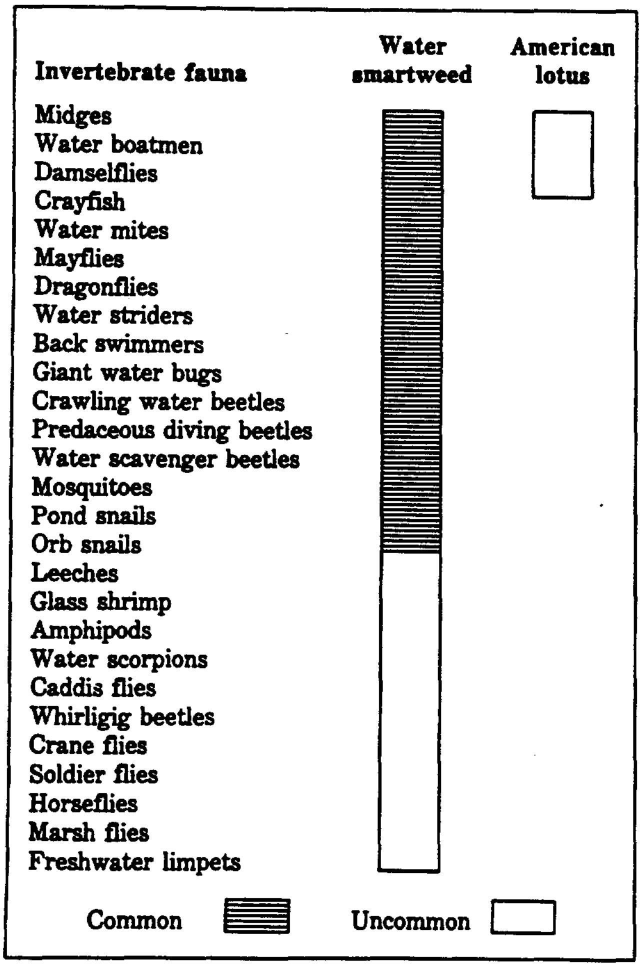

Figure 4. Macroinvertebrates associated with water smartweed and American lotus in seasonally flooded wetlands.

Management Implications

Acquisition of wetlands or protection of previously acquired wetland complexes will continue to be the best means to support diverse invertebrate fauna. The restoration of disturbed wetlands has its greatest potential in areas of marginal agricultural lands. Pesticide use should be eliminated on all refuge areas, regardless of proximity to urban sites where mosquito control is a concern, or the quality of such wildlife areas will be reduced. Inflow waters must be monitored for pollutants and pesticides. The timing of water movements should coincide with the exploitation of leaf litter by invertebrates. Waters should not be drained when nutrient export may be high, such as in early stages of leaf litter decomposition. Present knowledge of water manipulations suggests that management for specific aquatic or semi-aquatic plant communities may be the most practical means of increasing invertebrate production. Managers can enhance the potential for invertebrate consumption by waterfowl if peak periods of waterfowl use of wetlands coincide with reduced water levels. Exploitation of invertebrates by waterbirds can be optimized through shallow water levels, partial drawdowns that concentrate prey, and extended (3–5 week) drawdowns with "feather-edge" flooding to increase the available time and area for foraging.

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Appendix. Common and Scientific Names of Plants and Animals Named in Text.

Plants

American lotus	*Nelumbo lutea*
Smartweed	*Polygonum* spp.
Water smartweed *or* marsh knotweed	*Polygonum coccineum*

Birds

Northern pintail	*Anas acuta*
Northern shoveler	*Anas clypeata*
Blue-winged teal	*Anas discors*
Mallard	*Anas platyrhynchos*
Gadwall	*Anas strepera*

Invertebrates (Families)

Crayfish	Astacidae
Giant water bugs	Belostomatidae
Midges	Chironomidae
Water boatmen	Corixidae
Mosquitoes	Culicidae
Predaceous diving beetles	Dytiscidae
Water striders	Gerridae
Whirligig beetles	Gyrinidae
Crawling water beetles	Haliplidae
Water scavenger beetles	Hydrophilidae
Pond snails	Lymnaeidae
Water scorpions	Nepidae
Back swimmers	Notonectidae
Orb snails	Planorbidae
Marsh flies	Sciomyzidae
Soldier flies	Stratiomyidae
Horseflies	Tabanidae
Crane flies	Tipulidae

Invertebrates (Orders)

