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AMERICAN PRONGHORN ANTELOPE IN THE YELLOW WATER TRIANGLE, MONTANA

A Study of
Social Distribution, Population Dynamics, and Habitat Use

by

Duane B. Pyrah

Wildlife Division

MONTANA DEPARTMENT OF FISH, WILDLIFE AND PARKS

in cooperation with

Bureau of Land Management

UNITED STATES DEPARTMENT OF THE INTERIOR

1987

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the costs of printing this bulletin.

FOREWORD

"When I beheld the rapidity of their flight along the ridge before me it appeared reather (sic) the rappid (sic) flight of birds than the motion of quadrupeds" (DeVoto 1953:20). Thus, Captain Meriwhether Lewis in 1804 described some of the unique attributes of the unique *wavies of the prairie*—the American pronghorn antelope (*Antilocapra americana*).

Early explorers reported seeing vast herds of antelope, sometimes referred to as pronghorn, throughout much of their historical range—dry plains west of the 100th meridian. Before and during exploration and early settlement, antelope were the most abundant native ungulates throughout much of the semiarid shrub steppe (low brush/grass plains) of middle western North America. Montana populations, estimated at 2.5 million by Beer (1944), probably outnumbered those in any other state before settlement by Caucasian pioneers.

Approximately 100 years later, these legions of antelope had declined to approximately 0.1% of their original number in Montana. Primary causes for near annihilation were: destruction, disruption, and/or deterioration of the unique pristine vegetation (mainly through cultivation and overgrazing by domestic livestock), disruption and loss of habitat use traditions, forage competition with livestock (where little forage competition existed before), and unrestricted hunting.

Antelope survived, however, by subtle adaptations to utilize food, cover, and water resources in the dry plains. They demonstrated flexibility in traditional movement patterns in adjusting to environmental changes, pioneering behavior to disperse young animals into unoccupied habitats, migratory traditions to make use of seasonally usable habitats, and prolific production. Antelope populations recovered as regulated hunting reduced mortality, and new populations started from trapping and transplanting and natural dispersal. These increases in antelope populations, from all-time recorded lows in the early 1900s to relative abundance in the 1950s is one of game management's significant achievements. Bison (*Bison bison*), wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), and elk (*Cervus canadensis*), which also inhabited eastern Montana prairies, are now gone (except elk in a few cases) while antelope are common.

Antelope require extensive rangeland with predominantly native plains vegetation. The almost inseparable alliance between antelope and sagebrush (*Artemisia spp.*) communities contributes to the uniqueness and vulnerability of these resources.

The most important commercial use of native plains vegetation is grazing by livestock. Antelope depend upon this same rangeland and vegetation base. This bulletin intends to reduce potential conflicts by providing management planning keys for antelope populations and their habitat needs in relation to livestock and vegetation management.

Arnold Olsen, Administrator
Wildlife Division

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INTRODUCTION

Antelope in Montana have a high public use priority, as rated by big game hunting recreation days, being surpassed only by elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Land management activities that have changed the native plains vegetation have constantly whittled away the habitat base of antelope. During the 1950s, habitat reduction and deterioration increased rapidly, due to more miles of impassable fences, extended cultivation, intensified livestock management, and range vegetation conversions by spraying (with herbicides) and plowing. Efforts by public and private land managers to increase grass forage for livestock by reducing or eradicating sagebrush on rangelands occupied by antelope became of critical importance. Over much of the antelope range, the target plants, species of *Artemisia*, comprised the antelope's major food for 8 months of the year, including staple winter forage. In addition, as the dominant shrub over large areas of the plains, sagebrush provided important cover.

Much research had been conducted to substantiate and justify sagebrush removal to increase grass production for livestock forage. Little or no research had been directed at an evaluation of how much other plants and animals were affected by sagebrush control practices. Little was known about the impacts caused by removal of sagebrush and other broad-leaved plants important to game animals like antelope and sage grouse as well as small birds and mammals.

Mutual concern by the Montana Department of Fish, Wildlife and Parks (then the Montana Fish and Game Department) and the Bureau of Land Management (BLM) led to a cooperative funding of the Sagebrush Ecology Project from 1965 to 1975. The Yellow Water Triangle in central Montana was selected as the main study area because of data from previous studies by Cole (1956) and Eng (1954). Objectives of the overall study were to determine the ecology of various plants and animals and document changes after application of sagebrush control practices.

Objectives of the antelope study were to determine social distribution, population dynamics, use of habitat types, and relation to livestock grazing in order to better understand research results and interpret the effects of the treatments on antelope ecology. The primary period of study was December 1967 to September 1974. The population dynamics phase has been continued to determine long-term population characteristics. Winter observations of marked antelope during 1966–1967 were made by Bayless (1967).

HISTORICAL PERSPECTIVE

One of the first accounts detailing the number of antelope in the Yellow Water Triangle is the U.S. Biological Survey report by Nelson (1925:36), which stated:

"A band of 172 was counted along Elk River (Yellow Water Creek could have been called a fork of Elk Creek) on the Jack Rowley Ranch[1] about 50 miles southeast of Lewistown in Fergus County (present Petroleum County). Mr. Rowley states that for the past 10 (or more) years from 100 to 125 antelope have been ranging on the ranch . . . During the fall of 1923 he counted 172 in one band, which apparently covered the entire number.[2] He states that they ordinarily run in three or four bands but occasionally unite. They have many young; but, although efforts have been made by the owners of the ranch to protect them, they continually stray off and are shot by hunters.[3] When fired at, those not hit usually seek safety in the meadows of the ranch where they seem to appreciate the fact that they are protected. Mr. Rowley believes that since so many dry farmers have left that section of the state, conditions are more favorable for antelope, which are likely to increase in numbers."

Preliminary antelope surveys were initiated by the Montana Fish and Game Department in 1941 (Beer 1944) and aerial surveys were made in the Musselshell Unit in 1943–1944 (Bergeson and Thompson 1946). Antelope distribution was recorded for the Yellow Water Triangle in January 1946 (Couey 1946). Couey's observations were near the location of the 1923 herd and agree with the 1941 distribution survey (Beer 1944). Brown (1948) began intensified aerial surveys of the antelope in the Musselshell Unit and in the Yellow Water Triangle as a sub-unit. Results of antelope surveys are shown in Table 1.

The probable spread of antelope in the study area (as indicated by Nelson's report in 1923, Beer's survey in 1943, and Brown's report in 1948) is shown in Figure 1. Much of the spread occurred, as Mr. Rowley had predicted, after the major land use reverted to rangeland grazing. If not completely accurate in depicting expanding distribution, the records indicate increased abundance, although some apparent increase also resulted from improved techniques for surveying antelope. Antelope now occupy nearly all suitable habitat in the Yellow Water Triangle.

Antelope were not hunted legally from 1903 to 1943 over most of the state (Compton et al 1971) and until 1945 in the Yellow Water Triangle (Couey 1946). Rancher pressure in the Musselshell Unit for open hunting seasons, to reduce or control increasing antelope populations, produced the first special permit hunting seasons (bucks only from 1945 to 1949, Couey 1946, Brown and Johnson 1952). Table 2 presents a summary of hunting seasons.

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[1]A cattle ranch when most other livestock operations in the area were sheep ranches.

[2]An interview survey with contacts made by predator control field men of the U.S. Biological Survey. Several area residents, who are still living, indicated that antelope in the area were more prevalent than reported by Nelson.

[3]Illegal hunting.

Table 1. Antelope surveys in the Yellow Water Triangle[1], 1923–1978.

Year	No. Adult Males	No. Adult Females	No. Fawns	No. Uncl.	Total	Area (mi²)	Density	Males per 100 Females	Fawns per 100 Adult Females
1923[2]	–	–	–	–	172	–	–	–	–
1944[3]	–	–	–	–	218	230	0.95	–	–
1946	–	–	–	–	352	193	1.82	–	–
1948	99	185	165	187	636	193	3.30	54	89
1950	185	401	294	109	989	193	5.12	46	73
1951	317[4]		195	302	814	193	4.22	–	–
1952	–	–	–	–	892	193	4.62	–	–
1953	228	541	424	–	1193	193	6.18	42	78
1954	–	–	–	–	1246	193	6.46	–	–
1955	167	320	301	421	1209	193	6.26	52	94
1960[5]	139	287	222	–	648	213	3.04	48	77
1962	239	504	428	–	1171	213	5.50	47	85
1963[5]	61	310	280	23	674	300	2.24	20	90
1964	230	608	360	–	1198	300	3.99	38	59
1966	89	246	181	13	529	213	2.48	36	74
1968	118	202	233	–	553	213	2.59	58	115
1969	123	316	253	–	692	213	3.25	39	80
1970[6]	150	411	299	–	860	213	4.04	36	73
1971[6]	201	390	306	–	897	213	4.21	52	78
1972[6]	231	492	367	–	1090	213	5.12	47	75
1973	225	537	371	–	1133	213	5.32	42	69
1974[6]	241	476	204	–	921	213	4.33	51	43
1975[6]	163	521	275	–	956	213	4.49	31	53
1976[6]	171	492	288	–	951	213	4.47	35	59
1977[6]	171	412	273	–	856	213	4.02	42	66
1978[6]	153	353	246	–	752	213	3.53	43	70

[1] Included more of H.D. in 1963 and 1964.

[2] Nelson (1925).

[3] Bergeson and Thompson report for Musselshell Unit, 1946.

[4] Unclassified adults.

[5] Survey appears too low to reconcile with the next survey.

[6] Totals do not agree with Table 6 due to inclusion of the area between McDonald Creek and Highway 200 in these survey numbers.

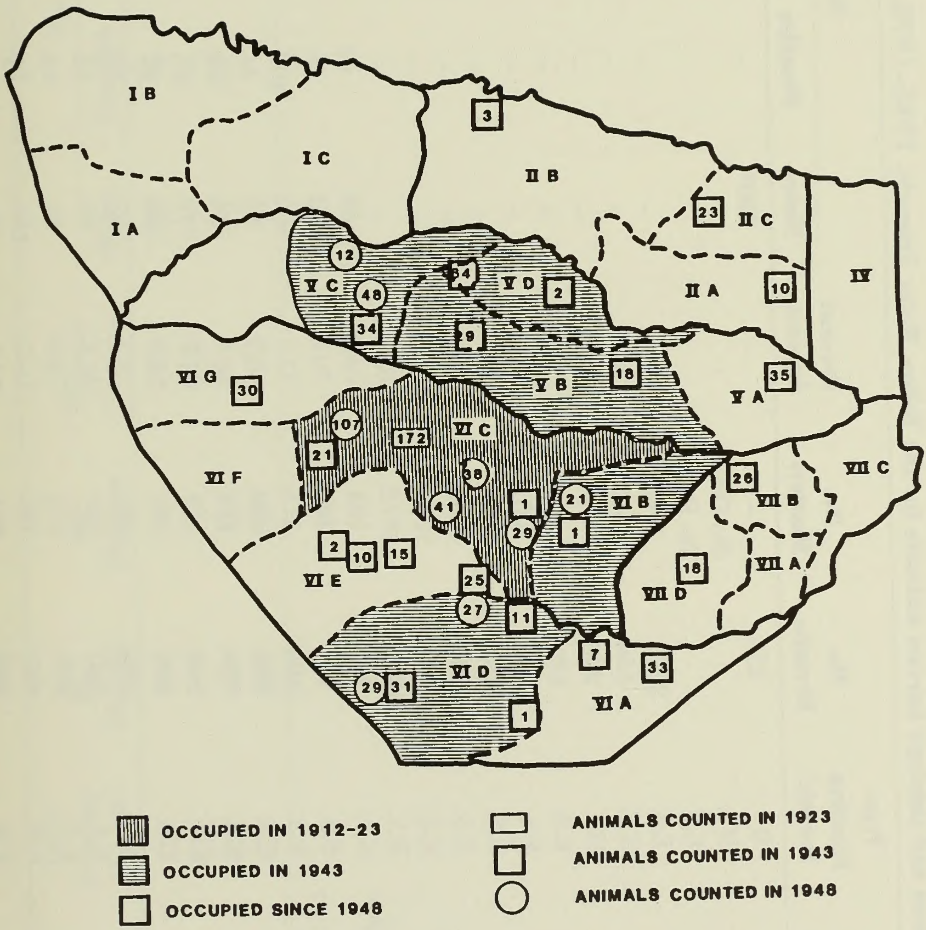


Figure 1. The apparent spread of antelope in the Yellow Water Triangle, Montana, 1912-Present.

Table 2. Hunting season and antelope harvest statistics for the Yellow Water Triangle, 1945–1978.

Year	Hunt. District	Type Hunting Permit[1]	No. Permits	No. Hunters	Percent Success	No. Harvested				
						Males	Females	Fawns	Uncl.	Total
1945	MU[2]	M	250	–	–	200[3]	–	–	–	–
1946–49	53	M		(No Data)						
1950–54	53	E.S.		(No Data)						
1955	53	E.S.	2207	1948	90.5	–	–	–	–	1796
1956	53	E.S.	550	475	61.2	–	–	–	–	291
		M	200	200	27.5	–	–	–	–	55
1957	53	E.S.	601	530	77.5	–	–	–	–	411
1958	53	E.S.	1200	1051	92.4	–	–	–	–	971
1959	53	E.S.	1200	1068	83.1	–	–	–	–	888
1960	53	E.S.	1200	1006	84.0	–	–	–	–	846
1961	53	E.S.	1199	1059	83.3	–	–	–	–	883
1962	53	E.S.	1800	1672	81.6	–	–	–	–	1365
1963	420	E.S.	200	183	76.0	88	49	0	2	139
1964	420	E.S.	400	389	70.6	180	88	6	1	275
1965	420	E.S.	400	375	71.7	166	102	0	1	269
1966	420	E.S.	200	169	66.2	50	56	6	0	112
1967	420	E.S.	200	176	68.2	74	40	6	0	120
1968	420	E.S.	200	168	67.3	75	35	3	0	113
1969	420	E.S.	200	171	72.0	89	23	11	0	123
1970	420	E.S.	200	161	75.3	97	33	2	0	132
1971	420	E.S.	200	180	81.2	90	52	0	0	142
1972	420	E.S.	200	178	73.0	81	44	4	0	129
1973	420	E.S.	400	316	76.5	149	74	19	0	242
1974	420	E.S.	400	353	74.7	183	75	7	0	264

Table 2. Continued.