Scuds *or* sideswimmers	Amphipoda
Leeches	Annelida
Fairy shrimp	Anostraca
Water fleas	Cladocera
Beetles	Coleoptera
Clam shrimp	Conchostraca
True flies	Diptera
Mayflies	Ephemeroptera
Water mites	Hydracarina
Isopods	Isopoda
Damselflies, dragonflies	Odonata
Caddis flies	Trichoptera

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WETLAND INVERTEBRATES IN RELATION TO HYDROLOGY AND WATER CHEMISTRY

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Mosquito control, especially as a restraint to the vector of malaria and encephalitis, was one justification for drainage of North American wetlands in the early 1900's. The decline of yellow fever and malaria after swamp and marsh drainage associated with the Panama Canal project was often cited to defend agricultural "reclamation" of other "wasteland" wetlands (Nolen 1913).

Today the economic, political, recreational, and scientific values of functioning wetland ecosystems are increasingly recognized (Odum 1978). Unfortunately, vast areas of North American natural wetlands have been lost to agricultural, industrial, and urban developments (Weller 1981). Many remaining wetlands have suffered major perturbations in water quality, hydrologic regimes, and habitat isolation. A holistic management philosophy for public wetlands has recently been adopted by most natural resource agencies. These long-term management plans often include restoration of certain drained wetlands. Although the ecological functions of natural wetlands cannot be completely duplicated, water impoundments have proven effective in many wetland restoration programs. Monies from license fees and taxes on hunting and fishing equipment have allowed public acquisition of many wetlands by state and federal agencies.

While the general public has a positive attitude toward wetland birds, mammals, herpetofauna, and fish, their interest has not been expanded to include aquatic invertebrates. Many recent studies have demonstrated that these lower trophic forms are extremely important in maintaining a functional wetland habitat, not only as a protein food base for vertebrates, but also in nutrient cycling (Anderson and Sedell 1979). The purpose of this manuscript is to provide resource personnel with ecological information on both wetland invertebrates and, more specifically, how these organisms may respond to wetland management techniques.

INVERTEBRATE ADAPTATIONS TO HYDROLOGIC CHANGES

Long-term, regional hydrologic cycles have shaped the life history strategies that wetland invertebrates have evolved. Short-term water regimes, physical factors (basin morphology and complex structure), chemical factors (nutrient inputs), and biotic factors (hydrophyte structure and predator density) may, however, determine actual occurrence and abundance at any given time. Present knowledge regarding ecological strategies available to temporary pool invertebrates has been well summarized (Wiggins *et all.* 1980). The basic life history groups from that manuscript are summarized using examples of genera (table 1).

Basic invertebrate adaptations for temporary wetlands include rapid development, marked seasonality in life cycle, and egg or pupal stages that can tolerate drought periods. The groups of Turbellaria (flatworms), Lumbriculidae (freshwater worms), Bryozoa (ectoprocts), Anostraca (fairy shrimp), Conchostreaca (clam shrimp), Cladocera (water fleas), Ostracoda (seed shrimp), Ephemeroptera (mayflies), Chaoboridae (phantom midges), Culicidae (mosquitos), and Sciomyzidae (marsh flies) all contain species with drought resistant egg, ephippia, or statoblast stages. Many organisms demonstrate an obligate diapause (period of non-development) which appears tied to seasonal flooding. Eggs of *Caenestheriella* phyllopeds may remain viable for 5 years under dry conditions (Mattox and Velardo 1950). Some midge larvae construct cocoons during dry periods (Grodhaus 1976). Fairy shrimp are dependent on wetland habitats which remain dry in winter, but reflood in spring (Broch 1965). Other adaptations include self-fertilization in some pulmonate snails and parthenogenetic reproduction in cladocera. As reflooding occurs, *Daphnia pulex* may direct a mere 5 percent of its gross energy

Table 1.--*Invertebrate groups according to life history tolerance or avoidance of drought period and period of recruitment in the community (Wiggens* et al. *1980)*

Group 1--Overwintering residents:
  Passive dispersal only.
  Examples include *Phagocata, Nais, Helobdella, Daphnia, Cyclops, Procambarus, Hyallela, Asellus, Physa, Gyraulus, Sphaerium.*
  (Most oligochaetes, leeches, zooplankton, crayfish, amphipods, isopods, gastropods, pelecypods)

Group 2--Overwintering spring recruits:
  Oviposition dependent on water; most reproduce in spring water.
  Examples include *Agabus, Haliplus, Hydrobius, Tanytarsus, Chironomus, Tabanus.*
  (Some beetles, most midges.)