Year	Hunt. District	Type Hunting Permit[1]	No. Permits	No. Hunters	Percent Success	No. Harvested				
						Males	Females	Fawns	Uncl.	Total
1975	420	E.S.	400	320	71.2	135	74	18	0	228
1976	420	E.S.	400	363	66.1	144	91	5	0	240
1977	420	E.S.	400	354	78.2	148	120	6	0	274
1978	420	E.S.	150	120	74.2	51	37	0	0	89

[1]M = Males only; E.S. = Either Sex.
[2]Musselshell Unit.
[3]Estimate for 1945 (Couey 1946:6).

Overall, the major recovery of antelope populations on the study area appears to have been a response to a combination of natural and human related events that increased antelope carrying capacity and/or reduced mortality. The widespread and long range influence of each condition suggests that they acted together as a complex of interrelating and compensating factors. Some of those events include:

1. A 20-year drought ended as World War II was beginning (Climatological Data, Montana). The average annual precipitation at Flatwillow during 1919–1936 was 11.4 inches and 13.5 inches during 1937–1955 (Appendix A). During 1941–1944, annual precipitation averaged 17.4 inches. A succession of wet years could have had a great impact on antelope population build-up. Antelope can almost double their population each year when outstanding food conditions and low populations prevail, as happened in 1968.

2. Habitat conditions stabilized, allowing time for antelope to adapt to new food and cover conditions, and to pioneer new seasonal movement and habitat use traditions. Antelope had insufficient time to adjust to the overwhelming changes of widespread livestock grazing and homestead agriculture as departures from pristine environmental conditions.

3. Unlawful antelope hunting was reduced. Earlier, illegal hunting apparently had been widespread even though hunting was prohibited.

4. The Taylor Grazing Act (1934) provided for the first controls on livestock grazing on public lands. This Act licenses livestock numbers and required domestic livestock to leave public land during winter (in most places) which reduced winter competition with antelope. Livestock left private land during summer, making this better antelope summer habitat. Much public and private rangeland had been grazed yearlong before the Taylor Grazing Act. The Bankhead-Jones Act (1937) provided for reseeding many abandoned cultivated lands and changed management of public rangelands.

5. Land use changed further as drought and depression eliminated small uneconomic landholdings along with their dependent human population; these changes began in the early 1920s (Gieseker et al 1953).

Abandoned homestead on the Yellow Water Triangle. *(Photo by: Author)*

6. World War II (1941–1945) marked a change in the livestock industry. A prewar sheep economy became a postwar cattle economy, which still persists. Cattle competed less for food with antelope than sheep did.

7. Antelope hunting in the Musselshell Unit was initiated in 1945 (Couey 1946). This might have influenced antelope movements and expanded distribution (Russell 1964). They had not been hunted legally for 42 years.

8. The toxicant thallium was replaced by less expensive Compound 1080 (C-1080) in 1947 resulting in more widespread poisoning of coyotes, although high and expanding antelope populations preceded the introduction of C-1080. By the early 1940s many ranchers were concerned that antelope populations were too high, competing with livestock for forage and depredating cultivated crops (Cole 1956, Cole and Wilkins 1957). High antelope populations since 1972, when predator control by use of C-1080 was discontinued, would indicate that the role of C-1080 in increasing survival of antelope (Knowlton 1968) may have been overrated for eastern Montana.

9. "Wild" horses were removed from open rangeland prior to 1941 as the livestock industry became mechanized. These animals were year-round grazers and competed with antelope on already overgrazed rangelands.

10. The Federal Aid in Wildlife Restoration Act (1937) provided increased funding for wildlife research and management. Coupled with the GI Bill (1945) which helped produce a new generation of range and wildlife professionals, this act led to increased staffs of fish and game departments and other government agencies, as well as remarkable improvements in range and wildlife management techniques, wildlife regulations and law enforcement.

11. More intensive antelope management followed World War II; underemployed postwar pilots and aircraft stimulated development of new techniques in aerial surveying, trapping, and transplanting.

STUDY AREA

Excellent descriptions of geology, soils, climate, vegetation, and history of the study area are provided in Gieseker et al (1953), Cole (1956), Bayless (1969), and Jorgensen (1979). The following summarizes those accounts while adding details particularly relevant to antelope ecology.

Location

The Yellow Water Triangle (266 mi^2) is near the geographic center of Montana (Fig. 2); 62% of the land area falls within Petroleum County and 38% within Fergus County (Jorgensen 1979). The area is enclosed by U.S. Highway 87 (20 mi from Grass Range to Flatwillow Road), Montana Highway 200 (23 mi from Grass Range to Winnett), Montana Highway 244 (18 mi from Winnett to Flatwillow Road), and Flatwillow Road (5 mi from U.S. Highway 87 to Montana Highway 244). Drainages of two minor permanent streams (Flatwillow and McDonald Creeks) and three intermittent streams (Pike, Elk, and Yellow Water Creeks) parallel one another across the study area. The name "Yellow Water" is derived from the discoloration of the stream by yellowish bentonite from certain geological formations (Jorgensen pers. comm.).

Geology and Soils

Relief slopes upward from east to west. All geological formations tilt easterly and thus have lower strata exposed at higher elevations toward the west.

Elevations range from 3,000 ft at Winnett to 4,500 ft atop Button Butte in the northwest quarter near Grass Range. The topography varies from flat to gently rolling along an elevational gradient that increases an average of approximately 20 ft/mi along McDonald Creek between Winnett and Grass Range. Most topographical relief stems from geological relics of hills, buttes, and ridges or stream erosion valleys, coulees, and draws cut below the level of the prairie plateau. Most of these topographic relics have immediate elevational changes of less than 100 ft.

Predominant geological formations are shales and sandstones. Soils are clayey over shale and sandy loams over sandstone. Topsoil profiles are mostly very shallow.

Weather and Climate

The climate of the study area is semiarid. Two months, October and April, are cool and 5 months, November-March, are cold. Figure 3 shows the annual cycle in average monthly *heating degree days*, a negative value of degree days below 60°F (Climatological Data, Montana) which provides a guide to monthly conditions of potential cold stress or heat loss. For November-March, monthly degree days range from 746 (March 1968) to 1954 (January 1969).

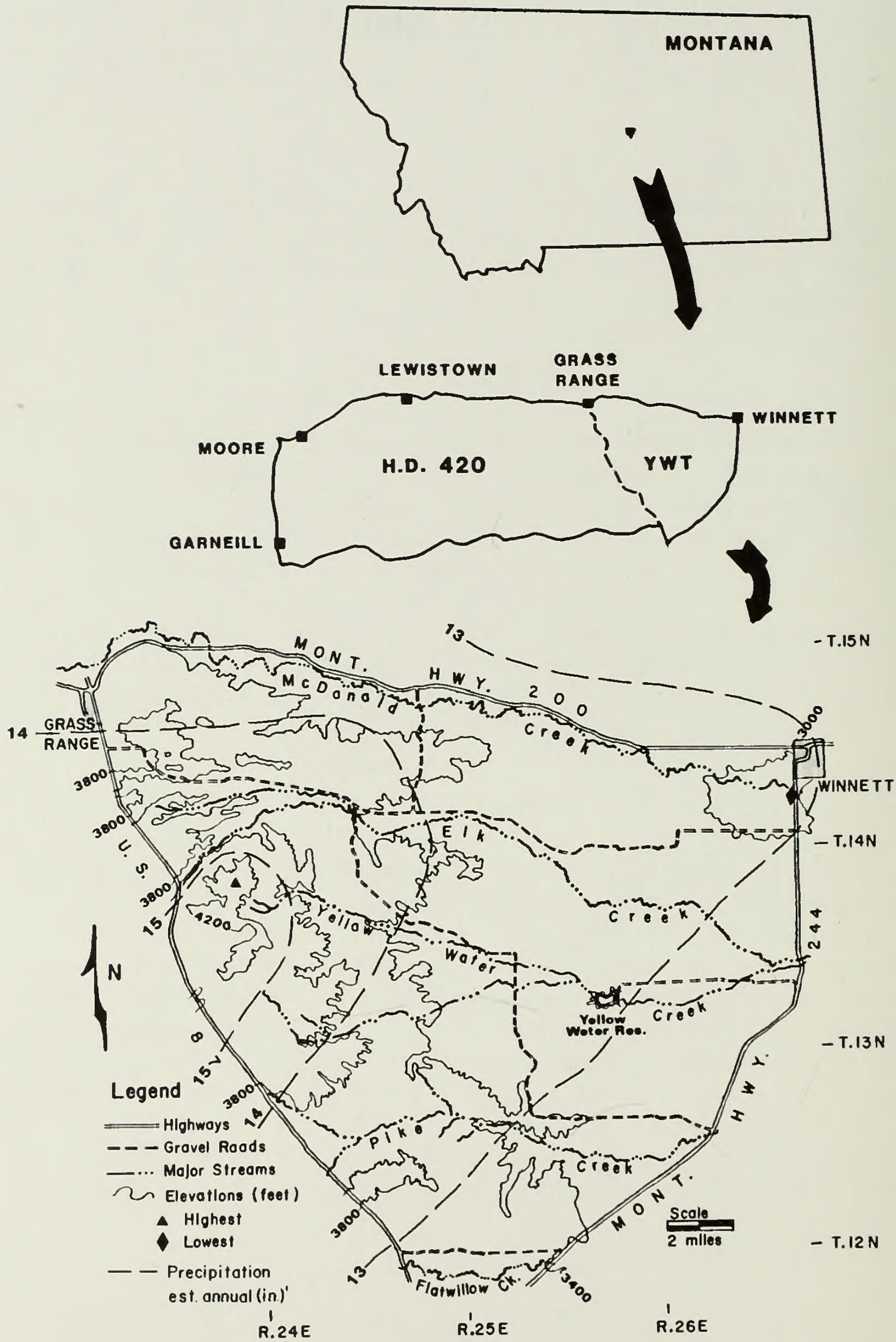


Figure 2. The Yellow Water Triangle Study Area, Montana.

On the average, mid-July (17 degree days) and mid-January (1,438 degree days) approximate the warmest and coldest periods, respectively. A theoretical straight-line curve of increasing heating degree days extends from July through January and a decreasing heating degree days regime extends from January through July (Fig. 3). Actual average temperature departures from this theoretical condition typically consist of the warmer than expected temperatures from August through October (Indian Summer), during February (chinooks), and from April through June. Temperatures average colder than expected during December. November and March average temperatures lie near the theoretical.

Average degree days (1959–1979) for November through March totalled 5,706. Severe winters, identified as above average number of degree days during November-March, were 1961–1962, 1964–1965, 1968–1969, 1970–1971, 1971–1972, and 1977–1978. The 1968–1969 winter (6,772) was the coldest in this 20-year span, followed by 1977–1978 (6,542) and 1964–1965 (6,492). These severe winters coincide with those identified by Hamlin (1979) on the basis of temperature and snow depth, except for 1961–1962 and 1970–1971, which were relatively snow-free.

A long, cold winter results in negative energy balance for antelope. These problems arise from reduced energy intake and increased energy demand. Reduced energy intake reflects the November-March dormancy of herbaceous plants, which while growing, provide more available energy and protein than shrubs. Increased energy demand results from air or wind chill temperature below the comfort threshold. Moen (1968a) indicates there is a "variable critical environment," depending on several factors, that determines lower limits for the thermoneutral range. Studies of white-tailed deer (Gerstell 1937) indicate this critical temperature zone lies between 30° and 40°F. This comfort threshold probably lies near 900 heating degree days per month. The average monthly heating degree days in the Yellow Water Triangle exceeds 900 from November through March (Fig. 3).

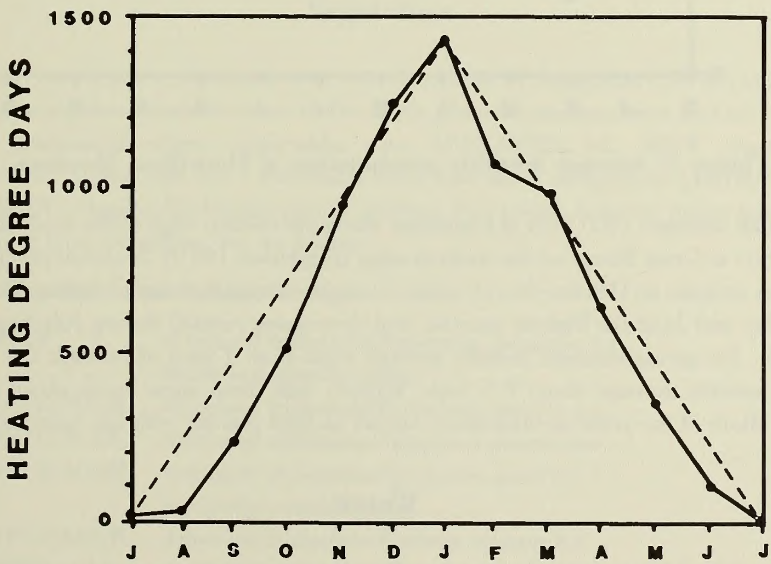


Figure 3. Cycle of average monthly heating degree days. The dotted line is a theoretical line from July to January; the solid line is the 20-year average.