Group 3--Overwintering summer recruits:
  Oviposition independent of water; egg deposition in mud.
  Examples include *Lestes, Aedes, Chaoborus.*
  (Odonates, mosquitoes, phantom midges.)

Group 4--Non-wintering spring migrants:
  Adults leave temporary water before drying; overwintering mostly in permanent water.
  Examples inlcude *Sigara, Notonecta, Belostoma, Gerris, Ranatra, Dytiscus,* Gyrinus.
  (Most hemipterans, some beetles.)

budget (in excess of maintenance) toward growth, but then spend the remainder in reproductive effort (Richman 1958).

Behavioral adaptations to drying conditions may include burrowing in sediments, moving toward deeper water or emigrating from the basin. Leeches, oligochaetes, clams, and crayfish may burrow into the water table to avoid desication. Imago beetles and hemipterans demonstrate well developed flight dispersal in relation to water drawdown (Fernado 1958). This migration strategy requires high energy food for flight and, correspondingly, a reduced fecundity. Physical conditions, such as exposed mudflats or increased prey are necessary for such flight, but behavioral interaction with species that are competitors or predators may influence the timing of these movements. Movements may involve only a short flight within a wetland complex to another basin or may extend 80 km or more (Popham 1964).

Food availability and developmental potential are determined by the extent and duration of flooding. Invertebrates that have adapted to such fluctuating conditions demonstrate diverse trophic and developmental strategies. Figure 1 represents the response of four common freshwater invertebrate genera to five separate annual hydrologic regimes in a mid-latitude North American wetland. None of the represented hydrologic regimes meets all the requirements for all four of these common organisms. The adaptive timing of reproduction is based on genetic potential, physiological condition, and habitat availability. The specificity of a population's breeding schedule varies between species, but a wide range of schedules and high fecundity allow for greater success in a fluctuating aquatic environment.

WATER CHEMISTRY AND INVERTEBRATE-HYDROPHYTE ASSOCIATION

As wetland waters fluctuate, ions and nutrients may concentrate or become dilute. These chemical changes influence the richness of invertebrate species, abundance, growth, and behavior. Temperature and oxygen levels seem to have the most pronounced effects. Temperature directly affects metabolic activity. Timing of molt (voltinism), feeding activity, emergence patterns, and hatching are all influenced by water temperature. Turbellaria require temperatures above 5° C to stimulate egg development and above 8° C for hatching (Young 1974). *Phagocata* (flatworms) will fragment into resistant cysts at high temperatures (Castle 1928).

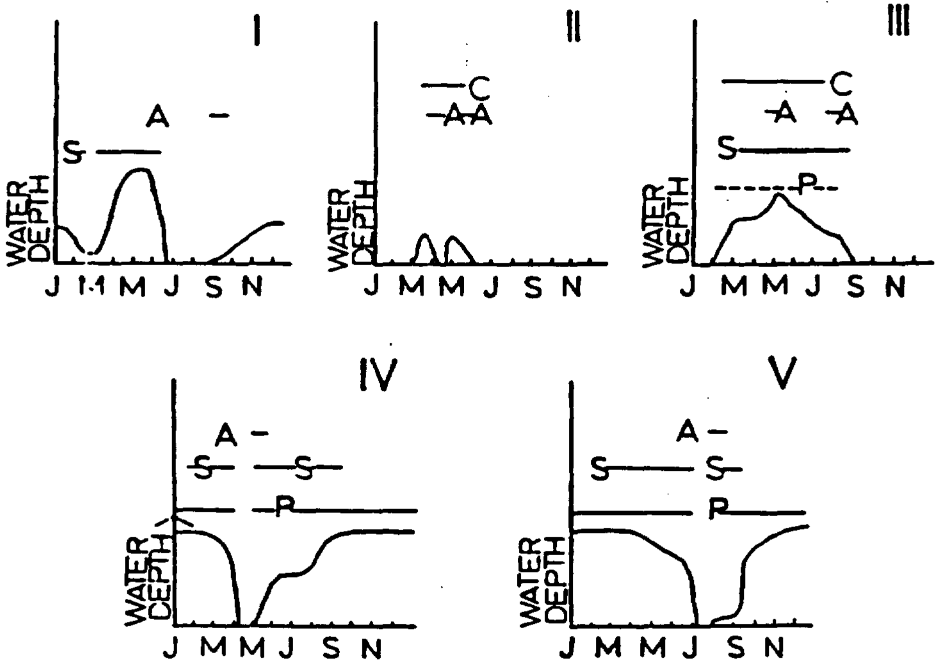

Figure [illegible].--*Response of four wetland invertebrates (P-*Physa *snail, S-*Sigara *corixid, A-*Aedes *mosquito and C-*Chirocephalopsis *fairy shrimp) to five separate mid-latitude, emergent wetland basins under various annual hydrologic regimes. I-Autumnal Basin, II-Short Vernal Basin, III-Long Vernal Basin, IV-Moist Soil Early Drawdown, V-Moist Soil Late Drawdown. Dashed line indicates occurrence only if pioneering occurs. Letters indicate period of oviposition. (After Wiggens* et al *1980, Broch 1965, Reid* et al. *in prep.)*

Fairy shrimp are not only dependent on fluctuating water conditions, but all egg development is stimulated by decreasing temperatures and high oxygen levels. As spring flooding occurs and oxygen levels drop as hydrophytes decompose, the fairy shrimp hatch (Broch 1965). Many other organisms require a strict progression of rising temperatures (Danks 1971). The hatching stimulus for the water flea *Diaptomus stagnalis* is controlled by decreased oxygen levels (Brewer 1964), while the hatching of the playa shrimp *Branchinecta mackini* is controlled by O_2 tension and percent salinity (Brown and Carpelan 1971). Populations of Molluscs are not large in impoundments in the forested Lake States if calcium and magnesium needed for shell development are low (less than 50 micromhos specific conductance) (Verry, personal communication; Baldassare 1978)

As water fluctuations influence chemical composition of waters, they also influence hydrophyte germination (van der Valk and Davis 1980). One of the earliest recognized habitat relationships for aquatic invertebrates was that with aquatic plants. Hydrophyte leaf shape, structure, and surface area are related to invertebrate abundance (Wieser 1951, Rosine 1955). Several investigators (Krecker 1939, Andrews and Hasler 1943, Krull 1970) have found higher densities of insects associated with aquatic plants containing highly dissected leaves.

Hydrophyte conditions are not stable and changes in growth and senescence influence the invertebrates associated with them. Annual fluctuations in the amphipod *Hyallela azteca* associated with *Chara* and smartweed *Polygonum* can occur, as seen in a shallow Colorado lake (Rosine 1955). The largest standing biomass of invertebrates in Mississippi wetlands occurred in association with coontail *Ceratophyllum* and fanwort *Cabomba* (Teels *et al. 19176)*. These submergents become established only after flooding and after resulting turbidity has subsided. Investigations of Lake Erie waters revealed that "thrifty" (or healthy) plants maintain the greatest invertebrate abundance (Krecker 1939). Smartweed leaf drop associated with drought stress and reflooding resulted in a depauparate invertebrate fauna the following spring in a Mississippi River floodplain wetland (Reid *et al.* in prep.).Community composition is dependent on plant condition and food habits of the invertebrates. Seasonal senescence of emergents encourages colonization by detritivore communities (Danell and Sjoberg 1979). Biochemical inhibitors from submergents may influence associated periphyton (Abdel-Malek 1948) and invertebrate feeding, growth, and hatching. Annual periphyton shifts (Young 1945, Millie 1979) undoubtedly influence grazer community composition.

Despite the wide diversity of species present in most natural or impounded wetlands, certain taxonomic groups are usually dominant. Although techniques and sampling periods vary among studies, chironomids or freshwater worms are usually the most numerous in shallowly flooded emergent wetlands or typical littoral regions of eutrophic lakes (table 2). Dipterans are the most numerous of emerging insects, while mayflies and odonates are somewhat less numerous. In Ontario wetlands 87 and 98 percent of all emerging adult insects were dipterans (Judd 1953, 1958, 1960) and chironomids and culicids dominated the species composition. Snails, mayflies, corixids, and amphipods may form the next most common aquatic groups. Impounded water with minimal hydrologic modifications or shallow lakes may encourage submergent hydrophyte growth and associated amphipods (Cooper 1965, Whitman 1976). Invertebrate production may be less than in seasonally fluctuating wetlands.