Cold wind and deep snow increase stress imposed by cold temperature, making heating degree days less accurate as an estimator of cold stress; however, antelope avoid or modify these highly variable accessory stress conditions as much as possible. Uniformly deep snow covers much of the short vegetation and makes it unavailable as forage. Movement through deep snow taxes antelope energy. Wind can be beneficial because it clears snow from ridges, making travel easier, and warm chinook winds rapidly sublimate snow, expose forage, and reduce deep snow hazards.

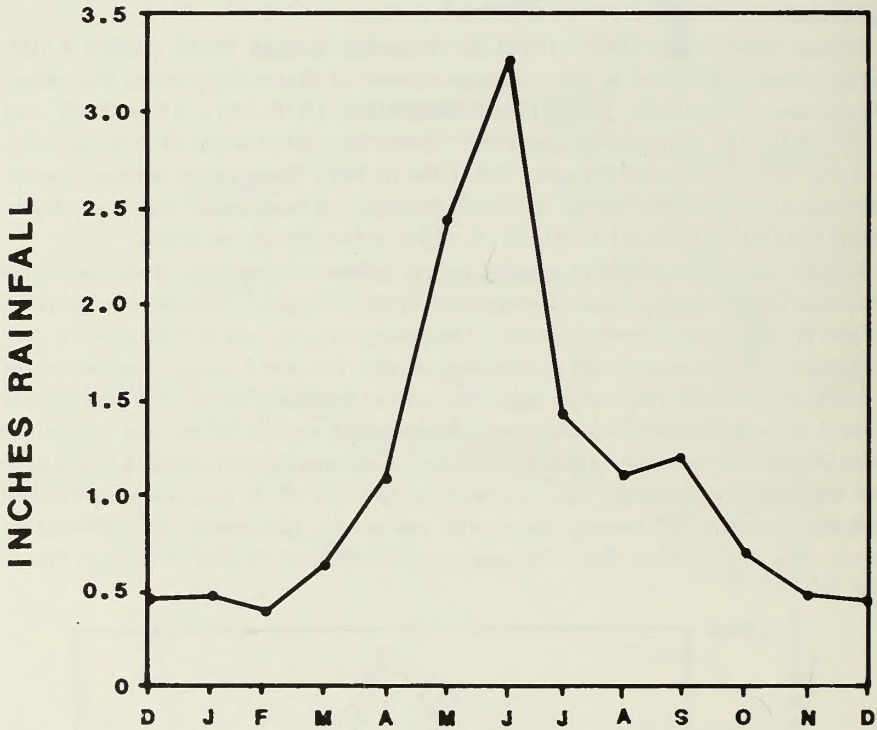


Figure 4. Average monthly precipitation at Flatwillow, Montana.

Rainfall averages 13.0 in/yr at Flatwillow along the eastern edge of the study area and 15.8 in/yr at Grass Range on the western edge (Jorgensen 1979). Seasonal precipitation changes indicate an October-March winter drought, increasing rainfall during April-June with May and June the highest months, and decreasing rainfall during July-September (Fig. 4). Six spring-summer months average more than 1 inch of rainfall; the six fall-winter months average about 0.5 inch. Winters with deep snow occur about every 5 years. Much of the snow accumulation occurs as light powder with low water content.

Water

Many of the 150 stock ponds provide relatively permanent sources of free water during spring-fall. These reservoirs, plus natural catchments, springs, seeps, and a few permanent streams, distribute free water throughout the area during most of the year. Antelope use free water infrequently except during dry periods in central Montana. When little or no snow has accumulated and water in reservoirs has frozen, free water during late fall-early spring may be more important than commonly assumed (Couey 1946). Shrubs usually have less succulence over winter due to low soil moisture, a common fall-spring condition in the study area. Forbs appear to provide most of the necessary moisture during spring and summer.

Stockwater reservoir in the Sibbert Treatment Area. *(Photo by: Richard J. Mackie)*

Vegetation

Habitat types (h.t.s) on the study area were described by Jorgensen (1979) (Appendix B). In adapting those classifications to this study, phase dominants were included in the symbol designation where applicable; e.g., ARTR/AGDA h.t., SAVE phase was ARTR/SAVE. Cover type (c.t.) dominants were also used in symbols (ARTR/BOGR, ARTR/AGDE). Applicable habitat groups showing the relation between major types and their minor type inclusions, are as follows:

Shrub-Grassland and Habitat Groups

ARTR/AGSP	*Artemisia tridentata/Agropyron spicatum* h.t., *Bouteloua gracilis* phase
ARTR/BOGR	*Artemisia tridentata/Bouteloua gracilis* c.t.
ARTR/AGDE	*Artemisia tridentata/Agropyron desertorum* c.t.
ARTR/AGSM	*Artemisia tridentata/Agropyron spicatum* h.t., *Agropyron smithii* phase
ARTR/KOCR	*Artemisia tridentata/Koeleria cristata* h.t.
ARTR/FEID	*Artemisia tridentata/Festuca idahoensis* h.t.
ARTR/AGDA	*Artemisia tridentata/Agropyron dasystachyum* h.t.
ARTR/SAVE	*Artemisia tridentata/Agropyron spicatum* h.t., *Sarcobatus vermiculatus* phase

SAVE/AGDA	*Sarcobatus vermiculatus/Agropyron dasystachyum* h.t.
ALFALFA	Alfalfa (grass hayland) c.t.
ARCA/AGSM	*Artemisia cana/Agropyron smithii* h.t.
ATDI/XASA	*Atriplex dioica/Xanthocephalum sarothrae* h.t.

Grassland Habitat Group

AGSP/AGSM	*Agropyron spicatum/Agropyron smithii* h.t.
MUCU/ANSC	*Muhlenbergia cuspidata/Andropogon scoparius* h.t.
POPR/ARLU	*Poa pratensis/Artemisia ludoviciana* h.t.
AGDE	*Agropyron desertorum* seeding c.t.
GRAIN	Mainly winter wheat, seeding or fallow, c.t.

Exposed Raw Shale Habitat Group

ROAR/THRH	*Rosa arkansana/Thermopsis rhombifolia* h.t.
JUHO/CAPA	*Juniperus horizontalis/Carex parryana* h.t.

Mesic/Riparian Habitat Group

PODE/SYOC	*Populus deltoides/Symphoricarpus occidentalis* h.t.

Conifer Forest Habitat Group

PIPO/ARTR	*Pinus ponderosa/Artemisia tridentata* h.t.
PIPO/AGSP	*Pinus ponderosa/Agropyron spicatum* h.t.

Wetland Habitat Group

SCIRPUS/CAREX	*Scirpus/Carex* marsh h.t.
SUAEDA/SARU	*Suaeda/Salicornia rubra* alkali h.t.

Shrub-grassland predominates in the Yellow Water Triangle. The ARTR/AGSP h.t. includes much of the sagebrush-grassland described by Cole (1956) and Bayless (1969) and occurs where soils have some profile development (Jorgensen 1979). Historically, before heavy livestock grazing, this vegetation doubtless covered much more of the study area. It now occurs mainly in areas of rough topography or distant from water. On level lands, grazing and seeding disclimaxes, ARTR/BOGR c.t. and ARTR/AGDE c.t., have replaced ARTR/AGSP. Evidence from exclosures indicate that ARTR/STCO may be the intermediate stage between ARTR/AGSP and ARTR/BOGR. A thick stand of BOGR in the long Iverson exclosure was replaced quickly by STCO, a response to protection also reported by Mueggler and Stewart (1980).

Jorgensen (1979) indicated that AGSP in this area is on the margin of its climatic optimum. The species grows through several phenological stages during early spring when soil moisture is often below optimum (see Fig. 4). Because of this, AGSP is highly susceptible to overgrazing and drought, which reduce vigor and lead to replacement by the aggressive seeding STCO. Continued overgrazing and absence of seed production by AGSP and STCO results in more rhizomatous grasses (BOGR, AGDA, and AGSM).

American vetch (*Vicia americana*), a native forb with nitrogen-fixing capability (Jorgensen 1979), increased in the Iverson exclosure while STCO was replacing BOGR. The lack of desirable forbs could indicate past years of overgrazing. Antelope would probably benefit by grazing management which would direct plant succession toward climax and increase desirable forbs (Cook 1983).

Antelope spring band in shrub-grassland habitat, predominantly ARTR/BOGR c.t.
(Photo by: Author)

AGDE seedings were attempts to reclaim abandoned homesteads where cultivation was unsuccessful. In the nearly 40 years since the seedings were established, sagebrush and native herbs have reinvaded in varying degrees, but AGDE remains a dominant on many areas. Yellow sweetclover (*Melilotus officinalis*) also occurs commonly on these disturbed soil sites, indicating that a much longer time is needed for the soil and vegetation to become stabilized again.

ARTR/AGSM and ARTR/KOCR occur as narrow inclusions within major types of ARTR/AGSP or ARTR/BOGR. ARTR/AGSM occurs as small meadows in swales, footslopes, and some bottomlands. The relatively small acreage of ARTR/AGSM includes the area of POPR/ARLU (swale vegetation in grasslands). The two swale types could not be reliably separated on aerial photos (Jorgensen 1979). ARTR/KOCR occurs as narrow strips along ridge edges.

The remaining upland sagebrush-grass consists of ARTR/AGDA h.t., occurring on clayey soils which do not have profile development. This habitat type might be a soil developmental stage of ARTR/AGSP because both types occur over most of the same members of the Colorado shale formation (Jorgensen 1979).

ARTR/SAVE consists of ARTR/SAVE and SAVE/AGDA. ARTR/SAVE occurs on uplands where saline soil conditions and surplus ground water favor SAVE. SAVE/AGDA grows on bottomlands but often includes varying amount of ARTR also. Valley bottoms near drainages include SAVE/AGDA and ALFALFA hayfield conversions. ARCA/AGSM covers narrow strips along stream courses within the SAVE/AGDA h.t.

AGSP/AGSM h.t. comprises most of the grassland on the study area (Jorgensen 1979). Small, visually inconspicuous spots of MUCU/ANSC h.t. occur in sandy soil on and around sandstone outcrops. Level, rock-free areas of grassland contain plantings of AGDE and GRAIN.

Exposed raw shale soil supports two communities: ROAR/THRH h.t. the major type, and JUHO/CAPA h.t., the minor type. These types were not separated during the study.

The mesic riparian habitat group is the PODE/SYOC h.t. Mesic sites on uplands and along intermittent streams frequently lack trees.

The conifer forest habitat group includes the PIPO/ARTR and PIPO/AGSP h.t.s. These types were combined due to the presence of pine trees. Antelope seldom used sites with trees.

Antelope did not use marshes (SCIRPUS/CAREX h.t.), alkali spots (SUAEDA/SARU h.t.), bentonite spots (ATDI/XASA h.t.) or tops of small buttes (ARTR/FEID h.t.). All of these types covered small areas.

Antelope used treeless mesic areas, especially in late summer, but were not observed in marshes. *(Photo by: Montana Department of Fish, Wildlife and Parks)*

Complexes of two or more soil and vegetation types cover much of the study area (Jorgensen 1979). These complexes are intermixed to the extent that it is impractical to separate them. In these cases, the complex was included in the most widespread type.

Vegetation in the Yellow Water Triangle is unique in several other ways that may be noteworthy in relation to antelope. Sagebrush ranges in eastern Montana support the *A.t. wyomingensis* subspecies, which is palatable to both wildlife and livestock. This species rarely grows over 24 inches tall and often has less than 25% canopy coverage in central Montana. It is probably more abundant now over much of the study area than during pristine time, except on areas where it has recently been eliminated. Historical references (Dana and Grinnell, quoted by Silliman 1974) indicate that sagebrush probably was present before settlement in most of the types in which it now occurs on the study area. One of the important exceptions is invasion into the meadow vegetation of bottoms, swales, and footslopes. In one instance, exclusion of a meadow site from livestock grazing provided important cover for voles (*Microtus* spp.) which girdled and subsequently eliminated many of the sagebrush plants. Sagebrush would not be able to reinvade into the dense western wheatgrass stand presently growing in the exclosure.

Most sagebrush range west of the Continental Divide has a winter moisture pattern. The spring-summer rainfall pattern characteristic of central Montana appears to be less suitable for this species. Thomas (pers. comm.) found sagebrush seedlings germinating in central Montana during February when the ground became snow-free. These seedlings invariably died of inadequate soil moisture when winter snow melt evaporated before spring-summer rains arrived.

Poor reproduction has largely prevented sagebrush from successfully reinvading places where it has been killed. Burns over 10 years old (Sibbert fire of 1960, Bratten fire of 1971) remain relatively free of sagebrush, and those nearly 50 years old (Carey Act Fire of 1936, Winnett railroad fire of 1940) have only spotty sagebrush distribution. Thomas (pers. comm.) also found very few sagebrush seedlings surviving to reinvade the total kill spray strips in the spray/leave strip treatment associated with this study.

Sweetclover grows profusely in much of central Montana during years of suitable moisture, most commonly on disturbed sites and other areas bare of vegetation. Old crested wheatgrass seedings usually have more sweetclover than undisturbed stands of native vegetation. Sweetclover plants are also common under sagebrush plants and in pan spots where deer mice (*Peromyscus maniculatus*) have planted seeds by establishing seed caches in bare soil. The flowering phase (2nd year) produces the best food and cover for antelope. However, because of moisture requirements for germination and growth, occurrence is highly variable and unpredictable in the area.