Forested wetlands contain a very different community structure than emergent marshes. Fingernail clams *(Sphaerium* and *Musculium)* make up between 58 and 98 percent of invertebrate biomass in Mississippi and Alcovy River floodplain samples (Eckblad *et*

Table 2.--*Dominant macroinvertebrates in selected shallowly flooded, emergent wetlands*[1]

Organisms	Percent of sample	Reported form	Site	Source
Chironomidae	80.1	N[2]	North Slope,	Bergman *et al.*
Oligochaeta	19.9		AK, USA	1977
Gastropoda	36.2	N	Lizard Lake,	Tebo 1955
(Helisoma/Physa)			IA, USA	
Chironomidae	19.1			
Oligochaeta	17.6			
Chironomidae	70.4	N	< 1 yr age	Whitman 1974
Planorbidae	20.3		Managed wetlands	
Corixidae	8.0		NB, CAN	
Chironomidae	42.5	N	1-4 yr age	Whitman 1974
Gastropoda	46.5		Managed wetlands	
Planorbidae	(22.5)			
Physidae	(6.5)			
Lymnaeidae	(17.4)			
Corixidae	6.2			
Chironomidae	61.9	N	7 + yrs	Whitman 1974
Planorbidae	6.2		Managed wetlands	
Corixidae	13.1		NB, CAN	
Talitridae	7.9			
Chironomidae	60.2	N	NB, CAN	Whitman 1974
Planorbidae	9.3			
Corixidae	6.8			
Talitridae	7.0			
Tanytarsus (Chironomidae)	74/54	N/V	S. Michigan Lake	Anderson and Hooper
+			MI, USE	1956
Hyalella (Talitridae)				

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[1] Data does not include zooplankton (Cladocera, Copepoda, Ostracoda).
[2] N = numbers, V = volume.

al. 1977, Parsons and Wharton 1978). *Asellus* isopods, *Crangonyx* amphipods, fingernail clams, and crayfish dominated the invertebrates of lowland hardwood forests of Louisiana, Illinois, and Missouri (Moore 1970, Hubert and Krull 1973, White, 1982).

MANAGEMENT IMPLICATIONS

Although water manipulation is a common tool for wetland management, little is known about its effect on macroinvertebrate ecology (Weller 1978). A dramatic decrease in invertebrate abundance after a drawdown was noted in a Michigan wetland (Kadlec 1962). Herbivores decreased, but predator species increased in another drawdown (Wegener *et al.* 1974). The species diversity of an aquatic invertebrate community dropped rapidly in natural wetlands of Minnesota just prior to drying (Hohman 1977). Available biomass during drawdown depends on emigration or aestivation tactics. Most of the information related to drawdown has not considered semi-aquatic organisms such as *Stenus* rove beetles or *Pirata* spiders. These organisms rapidly respond to mudflat conditions and may greatly increase biomass estimates. Response to artificial, shallow flooding is also rapid, especially if timed to natural hydrologic increases and invertebrate growth and hatching strategies. Invertebrate abundance was greatest 6 weeks after Green Tree reflooding (Hubert and Krull 1973).

The duration of flooding influences invertebrate occurrence. Semi-permanent wetlands appeared more productive than seasonal basins in Minnesota (Hohman 1977). Whitman (1974) found 1.5-5 years as optimal for invertebrate production on shallow impounded water of Nova Scotia, while Reinecke (1977) found the greatest abundance and biomass of invertebrates in 3- to 5-year-old beaver ponds. Highly turbid waters will restrict the development of submergents, and if the basin is flooded to depths greater than a few centimeters, the area will rapidly decline in invertebrate usage Seasonal or semi-seasonal wetlands may be most productive where input waters are highly turbid.

The relationship between invertebrates and vegetation suggests there may be major faunal shifts with vegetation succession. Voights (1976) documented this shift in summer studies of Iowa marshes. Isopod and snail biomasses increased as emergent and dead vegetation increased, while midges cladocera, and copepods dominated more open areas and amphipods increased in dense beds of submerged vegetation. The number of organisms, biomass, and number of taxa all increased when the ratio of cover: water approached 50:50 at the Delta Marsh in Manitoba (Kaminski 1979).

Investigations related to physical treatments (mowing, disking, burning) are few. At the Delta Marsh, mean number of invertebrates was greater on the control site than on mowed or rototilled sites after spring reflooding, but mowed sites showed higher numbers a year later (Kaminski 1979). Density, biomass and taxa richness of aquatic invertebrates increased dramatically 4 weeks after cattails (*Typha latifolia)* were cut and removed from plots in southern Manitoba (Murkin *et al.* 1982). Early fall flooding may produce greater invertebrate numbers in disked areas because of the conditoned plant material (Reid *et al.* in prep.). Most numerous at these sites will be highly mobile aquatic forms (Hydrophilidae, Dytiscidae) or larvae of emergent forms (Culicidae, Ephyridae).