The prevalence of sweetclover on less productive sites may also be related to its ability to obtain nitrogen from nitrogen-fixing bacteria in root nodules. The soils of semi-arid rangelands of central Montana are low in nitrogen. Tests have shown that plant yields can be increased when nitrogen is added, even in the absence of increased moisture (Schlatterer 1970, Jorgensen 1971).

Feral alfalfa also has the nutrient advantages provided by its nitrogen-fixing property. Alfalfa plants survive for many years along fenced highway rights-of-way when they are ungrazed during the summer. On one site, a right-of-way fence change enclosed an alfalfa stand within a pasture grazed throughout the summer; the grazed alfalfa plants were destroyed in a short time. The deep root system of alfalfa obtains soil moisture from deeper soil layers and contributes to its significant regrowth capability. Alfalfa would be highly desirable for seedings or interseedings to increase rangeland production and improve habitat for antelope; however, these plants cannot survive unless a grazing system is used that protects them from heavy summer-long use. Alfalfa seedling establishment is also risky in this area of highly variable rainfall.

Dandelion (*Taraxacum officinale*), goatsbeard (*Tragopogon dubius*), and prickly lettuce (*Lactuca serriola*) are exotics associated with disturbed vegetation. They are extremely palatable and are preferred food plants for many kinds of wild and domestic animals. They are also less obvious on grazed than on ungrazed sites.

Land Use

The primary land use is cattle grazing. Only 6% of the land is cultivated. Twenty-four percent of the area is administered by the BLM; most of the remainder is privately owned or leased state land.

The Yellow Water Triangle is a popular area for hunting antelope, sage grouse (*Centrocercus urophasianus*), mule deer, white-tailed deer, sharp-tailed grouse (*Pediocetes phasianellus*), pheasant (*Phasianus colchicus*), and waterfowl. Fur hunters and trappers take coyote (*Canis latrans*), bobcat (*Lynx rufus*), beaver (*Castor canadensis*), and other furbearer pelts. Yellow Water Reservoir contains a popular fishery.

METHODS

Definitions

Social Distribution

"Herds" and "bands" are the terms most frequently used in antelope literature to denote social groupings. Their use, however, has been highly variable, with little consistency for the social units represented. They are often used interchangeably for the same social group. Despite this, extensive use has demonstrated their acceptance and they will be used here, though only in the sense of definitions given below.

Social distribution (Pyrah 1984) is defined as the spacing of herds and doe bands as traditional social units. It reflects the combined influences of social behavior, tradition, genetics and habitat response. *Social organization* is often used in its broad sense to include social distribution; however, for this study, social organization identified the hierarchical profiles of individuals as developed through their behavioral interactions within groups. Social organization hierarchies mainly involve groups at the doe band level. *Dispersion* sometimes implies social distribution but it ignores traditional social units.

Social distribution reflects social behavior, which changes seasonally. During winter, males freely associate with females and fawns, and doe bands combine. At this time, social distribution relates to herds and winter ranges. During summer, however, fawning, summer fawn rearing, and breeding occur; social distribution shows the peculiar behaviors of doe bands, territorial bucks, and bachelor bucks around doe band areas to optimize reproductive success. Over time, these seasonal associations become traditional as learned or imprinted behaviors.

Social distribution can be considered at several population levels: the gradient of increasing size of area or number of animals usually accompanies a dilution of immediate genetic traits. Doe bands, and their more related subbands, probably represent the maximum in genetic kinship. Gene flow between doe bands probably occurs when doe bands converge periodically; however, gene flow between larger social units, such as hunting districts and geographic regions, becomes progressively weaker.

Herds function as discrete populations. A herd is defined as all of the resident antelope summer groups on a particular land area that have routine social interactions—often as a single winter herd. Several herds may be consolidated for surveys and hunting season regulations. However, each herd functions independently; its population characteristics being related to habitat, land use, and other environmental or population influences within its own distribution or "herd" range. Genetic exchange between adjacent herds is minimal due to limited interherd movements.

A *herd range* is the geographic area used almost exclusively by a resident antelope herd. Herd ranges are often bounded by visible movement barriers (topography, vegetation, water, or fences) but can be separated by more subtle factors which possibly are related to incompatible land use or to social relationships between groups. In this study, most herd ranges were separated by drainages.

In central Montana, each herd range must have both winter and summer range. Parcels of winter range may be separate with connecting corridors. Migratory antelope may have a winter range, summer range, and a migration route or corridor connecting them.

Bands are subdivisions of herds. A *doe band* is the primary subdivision of a herd during summer. It is composed of female associates which have a traditional summer range called a *doe band area*. These geographic areas have nearly exclusive use by the resident doe band. Summer bands also include *bachelor buck bands*. In winter, the herd may be separated into several *winter bands* which are essentially one or more doe bands.

Territorial bucks are associated with doe bands most of the year. Summer movements of territorial males are restricted to defended territories within doe band areas. A doe band can be exclusive for one territorial buck; however, most doe bands use a land area larger than a male can defend and consequently doe band areas usually encompass more than one male territory (Kitchen 1974). Thus male territories are adjunct to doe band areas and are not a separate social order.

A *dry-doe band* is a transitory social group of non-breeding females, usually yearlings (Autenrieth and Fichter 1975). They exist mainly during the fawning isolation period of mature females.

A *bachelor buck band* is a transitory summer social group of young nonterritorial males (mainly 1 and 2 years old). It usually occurs during the interval between spring dispersal and the onset of rut when males leave to be near doe bands. Bachelor buck bands usually occupy doe band areas where habitat is poorest and often at the edges of two or more doe band areas.

Subbands are the frequent divisions of the major social groups. No attempt is made here to attach terms to these temporary, changeable groups.

Pioneering is used to describe the movements and behavior in spring of yearlings having no apparent social attachment. In this process of social readjustment, yearlings of both sexes can be seen following 2- or 3-year-old males. Young females are herded away as they cross male territories and young males eventually congregate into bachelor buck bands. These groups probably represent dispersing *pioneer bands*.

Population Dynamics

Fawns are young of the year until about April 1. *Summer fawn production* refers to fawns alive at the time of the summer aerial survey, and is usually given as fawns/adult or mature female. *Yearling* refers to a fawn of the previous year during the period from 1 April to 31 March (i.e., 10½ to 22½ months of age). *Yearling recruitment* refers to yearlings alive in the herd/population during the summer aerial survey as compared to the number of fawns counted during the previous summer aerial survey. *Mature* refers to adults older than yearlings (>22 months). *Adult* refers to all antelope of yearling age or older (>10½ months).

Survival is the percent of a previous number (usually a sex/age cohort) alive after a given length of time (usually one year). *Mortality* is the percent of a cohort which is no longer present and the complement of survival. Mortality is divided into *hunting* and *natural* causes. *Hunting mortality* includes only the number of antelope kills estimated by the hunter questionnaire. Crippling loss estimates should also be included; however, there is no currently acceptable method to accurately determine this loss. *Natural mortality* includes all other types of mortality, including crippling loss. *Total mortality* represents total numbers/percentages of animals lost from the population between successive summer aerial surveys. Unknown, but probably slight, amounts of emigration and immigration add small errors to the mortality data, as do animals missed by the survey.

Density is the number of individuals per square mile.

Vegetation

Terminology related to vegetation classification generally follows the habitat type concepts of Daubenmire (1970). Habitat type names follow descriptions by Jorgensen (1979).

Canopy coverage or cover represents average percent of the ground surface covered when a polygon of the foliage of a plant species (or class) is projected toward the ground (Daubenmire 1959). It is assumed that average percent canopy coverage also represents average square feet per 100 square feet ($ft^2/100\ ft^2$) or the metric equivalents.

Cover index represents the approximate *effective cover volume.* Cover index is obtained by multiplying percent canopy coverage (as $ft^2/100\ ft^2$) by 0.5-ft. height class midpoints and summing for all height classes (Pyrah 1973b), which gives a cover volume approximation in cubic feet per 100 ft^2 ($ft^3/100\ ft^2$).

Procedures

Social Distribution

Antelope were captured by drive-trapping using a helicopter and a corral-type trap (Fig. 5) (McLucas 1956, Russell 1964). Captured animals were marked with individually recognizable neckbands or radio-transmitter collars (Fig. 6). Social distribution was determined by analysis of 1,699 reobservations of 164 marked antelope between December 1967 and September 1973.

Figure 5. Antelope in a corral trap on the study area, December, 1967. (Photo by: Montana Department of Fish, Wildlife and Parks.)

All observations were made with binoculars and spotting scope from a pickup truck. The location of each group observed was recorded by coordinates of a 10×10 grid of each land section (640 acres); these were identified by a letter (E-W)/number (N-S) grid (Example: U.4/21.6). The base map included excellent detail of drainages, roads, fences, reservoirs, and section lines.

Coefficients of association, association tables, dot maps, and area association were used to determine social grouping and land area fidelity.

Figure 6. A. Top left— antelope radio collar (Photo by Steve Bayless).
B. Top right—radio collar being put on a doe antelope (Photo by: Steve Bayless).
C. Bottom left—visible neck band on a buck fawn antelope (Photo by: Steve Bayless).
D. Bottom right— radio collar on a yearling buck antelope (Photo by: Roger Fliger).

Population Dynamics

Thirteen years (1966–1978) of annual antelope aerial surveys and 9 years (1970–1978) of yearling classifications during this study yielded detailed information on population characteristics and dynamics.

Aerial Surveys.—Annual aerial surveys, with flight lines at 1-mile intervals, were made during late summer (late July–early September) in a fixed-wing aircraft (Piper Super Cub). North-south flight lines were monitored closely on detailed maps. Counting periods were limited to early morning and late afternoon, depending upon conditions of clouds, wind, temperature, and antelope activity. Antelope were approached by the aircraft only near enough to verify classification. Antelope locations were plotted on maps at the time of the observation.

An experimental survey by helicopter in 1971 covering the study area produced results nearly identical with the Super Cub survey; therefore, helicopter surveys were discontinued (Pyrah 1973a).

Classification.—Binoculars and spotting scope were used to classify yearling and adult antelope from vehicles during 1970–1974. Males with large horns, approximately one and one-half or more times the height of their ears and noticeably large in basal circumference, were classified as mature. Males with small horns, usually near the same height as their ears (Fig. 7), were classified as yearlings. Average horn height, for age classes indicated by dentition classes (Hoover et al 1959, Dow and Wright 1962), was determined at two checking stations during the 1975 hunting season; 40 yearling males averaged 6.8 in (range, 4.8–8.5 in) and 78 mature males averaged 10.1 in (range, 8.5–12.5 in). Yearlings and mature males were classified by these characteristics on aerial surveys during 1974 and thereafter.

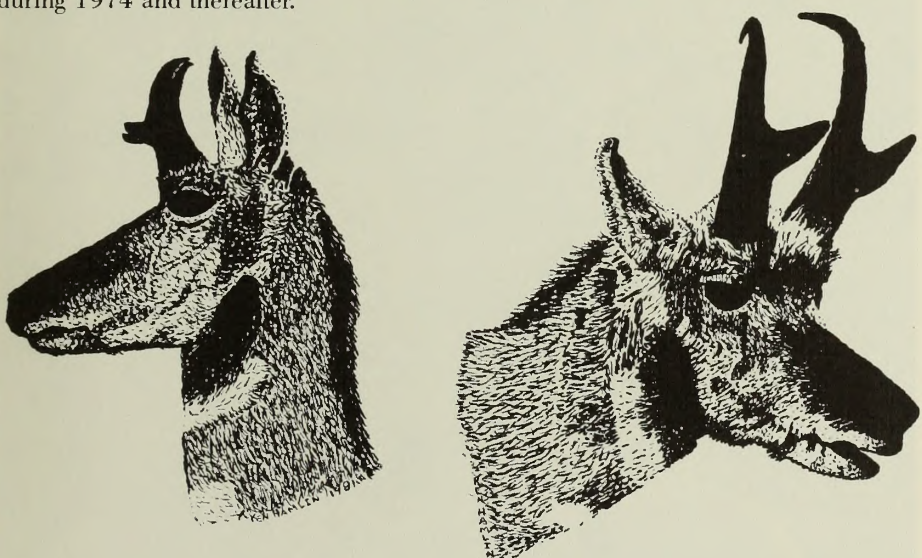


Figure 7. Yearling (left) and mature (right) male antelope. (Graphic by: Kenneth L. Hamlin).

Mature females were identified by indication of pregnancy (distended abdomen) or lactation (enlarged udder). Yearling females were identified during spring by the absence of these signs. Yearling females also retained slight fawn characteristics such as small head, small size, and slim body contour; however, these characteristics were subjective and probably less reliable than the presence or absence of an enlarged udder which was the most useable criterion. It was assumed that almost all adult females bred each fall, that nearly all carried two fetuses to birth, and that the enlarged udder was visible for approximately one month following parturition, whether or not the young survived.

Classification of yearling antelope from the ground during 1972– 1973 indicated male:female sex ratios near 50:50. Subsequently, the number of yearling females was estimated as being equal to the number of yearling males counted during aerial surveys.

Production Estimates.—Antelope production is usually expressed as fawns/female or fawns/100 females. Because yearling females rarely have fawns and the yearling cohort varies numerically and proportionately from year to year, fawns/female does not accurately measure production. Fawns/mature female actually shows the average number of fawns produced by each breeding-age female.

Fawns/mature female could not be measured at the herd level. Yearling males crossed herd boundaries and thus biased estimates of yearling females. Data limitations precluded estimating yearling females from yearling/mature ratios. Hence, production based on fawns/mature female was limited to the entire study area.