The importance of wetland invertebrates to avain omnivores has been documented only recently (Chura 1961; Sugden 1973; Swanson and Meyer 1973, 1977; Taylor 1977). Because impounded waters are often managed principally for these predators, it is important to know where and how exploitation occurs. The broad term "aquatic invertebrate" has masked the diversity of life history strategies and wetland basins utilized by these prey organisms. Breeding pintails concentrate on chironomids and snails in shallow potholes (Krapu 1974); white-winged scoters feed exclusively on the amphipod *Hyalella azteca* in semi-permanent lakes (Brown 1981); wood ducks eat amphipods, isopods, and snails of lowland hardwood forests (Drobney 1977); while migratory sora feed on semi-aquatic beetles and grasshoppers (Rundle 1980). Variation in emergence and egg laying dates within single insect genera (Meyer and Swanson 1982) allow for potential vertebrate predation over an extended period. Predators may select certain basins because the presence or conditions of plants save as a proximate cue to invertebrate prey. Availability of prey organisms initially increases with decreasing water levels, provided the invertebrates do not emigrate. Predators shift to wetland basins where the least energy is expended to forage.

Invertebrate mortality of 84 percent (Schneider 1978) and up to 90 percent (Schneider and Harrington 1981) has been reported on intertidal mudflats. Wading birds reduced fish biomass by 76 percent in a drying Florida wetland (Kushlan 1976). Invertebrates with low mobility and emigration tactics are most vulnerable when interior marshes dry in mid- to late summer. The behavior of predators may also change (Swanson and Sargent 1972, Watmough 1978) as foraging efficiency increases. Not only the numbers of prey, but the caloric and nutrient value of prey to the predators should be considered in management options (Driver 1981).

IMPORTANCE AND PROBLEMS OF WETLAND DATA INTERPRETATION

Wetland invertebrates were first considered important in diets of obligate animal predators. Recent food habit studies have shown that invertebrates are highly utilized during critical physiological periods of many vertebrate omnivores. Aquatic invertebrates are also important in vegetative decomposition and processing of nutrients in aquatic systems.

Several problems with wetland invertebrate investigations should be considered when evaluating research for management. Shallow water bodies, often typified by dense stands of emergent vegetation, present a challenge to organism collection. Several techniques have recently been developed or modified (Lammers 1977, Swanson 1978a, 1978b, LeSage and Harrison 1979) by wetland investigators. Different mesh sizes among studies makes direct comparisons of density and production data difficult. The few quantitative studies that deal directly with shallow-impounded wetlands or wetland techniques restrict viable options available to managers. In addition, many of these studies were conducted using broad systematic descriptions of organisims, such that trophic relationships or species life history strategies are impossible to determine. Considering the richness of invertebrate species in wetlands and the myriad of adaptations they employ to deal with water fluctuations, ecological projections based on taxonomic groupings above the level of family or genus are probably suspect.

CONCLUSIONS

Long-term hydrologic cycles have shaped the life history tactics of wetland invertebrates. This diverse group exhibits a wide range of feeding and reproductive strategies in association with dynamic water chemistry and vegetation patterns. The manipulation of water basins will directly influence availability of aquatic habitat and indirectly affect invertebrates through the physiological responses of hydrophytes. Wise, ecologically-based decisions will yield productive wetland systems.

Aquisition of potentially impounded wetlands should favor restoration of natural wetland areas which have been degraded. Construction should emphasize a complex of wetland types which may include green tree and seasonally flooded emergent types. Wetland management should strive to emulate water fluctuations of the region because invertebrates have adapted to such dynamic conditions. The degree and timing of fluctuations depends on desired species composition. Fall flooding will stimulate the hatch of many species and larval forms may continue to develop over the winter. Our present knowledge of water manipulations suggests that management for specific hydrophyte communities may be the most practical means of increasing invertebrate production. A diversity of plants with high seed production, as well as plants with finely dissected leaves may result from integrated management. Inflow water should be monitored for pesticides and pollutants. Management should strive for pesticide education in urban wetland areas because mosquito or agricultural pest control measures may be highly detrimental to wetland invertebrate survival or growth.

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