Mortality and Recruitment Estimates.—Antelope hunting mortality (total and by sex class of adults) was determined from statewide harvest questionnaire data from HD 420, which included the Yellow Water Triangle (Fig. 2). Sex and age of hunter-killed antelope was determined at checking stations in some years. Mortality and survival could not be estimated on a herd basis because mortality from questionnaires was on a hunting district basis.

Antelope hunting mortality is determined from statewide questionnaires and check stations. *(Photo by: Frank R. Martin)*

Antelope hunting mortality for the Yellow Water Triangle herds was estimated to be 75% of the hunter questionnaire total for hunting district (HD) 420; 73% (921 of 1,261) of the antelope counted in HD 420 during the 1974 aerial survey were in the study area and 76% (1,193 of 1,577) in 1954 (Kencza 1954). The questionnaire estimated the annual harvest within 5% of actual hunting mortality by a 32% sampling of 200 permit holders and 18.5% of 400 permit holders (Gooch, pers. comm.).

Chaffee (1954) reported the sex and age composition of the 1953 harvest from checking stations in the study area. Department biologists operated checking stations covering the same areas during 1975–1978. Hunters harvested sex and age classes at comparable levels during 1953 and 1975–1978. Questionnaires indicated fawns comprised 3% of the total harvests compared to 20% determined at checking stations. Therefore, questionnaire data were adjusted to correct proportions of fawns in annual harvests. Total antelope harvested was assumed to be most reliably determined by the questionnaire. The Yellow Water Triangle estimate (75%) was applied to the total harvest; 20% of the harvest was estimated to be fawns; and adult male and female percentages (questionnaire) were applied to the remainder.

Repeated annual aerial surveys and reconciliation of data between years for identical cohorts were important in analyzing survival and mortality. The system of classification, particularly identification of yearlings, made it possible to recount some sex-age cohorts during two successive years.

Coyote Population Surveys

Coyotes were the most abundant, and potentially the most influential, predators on the study area. The effects on coyotes (and indirectly on antelope) of the poison restrictions on public land (Presidential Executive Order No. 11643, 1972) were not known; thus, a summer survey of coyotes, to coincide with the summer antelope survey, was initiated during 1972 and continued through 1978. This survey was based on howling responses to a siren sounded at selected listing stations scattered over the study area (USFWS 1971). The year-after-year presence of coyote litters near the same locations suggested the existence of traditional den areas, similar in spacing and distribution to those found during a more intensive survey in the Missouri River breaks (Pyrah 1984).

Habitat Relationships

Habitat types were mapped on aerial photos by Jorgensen (1979). The aerial photos were used to make a habitat type map of the study area. Acreages of habitat types were measured on the aerial photos and combined on the basis of the habitat type map.

Most vegetation surveys employed the canopy-coverage method (Daubenmire 1959). Sampling typically consisted of measurement of 20 0.1 m^2 (2 × 5 dm) plots per 100 feet of transect. Sampling experiments in two sagebrush stands during 1970 indicated superiority of 10 0.4 m^2 (4 × 10 dm) plots per 100 feet of transect line rather than 20 0.1 m^2 plots per 100 feet and the need of 2 or more 100 ft lines for measuring canopy coverage of sagebrush (Pyrah 1973b). These experiments also indicated the need to measure plant heights as another parameter of cover. Equal canopy coverage does not mean equal cover for wildlife; height measurements reveal important cover differences.

The modified canopy-coverage method was used to measure fawn bedding cover (Pyrah 1974). Ten 0.4 m^2 plots were spaced at 10-foot intervals along two or more 100-ft line transects. Canopy coverage (by 0.5-foot height class) of shrubs (by species) and herbs was determined at each fawn bedding site. The tallest foliar parts of plants (excluding flowering stalks) were used to determine height class due to the importance of "aspect cover" produced by the tall vegetative parts of plants.

Habitat use was determined by a *Use Index* (UI) calculated as the product of the ratio between percent of observed animals and percent of land area involved. A UI of 1.0 indicated no selectivity while values above 1.0 indicated preference and below 1.0 indicated avoidance. The UI is similar to number of observations divided by a unit of area, being reduced by a factor of the average number of observations per unit of area, but can be used more easily for comparison between areas of unequal size and number of observations.

Bedding sites of antelope fawns were located as fawns left their dams in typical bedding site selection behavior (Pyrah 1971, Fichter 1974). The exact spot of bedding was determined as precisely as possible by relating it to some easily identifiable object; most observations were made during afternoon and evening when fawns were active for a longer period. The cover was usually measured during the following forenoon after the fawn(s) had moved to a new location; fawns were not intentionally disturbed. Most field work was completed between 24 May and 10 June when cover selection appeared to be most crucial.

Bedding sites of older fawns were not measured. After fawns reach about 3 weeks of age, they apparently are less selective of good cover (Fichter 1974). Older fawns were identified by their larger size, more erect standing and running posture, less secretive bedding behavior, and grouping of fawns.

The effects of sagebrush control measures on antelope were studied on four treatment areas that were selected in 1966 and fenced in the fall of 1967. Chemical and mechanical treatments were applied in 1967 and 1968 to effect varying degrees of sagebrush removal. Chemical control was accomplished using aerial application of 2,4-D.

The Iverson area comprised approximately 1,240 acres and was located in the extreme southern portion of the Triangle. Three hundred and twenty acres were sprayed to obtain a partial kill of sagebrush. An additional 320 acres were treated in alternate 100-foot wide spray and leave strips. The remainder served as a control.

Herbicide treatments of sagebrush communities were applied by fixed wing aircraft.
(Photo by: Montana Department of Fish, Wildlife and Parks)

The King area covered nearly 4,000 acres in the northern part of the Triangle. Two hundred and forty acres were sprayed to obtain a total sagebrush kill and 511 acres were treated mechanically. Of this acreage 321 acres were treated with a model B contour-furrowing machine which plowed to a depth of 12 to 14 inches. Seventy of the 321 acres treated by furrowing were also interseeded. An additional 190 acres were also interseeded using a machine which scalped the soil surface 2 to 4 inches in depth and 18 inches wide. The remaining 3,249 acres served as a control.

The Sibbert area was located on the eastern edge of the Triangle and comprised about 910 acres. Two hundred and fifty-three acres on the west side of Highway 244 were treated to obtain a partial kill of sagebrush. The remaining 657 acres on the east side served as a control.

The Winnett area was located outside of the Triangle approximately 3 miles northwest of the town of Winnett. Of the 1,220 acres in the area, 480 were sprayed for a total sagebrush kill and 400 were treated in alternate 100-foot wide spray and leave strips. The remaining 340 acres served as a control.

Statistical procedures were selected from Freese (1967) and Snedecor and Cochran (1967).

SOCIAL DISTRIBUTION

Overall, the herd is the basic social unit as well as the active social unit during winter. Doe bands and their adjuncts are the summer social groups as well as the primary production units of the antelope population.

Herds and Herd Ranges

The study area supported six herds—five in their entirety (Herds I, II, V, VI, and VII), and one doe band (IV-A) that was partially isolated by a highway from the remainder of its herd range outside of the area (Fig. 8). Because Doe Band IV-A often wintered on the study area, it functioned somewhat as a separate population.

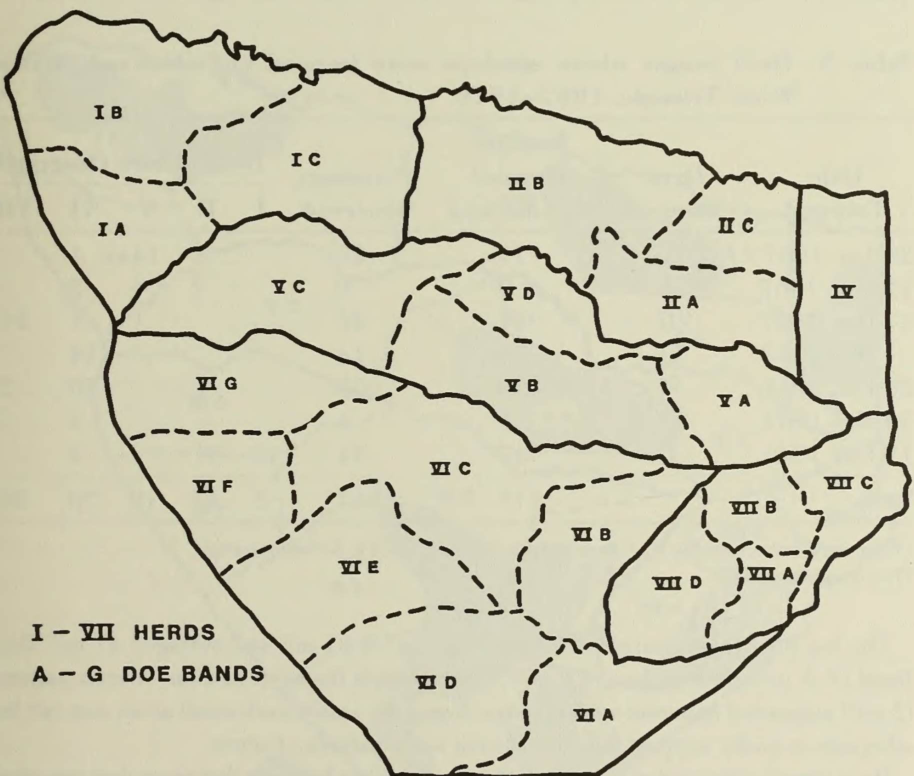


Figure 8. Social groups (herds and doe bands) in the Yellow Water Triangle, Montana.

Herd Ranges II, IV, V, and VII supported higher average fawn densities than herd ranges I and VI. Range condition (judged by the prevalence of the ARTR/AGSP h.t.) was good to excellent in Herd Range II. Two-thirds of Herd Range IV was ungrazed during summer (winter sheep pasture), nearly one-third was grazed by cattle during summer, and a small part was hayed. Summer range conditions were excellent in both sheep pastures and pastures containing hayfields, and fair to good in the cattle-grazed pasture. Herd Ranges V and VII were partially managed under rotational grazing, which appeared to increase antelope carrying capacity after initiation in 1970–1971. Herd Range VII also included a cattle winter pasture and a pasture used only periodically during summer.

Conversely, Herd Ranges I and VI included less suitable habitat and/or less favorable livestock grazing regimes. Herd Range I contained most of the timberland on the study area, which effectively separated areas of suitable habitat and reduced continuity. Heavy cattle grazing during summer also appeared to reduce antelope production. Herd Range VI included mainly the Yellow Water common use pasture that was grazed continually on a spring-fall schedule. During late summer, most antelope on that area retreated to livestock fall and winter pastures surrounding the common use pasture.

Herds occupied discrete herd ranges to which marked antelope exhibited high fidelity; 88% were consistently observed within their own herd ranges. Dot maps of individual relocations and association tables (Table 3) indicated little contact between herds; that which did occur largely involved dispersal.

Table 3. Herd ranges where antelope were trapped and observed, Yellow Water Triangle, 1967–1970.

Date Trapped	Herd Trapped	Number Trapped and Marked	Number Observed	Herd Where Observed				
				I	II	V	VI	VII
29 Jan. 1967	V	19	18		3[1]	14	1	
17 Dec. 1967	V	9	9		2	4	2	
17 Dec. 1967	VII	27	26			1	1	24
4 Mar. 1968	VI	14	14				14	
20 Feb. 1968	VI	58[2]	53		1		50	2
19 May 1969	VI	1	1				1	
19 Feb. 1970	II	47[2]	44	2	41		1	
Totals		175	164	2	47	19	70	26

[1]Three male fawns stayed in II, 3 does and doe fawns returned to V during spring.
[2]Two retraps.

The five herd ranges varied in size from 18 mi^2 to 81 mi^2 and averaged 41 mi^2. Doe Band IV-A occupied an area of 8 mi^2. Although both the latter and the Iverson pasture (2 mi^2) supported apparent social groups during the study, such small areas may not be adequate to totally support antelope during some periods of stress.

Herd ranges consisted of upland plateaus or benches between drainages that provided primary habitat for antelope. Boundaries typically were permanent and intermittent streams that restricted movement between herd ranges (Cole 1956); thus, most herd ranges had long axes oriented parallel to drainages. Tall, dense vegetation and steep-sided stream channels doubtless helped to curb antelope crossings. Also, bottomlands normally supported higher densities of small mammals and more coyotes and bobcats than uplands, such that more frequent contact with predators and/or predator sign could have reduced antelope use of those areas.

In some cases, combinations of streams, highways, railroads, and fences acted to restrict antelope movements and define herd range boundaries. In one, an old highway (as a herd boundary) may still act as a psychological constraint (Klopfer 1969:58) in maintaining traditional herd distribution and movement patterns. The boundary between Herds VI and VII had no evident environmental barrier, and herd separation apparently was maintained only by social behavior. However, the boundary is near an old country road that has little use and no right-of-way fences at present. At one time, Herds I and II apparently comprised a single herd that became separated by an incompatible land use (grazing by domestic sheep). When that restriction was removed, Herd II immediately occupied part of Doe Band Area I-C and two does from II-B emigrated to area I-C. A small area of winter habitat on Doe Band Area I-B appeared to be used similar to the semi-isolated Doe Band Area IV-A. Herd Ranges V and VI spanned the entire width of the study area.

Herd ranges included all areas used seasonally by all social units of the herd, except in winters of extremely adverse conditions. The normal or *traditional* winter range usually occurred near the center of the herd range (Fig. 9). Use of specific portions of traditional winter range varied, apparently depending upon such factors as harassment,

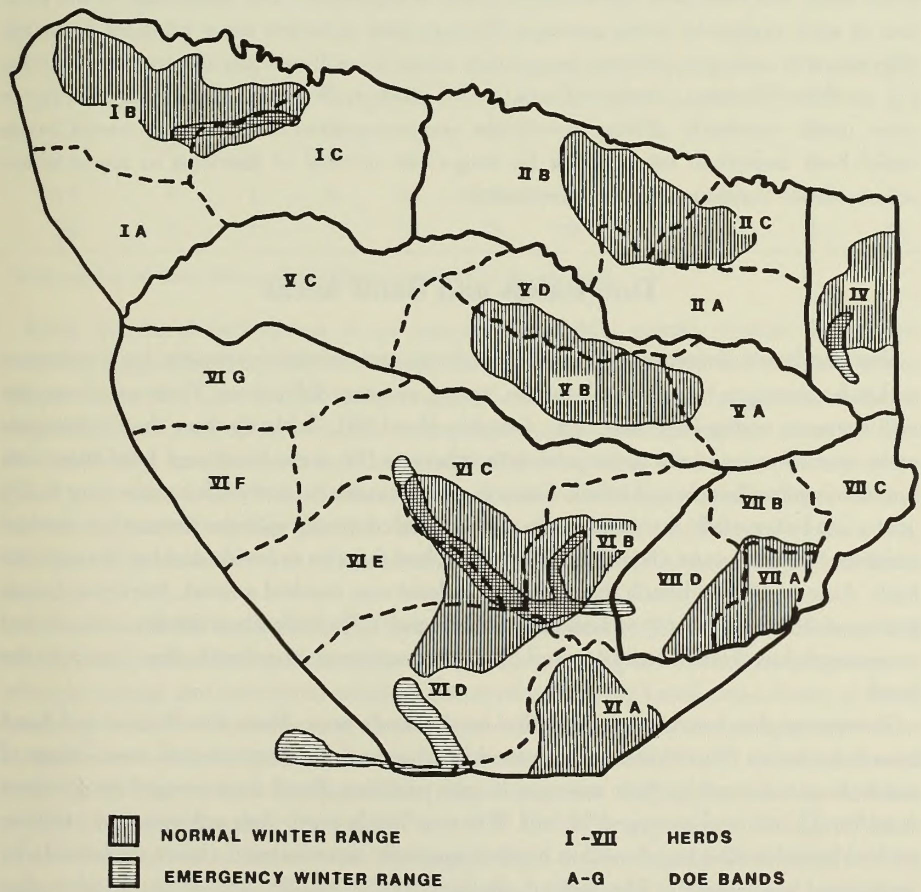


Figure 9. Traditional and emergency antelope winter ranges in the Yellow Water Triangle.

winter severity, and land use. Typically, doe bands gathered together in early winter as temperatures became colder and snow deeper. Sometime between December and February, most of the bands in each herd assembled either into one herd or in several groups in close proximity to one another. Periods of complete consolidation of bands often were short. During periods of warm weather, herds typically broke up, apparently into component doe bands or some combinations that formed the most common winter social groups.

Atypical movements and distribution during the 1977–1978 and 1978–1979 winters indicated that *emergency* winter ranges also existed (Fig. 9). In both of those years, when winter severity exceeded any of the previous 20 or more years (Hamlin 1979), herds assembled and traveled outside of normal herd ranges. During two other relatively severe winters, 1964–1965 and 1968–1969, antelope remained on their herd winter ranges.

Although winter severity may not exclusively determine when herds abandon their traditional winter range, it should be the most important factor during most years. The most recent winter approaching 1977–1978 and 1978–1979 in severity and causing winter migrations to emergency winter ranges was 1951–1952 (Brown 1953). Because of this, the consolidation and movement of herds to emergency winter ranges during this study could not have been the result of previous experience and knowledge of the location of such ranges by living antelope. Perhaps they reflected some inherent behavior. Migrations to emergency winter ranges may occur more frequently in some other areas; e.g. northern Montana, southern Canada, and southern Wyoming. An instinctive urge to move under extremely adverse conditions and recognition of emergency winter range could have important implications for long-term survival of antelope in areas where severe winter conditions occur infrequently.

Doe Bands and Band Areas

Doe bands are discrete social subunits of herds and occupied separate doe band areas within herd ranges during the 7-month, spring-summer-fall period. Patterns of association between marked animals (e.g., females, Herd VII, Table 4) show that individuals were much more closely associated with others in the same band and herd than with animals in other bands and herds. Some marked females, observed for periods up to 7½ years, used essentially the same areas and associated mostly with the same other marked animals year after year. Overall, fidelity of marked females to bands and band areas was high. Among 17 doe bands that included at least one marked animal, fidelity to bands averaged 86% and fidelity to band areas averaged 77%. Individual fidelity to band and area was reduced when bands moved to winter range and mixed with other bands in the herd.

Twenty-two doe bands were identified on the study area. Their distribution and band area boundaries (Fig. 8) were determined by observed distributions and associations of marked animals and by their association with pastures. Band areas ranged in size from 4 mi^2 to 21 mi^2, and averaged 10 mi^2. Whereas herds were often separated by environmental barriers, doe bands within herds apparently were isolated almost exclusively by behavioral mechanisms. The lack of physical separation, the knowledge of other doe band areas from winter movements, and escape reaction to human disturbance probably combined to cause more trespass and greater individual movement between band areas and bands than between herd ranges.

Table 4. **Number of times individual marked females were observed in association with other marked females within four doebands in Herd VII, Yellow Water Triangle, 1968–1973.**

Marked Antelope Id. No.	Doe Bands A 30	A 52	A 55	B 27	B 28	B 51	C 24	C 35	C 38	D 107
30	61[a]	22	26	5	10	7	6	3	2	0
52	22	37[a]	22	4	5	9	4	3	3	1
55	26	22	40[a]	4	6	7	4	5	4	2
27	5	4	4	37[a]	12	20	7	3	2	2
28	10	5	6	12	53[a]	10	6	3	0	3
51	7	9	7	20	10	44[a]	7	3	3	2
24	6	4	5	7	6	7	68[a]	26	7	0
35	3	3	4	3	3	3	26	32[a]	8	0
38	2	3	2	2	0	3	7	8	13[a]	0
107	0	1	0	2	3	2	0	0	0	20[a]
Others										
32	0	0	0	1	1	2	3	0	0	0
23	3	3	2	0	0	2	2	1	2	0
25	2	3	2	4	5	6	2	2	3	0
21	1	2	1	9	5	10	2	1	1	2
34	1	1	0	0	0	1	0	0	0	0
53	1	1	1	0	0	0	1	1	1	0

[a] Total number of times doe number (30) was observed in its own band.

Each doe band had access to an ungrazed or lightly grazed pasture during late summer, suggesting that such areas may be an important component of band areas. Observations by Cole (1956) also indicated that undisturbed (ungrazed) units of rangeland were especially attractive to antelope on the area during late summer. Two doe bands (I-C on Elk Creek and the band that developed in the Iverson Pasture when gates were closed in 1968, Becker 1972) dispersed when previously ungrazed and moderately grazed summer pastures became heavily grazed near the end of the study. The fate of those bands was not determined because intensive observations had been terminated.

In addition to the basic doe band that included productive females and fawns as well as yearling females during most of the spring-summer-fall period, various subgroups or other groupings and individual antelope occurred within doe band areas. Some of those involving females were temporary associations called *dry-doe bands* and appeared to be insignificant in herd organization or social structure. Typically, these included several yearling females of one doe band that ranged together during the fawning isolation period of mature females. During 1974, a year of low fawn production, unproductive mature females were observed with yearlings in large dry-doe bands. Observations of the nature and possible significance of other subgroups occasionally observed were hampered by the lack of marked antelope.

Territorial males characteristically occurred within doe band areas, usually excluding other males from the most desirable habitat in each area. A doe band area may include one or several buck territories (Bromley 1969, Kitchen 1974). Most territorial bucks were mature males 2-years-old and older; one yearling buck in the Iverson pasture was territorial (due to the lack of a mature male) and apparently bred successfully. Although two 2-year-old males were poached on a territory adjacent to a main road, several marked 2-year-olds were not territorial. Copeland (1980) reported that males usually become territorial at 2 years of age or older.

Territorial male antelope. *(Photo by: Montana Department of Fish, Wildlife and Parks)*

The size of territories varied greatly. The amount of area that is or can be defended apparently can be influenced by factors that restrict movements of other males into the territory; e.g., larger areas may be successfully defended if the main defensive effort is directed to one side rather than all directions.

Bachelor buck bands represent aggregations of immature males that apparently are not sufficiently developed sexually for the aggressive behavior of territoriality to override the gregarious behavior of fawn/doe groups. Young males are chased from the vicinity of doe bands by territorial males; their residual gregarious behavior causes them to band together. Frequencies of association between individually marked yearling males in bands were among the highest recorded for associations between any marked antelope on the area.

Banding together requires that bachelor males occupy poorer habitats than doe bands and territorial males (Copeland 1980); they also require less nutritious forage. Thus, bachelor buck bands typically ranged along the margins of doe band areas and frequently crossed doe band boundaries. At times they also crossed herd range boundaries. These bands broke up during the rut.

Dispersal

Dispersal involved permanent movement by individuals and groups of antelope between herds and off the study area. Return movements were uncommon.

Twenty (12%) of 164 antelope that were marked and subsequently reobserved exhibited some form of dispersal movement during the study. These included 8 (10%) of 86 females, and 12 (15%) of 78 males. The accuracy of these rates was confounded by the unknown fates of 11 marked antelope that were never reobserved. In addition, the original (pre-trapping) herd range of 7-9 antelope marked during 1967–1968 could not be determined.

Trapping may constitute a traumatic experience causing displacement and perhaps dispersal. Observations of marked antelope after trapping in the winter of 1966–1967 (Table 5), indicated that herds reassembled within a few days following release. Although the marked animals initially returned to their original herd range, within a few days the herd separated into two groups (probably Doe Bands V-B and V-D). The V-D group subsequently crossed Elk Creek, normally a deterrent to movement, and spent much of the winter in Doe Band Area II-B. During spring the group returned to Doe Band V-D, except for 3 immature males that remained in Herd Range II until killed by hunters. Several other animals marked during the 1966–1967 and other trapping operations dispersed immediately following release.

Table 5. Number of times individually marked antelope were observed with other marked animals within various winter groups in Herd V on the Yellow Water Triangle during winter 1966–1967 (data from Bayless 1967).

Winter	Winter Group A									Winter Group B						Singles		
Group	17	15	3	4	5	6	10	14	9	18	2	7	8	11	12	13	16	19
A																		
17	54[a]	35	33	32	29	33	29	29	10	1	5					2	1	1
15	35	36	31	30	27	33	24	25	6		2							1
3	33	31	38	30	26	28	24	26	6		6					1		4
4	32	30	30	38	28	29	25	27	6		3							2
5	29	27	26	28	34	27	25	25	6		4							
6	33	33	28	29	27	33	24	24	6		2							
10	30	24	24	25	25	24	37	28	10		6							
14	29	25	26	27	25	24	28	35	7	1	7					1	1	1
9	10	6	6	6	6	6	10	7	18	3	11	1				1		1
B																		
18	1							1	3	49	24	18	17	17	17		2	
2	5	2	3	3	2	2	7	7	11	24	34	17	17	17	17			
7									1	18	17	21	17	17	17			
8										17	17	17	20	18	19			
11										17	17	17	18	19	19			
12										17	17	17	18	19	21			
Singles																		
13	2	1	1				2	2	1		2					5		1
16	1							1		2							3	
19	1	1	3	2			1	1	1		1					1		43

[a] Total number of times antelope number (17), etc. was observed in its respective winter group.

Most known cases of dispersal involved movement to an adjacent herd range, and all returned collars, except one, were taken within the study area. Some hunters were reluctant to return collars; thus other marked animals may have been shot outside of the study area and not reported.

Pioneering unoccupied habitat is a unique behavior, and may be the ultimate role of dispersal, even though the likelihood of encountering such habitat is remote in occupied range. The more or less random wandering of small groups of immature antelope and apparently socially unattached animals, especially during spring when does and territorial males were returning to traditional ranges, might reflect some innate pioneering behavior. Some of those groups consisted of yearlings of both sexes following a 2- or 3-year old male.

One possible instance of pioneering was witnessed during 15–23 April 1968 when a group of 6 antelope was observed wandering near the edge of two doe band areas. The group consisted of a marked 3-year-old male (#104), a marked female fawn (#107), and 4 unmarked females. As the group neared the territory of another marked 3-year-old male (#54) on 23 April, the latter chased #104 away and drove the does into his territory. The marked fawn, and presumably does in the group, remained in #54's territory during summer. Other groups of this type were observed in other areas.

Although instances of dispersal during the study were few in relation to the total animals trapped and marked, dispersal could be important as a potential factor in pioneering and population regulation over time. Studies of mule deer (Hamlin pers. comm.), coyotes (Pyrah 1984), and prairie dogs (Knowles pers. comm.) indicate that dispersal may be a population controlling/regulating factor in some populations.

Discussion

Plains ungulates, including antelope, are characterized by gregarious social behavior. Etkin (1964) defined a social group as, "one whose members stay together as a result of their social responses to each other. . . . Groups which owe their existence to attractive factors in the environment . . . are called aggregations." This definition may be too general when considering antelope social distribution. Periodically, members of the same social group may be several miles apart; whereas, some aggregating, related to limited sustenance, comfort, or security factors, brings different social groups together during specific seasons. Etkin may have envisioned the bringing together of unrelated social groups. Even so, it may be difficult to accurately separate social and habitat attractions in social organization and distribution. Only animals that are somewhat aggregated can become organized (Allee et al. 1949).

Antelope social distribution results from discrete, autonomous herds and doe bands developing seasonal movement and habitat use traditions in separate and distinct geographic areas. Herds and doe bands are the basic social units; territorial bucks, bachelor buck bands, and dry-doe bands are auxiliary and/or transitory social units. Social distribution reflects the combined influences of genetics, social behavior, tradition, and habitat response. Social groups acquire stability through social, behavioral, and habitat traditions involving specific land areas with traditional land use management. Stable herd and doe band traditions produce stable social distribution of antelope in the Yellow Water Triangle.

Stability of social structure apparently originates from close kinship within each doe band. Low dispersal of female offspring and polygamy of territorial males cause doe bands to be essentially *sister groups*, a sociogenetic facsimile to brother groups in wild turkeys (Watts and Stokes 1971). Genetic interchange between doe bands causes herds to be families of sister groups. Because little exchange of individuals occurs between herds,

Large winter antelope herds exemplify gregarious social behavior.
(Photo by: Montana Department of Fish, Wildlife and Parks)

each herd theoretically represents a different gene pool (Urleston 1976 in Anderson 1981:36). Larger herds in other areas may be genetically more complex than the small herds in the Yellow Water Triangle.

Genetic closeness may strengthen group social bonds and decrease agonistic behavior. Near-identical genotypes may produce similar glandular odors, external appearances, behavioral traits, food preferences, and habitat use patterns, including migration. Adult females and their neonate daughters also may forge strong social bonds. Summer social groups often contain an adult male, a mature female, a yearling female and one or two fawns. Other larger groups involving more yearling and mature does and their fawns may also be closely related. Unrelated females may not be fully accepted into resident female social orders. Two of four marked immigrant females were observed to have unstable home ranges, and they resided part time in two different doe band areas.

While genetic similarities may influence social cohesiveness through individual and group recognition, group traditions, evolved in maximizing the occupancy of herd ranges and doe band areas, also support the individuality of social groups. Thus, a population unit is tied together genetically and socially as well as through habitat use traditions.

Knowledge of home range as well as of trespass may be readily determined by individual antelope. Scent signs of urine, feces, and tracks from males and females plus smell-paw-urinate-defecate and brush thrashing marks of males provide clues of individual recognition and sexual condition (O'Gara and Moy 1972). These signs may also provide continuous recognition to the social group occupying the area. In two observed trespass incidents, nonresident antelope fled from their location in a foreign doe band area as a response to the observer's presence (once in a truck and once in an airplane). Their unalterable return into their own herd range was especially significant; neither the airplane nor the truck could change their travel direction.

Some biologists consider that inbreeding weakens the gene pool; however, animal husbandry uses line breeding and inbreeding in domesticated animals to speed up selection of certain desirable physical qualities. Inbreeding potentially can speed up the selection process in antelope also. The ability to adjust quickly may be necessary for survival in rapidly changing environments. This may partially explain some short term changes in forage preferences and use of habitat types.

POPULATION DYNAMICS

Population Characteristics and Trends

Numbers

Total number of antelope counted annually on the Yellow Water Triangle averaged 842 but fluctuated widely during the 13-year (1966–1978) survey period, varying from 529 (1966) to 1,133 (1973) (Table 6). Although some of the variation probably reflected counting errors associated with conditions at the time surveys were made, the total counts should reasonably represent population trends. Numbers were low during 1966–1967, following the severe 1964–1965 winter, generally increased during 1968–1973, declined sharply in 1974, remained stable through 1977, and declined again during the severe 1977–1978 winter to the lowest level since 1969.

Table 6. Numbers of antelope counted and classified by sex and age during aerial surveys on the Yellow Water Triangle, 1966–1978.

Year	Adult Males			Adult Females	Total Adults	Fawns	Total Antelope
	Yrlg.	Mat.	Total				
1966[1,2]	56	35	91	252	343	186	529
1967[1,3]	64	40	104	263	367	181	548
1968[1]	72	46	118	202	320	233	553
				(279)	(397)	(322)	(719)
1969[1]	75	48	123	316	439	253	692
				(332)	(455)	(266)	(721)
1970[4]	92	58	150	411	561	299	860
	(94)	(59)	(153)		(564)		(863)
1971[4]	110	94	204	402	606	313	919
1972[4]	120	110	230	481	711	375	1,086
1973[4]	108	117	225	537	762	371	1,133
1974	119	121	240	474	714	199	913
				(497)	(737)	(209)	(946)
1975	67	95	162	518	680	273	953
	(77)	(110)	(187)		(705)		(978)
1976	87	83	170	487	657	284	941
	(89)	(85)	(174)		(661)		(945)
1977	83	86	169	399	568	257	825
1978	73	78	151	344	495	238	733
Average	88	79	167	400	567	275	842

[1]Yearling/mature ratio estimated from ground observation ratio in 1970.
[2]Adjusted for 13 unclassified.
[3]Partial coverage, totals estimated.
[4]Yearling/mature ratio determined by ground observations.
() Survey adjustments, averages based on the adjusted survey numbers.

Percentages of males and females remained near the same level throughout the study. Low and high populations contained nearly the same percentage of each class (Appendix C). The largest differences occurred during highest and lowest fawn production.

Individual herds were censused beginning in 1968 (Table 7). Average herd counts for 11 years (1968–1978) were: Herd I - 96, Herd II - 167, Herd IV - 59, Herd V - 195, Herd VI - 262, and Herd VII - 95. Average herd size was positively correlated with size

Table 7. Numbers of antelope counted and classified within individual herds during aerial surveys on the Yellow Water Triangle, 1968–1978.

Herd (Area of Herd Range)	Year	Adult Males			Adult Females	Total Adults	Fawns	Total Antelope
		Yrlg.	Mat.	Total				
	1968			7	23	30	31	61
I	1969			16	36	52	28	80
(32.26 mi^2)	1970			12	35	47	25	72
	1971			25	71	96	44	140
	1972			21	62	83	39	122
	1973			26	94	120	47	167
	1974	10	8	18	52	70	17	87
	1975	1	4	5	39	44	9	53
	1976	6	8	14	57	71	25	96
	1977	5	3	8	61	69	21	90
	1978	5	7	12	44	56	30	86
	Average	5	6	15	52	67	29	96
	1968			9	31	40	29	69
II	1969			26	38	64	35	99
(27.02 mi^2)	1970			35	72	107	59	166
	1971			41	80	121	63	184
	1972			67	124	191	94	285
	1973			53	89	142	52	194
	1974	33	32	65	91	156	36	192
	1975	8	13	21	105	126	54	180
	1976	14	11	25	86	111	40	151
	1977	21	22	43	69	112	40	152
	1978	18	19	37	71	108	52	160
	Average	19	19	38	78	116	50	167
	1968			11	11	22	15	37
IV	1969			6	23	29	22	51
(8.45 mi^2)	1970			12	36	48	17	65
	1971			9	23	32	15	47
	1972			17	40	57	39	96
	1973			27	40	67	30	97
	1974	10	15	25	41	66	12	78
	1975	2	9	11	26	37	16	53
	1976	6	2	8	26	34	20	54
	1977	0	3	3	17	20	17	37
	1978	4	1	5	14	19	18	37
	Average	4	6	12	27	39	20	59

Table 7. *(Continued).*

Herd (Area of Herd Range)	Year	Adult Males Yrlg.	Adult Males Mat.	Adult Males Total	Adult Females	Total Adults	Fawns	Total Antelope
	1968			38	43	91	52	143
V	1969			22	74	96	63	159
(46.44 mi²)	1970			27	75	102	49	151
	1971			50	61	111	56	167
	1972			55	84	139	95	234
	1973			44	107	151	95	246
	1974	29	28	57	94	151	52	203
	1975	17	26	43	130	173	76	240
	1976	33	30	63	133	196	67	263
	1977	11	23	34	80	114	69	183
	1978	29	23	52	61	113	37	150
	Average	24	26	44	87	131	65	195
	1968			39	62	101	76	177
VI	1969			48	117	165	84	249
(80.65 mi²)	1970			47	147	194	113	307
	1971			63	129	192	98	290
	1972			54	136	190	85	275
	1973			55	156	211	96	307
	1974	24	29	53	141	194	53	247
	1975	23	27	50	151	201	78	279
	1976	22	22	44	133	177	82	259
	1977	38	26	64	130	194	76	270
	1978	11	21	32	116	148	69	217
	Average	24	25	50	129	179	83	262
	1968			14	22	36	30	66
VII	1969			5	28	33	21	54
(18.07 mi²)	1970			17	46	63	36	99
	1971			16	38	54	37	91
	1972			16	35	51	23	74
	1973			20	51	71	51	122
	1974	13	9	22	55	77	29	106
	1975	16	16	32	67	99	40	139
	1976	6	10	16	52	68	50	118
	1977	8	9	17	42	59	34	93
	1978	6	7	13	38	51	32	83
	Average	10	10	17	43	60	35	95

of herd range ($r = 0.92$, 4 df, $P < 0.01$), indicating that the uninterrupted expanse of suitable habitat available strongly influenced herd size. Average total number of fawns ($r=0.92$), adult females ($r=0.95$), adults ($r=0.92$), and adult males ($r=0.83$) also correlated with size of herd range.

Total antelope in every herd increased between 1968 and 1973; however, maximum numbers were reached later in Herds V (1976) and VII (1975). Herd increases, except Herd VI, were near or above the 100+% reflected in total numbers.

Density

Density appears to be an important populaton parameter for antelope. Because density is the *result* of the effects of a number in interacting factors, density *per se* may not be as important as other factors: food abundance, competition, security, juxtaposition and interspersion of habitat needs, and a multitude of others.

Average antelope density for the study area (based on totals of antelope, area, and years) was 4.1/mi²; only Herd I had herd/year densities under 2/mi² (1968, 1975) and Herd IV had over 11/mi² during 2 years (1972, 1973) (Table 8). Average adult density was 2.8/mi² (Table 9), while average density of adult females was 1.9/mi² (Table 10).

Table 8. Total antelope densities (mi²) by herd and year, Yellow Water Triangle, 1968–1978.

	Herd						
Year	I	II	IV	V	VI	VII	Average
1968	1.89	2.55	4.38	3.22	2.14	3.65	3.38
1969	2.48	3.66	6.04	3.58	3.01	2.99	3.38
1970	2.23	6.14	7.69	3.40	3.71	5.48	4.05
1971	4.34	6.81	5.56	3.76	3.51	5.04	4.31
1972	3.78	10.55	11.36	5.27	3.33	4.10	5.10
1973	5.18	7.18	11.48	5.54	3.71	6.75	5.32
1974	2.70	7.11	9.23	4.57	2.99	5.87	4.24
1975	1.64	6.66	6.27	5.60	3.38	7.69	4.59
1976	2.98	5.59	6.39	5.91	3.13	6.53	4.44
1977	2.79	5.63	4.38	4.12	3.27	5.15	3.87
1978	2.67	5.92	4.38	3.38	2.63	4.59	3.44
Average	2.97	6.16	7.01	4.40	3.16	5.26	3.86

Table 9. Total adult antelope densities (mi²) by herd and year, Yellow Water Triangle, 1968–1978.

	Herd						
Year	I	II	IV	V	VI	VII	Average
1968	0.93	1.48	2.60	2.05	1.22	1.99	1.50
1969	1.61	2.37	3.43	2.16	2.00	1.66	2.06
1970	1.46	3.96	5.68	2.30	2.35	3.49	2.64
1971	2.98	4.48	3.79	2.50	2.32	2.99	2.85
1972	2.57	7.07	6.75	3.13	2.30	2.82	3.34
1973	3.72	5.26	7.93	3.40	2.55	3.93	3.58
1974	2.17	5.77	7.81	3.40	2.35	4.26	3.35
1975	1.36	4.66	4.38	3.89	2.43	5.48	3.19
1976	2.20	4.11	4.02	4.41	2.14	3.76	3.09
1977	2.14	4.15	2.37	2.57	2.35	3.27	2.67
1978	1.74	4.00	2.25	2.54	1.79	2.82	2.33
Average	2.08	4.30	4.64	2.94	2.16	3.32	2.78

Table 10. Density (mi^2) of adult female antelope by herd and year, Yellow Water Triangle, 1968–1978.

Year	Herd I	II	IV	V	VI	VII	Average
1968	0.71	1.15	1.30	1.19	0.75	1.22	0.95
1969	1.12	1.41	2.72	1.67	1.42	1.55	1.48
1970	1.08	2.66	4.26	1.69	1.78	2.55	1.93
1971	2.20	2.96	2.72	1.37	1.56	2.10	1.89
1972	1.92	4.59	4.73	1.89	1.65	1.94	2.26
1973	2.91	3.29	4.73	2.41	1.89	2.82	2.52
1974	1.61	3.37	4.85	2.12	1.71	3.04	2.23
1975	1.21	3.89	3.08	2.93	1.83	3.71	2.43
1976	1.77	3.18	3.08	2.99	1.61	2.88	2.29
1977	1.89	2.55	2.01	1.80	1.57	2.32	1.87
1978	1.36	2.63	1.66	1.37	1.40	2.10	1.62
Average	1.62	2.88	3.19	1.95	1.56	2.38	1.95

Density of adult females appeared to be a key parameter of antelope populations. Female density varied over years and between herds (Figs. 10, 11), suggesting that density was related to habitat quality. Using density of adult females as an indicator, each herd projected a different production potential, presumably as a result of inequality among the factors determining carrying capacity. Comparisons among herds, based on a theoretical maximum density of 5 adult females/mi^2, indicated higher average density and higher maximum density in Herds II and IV than in the other herds (Fig. 11).

Surprisingly, most herds were reduced to near their 1968 density following the high winter mortality during the 1977–1978 winter. Densities were more similar among all herds at low populations than at high populations.

Population Cycles

Long-term trends in antelope populations in the Yellow Water Triangle, together with data for 1966–1978, indicated an approximate 10-year cycle in antelope numbers on the area (Fig. 12). High populations on the study area occurred during the first 5 years of each decade; for periods with good census data, peak years were 1954, 1964, and 1973. Lows appeared to occur during the mid-to-latter years of each decade.

Because annual weather conditions influenced range conditions and antelope mortality during the 1960s and 1970s, it was possible that apparent population cycles were artifacts of weather patterns. A general review of weather patterns since 1913, when the Flatwillow weather station was established, and analyses of relationships between precipitation and antelope population parameters during the study period indicated that this was not the case.

Antelope population parameters during 1953–1978 (17 years, not continuous) had low correlations with annual precipitation. Correlations between annual precipitation and total population ($r = 0.176$) and fawn:doe ratio ($r = 0.052$) were insignificant, as was previous year precipitation and fawn:doe ratio ($r = 0.110$).

Periods of higher than average precipitation (Appendix A) were not consistently better for antelope production than periods of below average moisture. During a period of high

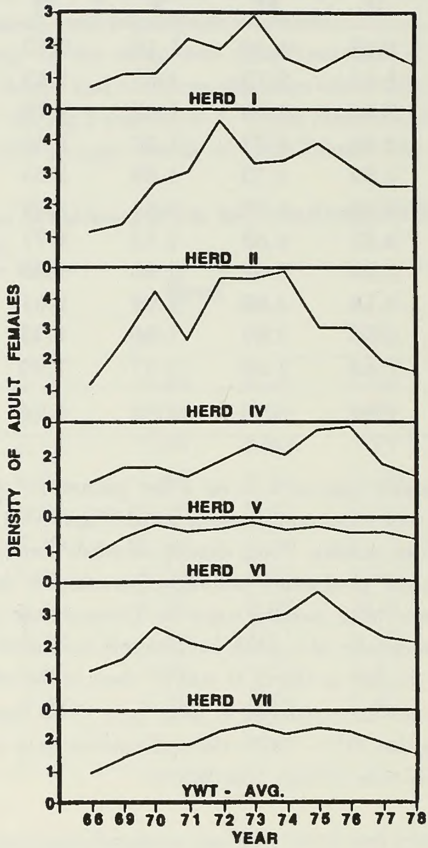


Figure 10. Trends in densities of adult females by herd unit, Yellow Water Triangle, 1968–1978.

precipitation (1962–1978), when 71% of the years were above average in annual precipitation, the antelope population varied from 529 (1966) to 1,133 (1973) and 1,198 (1964). During a period of lower precipitation (1945–1961), when only 35% of the years were above average, the antelope population varied from 636 (1948) to 1,246 (1954).

Nonetheless, weather/vegetation phenomena appear to affect antelope abundance cycles because down trends in antelope numbers usually followed cool, dry weather. Trends were reversed at a low population level when unusually good vegetation accompanied above average precipitation. The 1937–1944 period, when some of the greatest increases in antelope population occurred, was decidedly above normal. The extreme high, 17.4 inches during 1941–1944, could have been a key factor in the population increase.

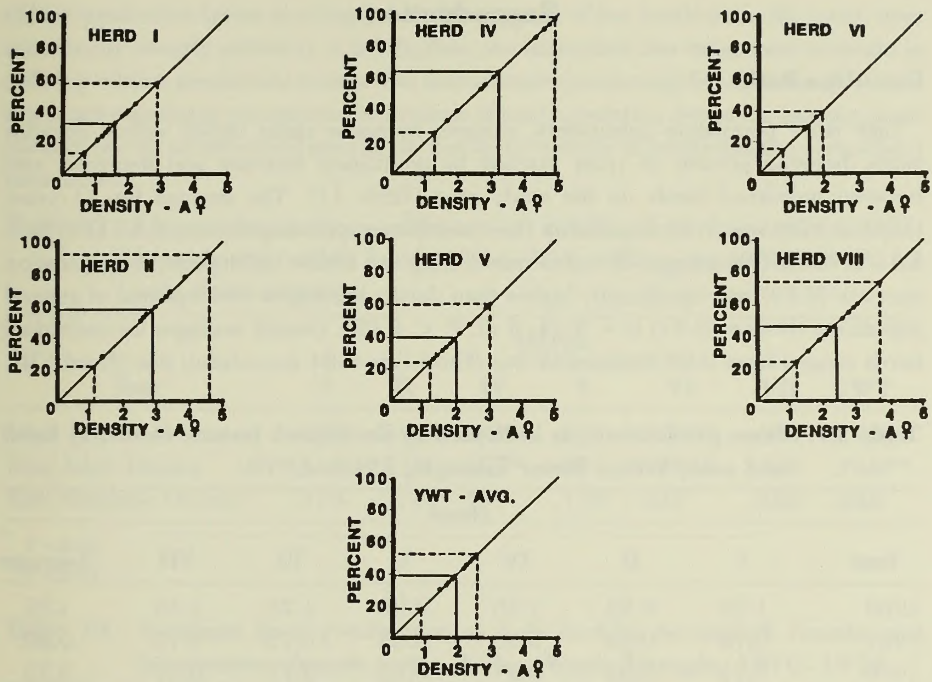


Figure 11. Differences in density of adult female antelope related to percent of maximum potential density (5 adult females/mi²) among herd units in the Yellow Water Triangle, 1968–1978.

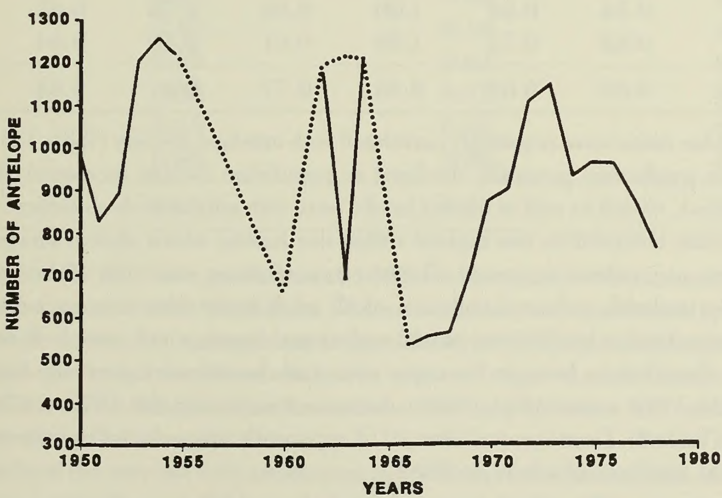


Figure 12. Antelope population trends ("cycles") on the Yellow Water Triangle, 1950–1978. Dotted line is reconstruction of apparent trend between counts.

Reproduction

Fawn:Doe Ratio

Like other population parameters, summer fawn:doe ratios varied widely between years, between periods of years marked by population increase and decrease, and between individual herds on the study area (Table 11). The average for 11 years (1968–1978) was 0.71 fawns/adult doe; yearly averages ranged from 0.42 (1974) to 1.15 (1968). The average fawn:doe ratio during the 1968–1973 period of population increase (0.84) was significantly higher than during the 1974–1978 period of general population decline (0.57) ($t = 3.24$, 8 df, $P < 0.05$). Overall averages for individual herds ranged from 0.60 fawns/adult doe (Herd I) to 0.84 fawns/adult doe (Herd VII).

Table 11. Fawn production, as indicated by fawn/adult female ratios, by herd and year, Yellow Water Triangle, 1968–1978.

	Herd						
Year	I	II	IV	V	VI	VII	Average
1968	1.35	0.94	1.36	0.98	1.23	1.36	1.15
1969	0.78	0.92	0.96	0.85	0.72	0.75	0.80
1970	0.71	0.82	0.47	0.65	0.77	0.78	0.73
1971	0.62	0.79	0.65	0.92	0.76	0.97	0.78
1972	0.63	0.76	0.98	1.13	0.63	0.66	0.78
1973	0.50	0.58	0.75	0.89	0.62	1.00	0.69
1974	0.33	0.40	0.29	0.55	0.38	0.53	0.42
1975	0.23	0.51	0.62	0.58	0.52	0.60	0.53
1976	0.44	0.47	0.77	0.50	0.62	0.96	0.58
1977	0.34	0.58	1.00	0.86	0.58	0.81	0.64
1978	0.68	0.73	1.29	0.61	0.59	0.84	0.69
Average	0.60	0.68	0.83	0.77	0.67	0.84	0.71

Fawn:doe ratios were negatively correlated with antelope density (Table 12), indicating that fawn production generally declined as population density increased. The highest correlations, overall as well as among herds, were with adult female densities. Apparently intraspecific competition was highest within doe bands, which shared forage and other resources, as numbers increased. The lowest correlations were with total antelope densities. This probably reflected inclusion of all adult males (the younger being excluded from better habitat by older, territorial males) and fawns, which were only weakly competitive. Correlations between fawn:doe ratio and density were generally higher during the 1968–1973 period of population increase than during the 1974–1978 period of decline (Table 8). Fawn survival after 1974 apparently was reduced by factors other than density as numbers of adults declined.

The accuracy and some of the variability in fawn:adult doe ratios (as an indicator of annual production) may have been influenced by inclusion of variable numbers of yearling (nonproducing) females. Data for 1970–1978, when yearling females were identified in field classifications, show an average 0.65 fawns/adult doe as compared with 0.83 fawns/mature (producing) doe (Table 13). The difference was significant ($t = 2.55$, 16 df, $P < 0.05$). Although differences in the two ratios were generally greater in years of high production (more yearlings) than during years of low production, the ratios were consistently linearly related (r = 0.99); thus, the fawn:adult doe ratios were accurate in defining relative production trends. The fawn:mature (producing) female ratios provided important population parameters for analysis of total population dynamics, but they were not accurate on an individual herd basis, due to movements of yearling males across herd boundaries.

Table 12. Linear correlation coefficients (r) relating fawn/doe ratios to antelope density within herds, Yellow Water Triangle, 1968–1978. All values are negative.

	Herds						
Year	I	II	IV	V	VI	VII	YWT
Adult Female Density	.480	.594	.723*	.503	.799**	.544	.772**
Total Adult Density	.399	.552	.658*	.487	.750**	.478	.766**
Total Antelope Density	.174	.376	.451	.179	.039	.262	.548

* $P<0.05$
** $P<0.01$

Table 13. Antelope fawn production as indicated by fawn/adult female and fawn/mature female ratios, Yellow Water Triangle, 1970–1978.

Year	Fawns/ Adult Female	Fawns/ Mature Female	Difference
1970	0.73	0.94	0.21
1971	0.78	1.07	0.29
1972	0.78	1.04	0.26
1973	0.69	0.86	0.17
1974	0.42	0.56	0.14
1975	0.53	0.61	0.08
1976	0.58	0.71	0.13
1977	0.64	0.81	0.17
1978	0.69	0.88	0.19
Average	0.65	0.83	0.18

The exceptionally high fawn production of 1968 was associated with successive years of excellent forage and cover conditions. These conditions were produced by above-normal rainfall during the spring-summer periods of 1967 (March-September) and 1968 (April-August), and doubtless resulted in improved vigor of adult females on the area. In addition, adult densities were low and the 1967–1968 winter was mild (5,377 degree days, 6% below average).

The cause(s) of the very low fawn production in 1974 was less evident. Both 1973 and 1974 were years of above normal precipitation, and the 1973–1974 winter was also mild (5,305 degree days, 9% below average). However, the month of May, when most fawns are born, was both very cold (coldest average temperature for May in 19 years) and wet (49% above normal precipitation) in 1974. Additionally, densities of adult antelope on the area and in most herds had peaked the preceding year, 1973. The possible involvement of other factors (e.g., disease and predation) could not be ruled out. As noted earlier, large numbers of dry mature does were observed in dry-doe bands during early June. Those bands, normally comprised of yearling does, were larger than usual in 1974 and included recognizable mature females which had neither enlarged udders nor distended abdomens. This indicated that either they had not been reproductively active (had not conceived fawns) or that reproductive activity had been minimal and ceased much earlier as a result of resorption or abortion of fetuses, or early postnatal mortality of fawns such that only small udders developed and quickly regressed. Coyote predation apparently contributed to above-average mortality of mule deer fawns in some central Montana populations during the period (Hamlin et al. 1984) and could also have affected antelope fawn survival.

Fawn Density

Fawn density refers to the number of fawns produced per square mile of habitat or herd range (Table 14). Year-to-year trends in fawn densities for individual herds and for the study area are illustrated in Figure 13.

Table 14. Fawn production, as indicated by fawn density (mi^2), by herd and year, Yellow Water Triangle, 1968–1978.

	Herd						
Year	I	II	IV	V	VI	VII	Average
1968	0.96	1.07	1.78	1.17	0.92	1.66	1.09
1969	0.87	1.30	2.60	1.42	1.02	1.16	1.18
1970	0.77	2.18	2.01	1.10	1.37	1.99	1.40
1971	1.36	2.33	1.78	1.26	1.19	2.05	1.47
1972	1.21	3.48	4.62	2.14	1.03	1.27	1.76
1973	1.46	1.92	3.55	2.14	1.16	2.82	1.74
1974	0.53	1.33	1.42	1.17	0.64	1.60	0.93
1975	0.28	2.00	1.89	1.71	0.94	2.21	1.28
1976	0.77	1.48	2.37	1.51	0.99	2.21	1.28
1977	0.65	1.48	2.01	1.55	0.92	1.88	1.21
1978	0.93	1.92	2.13	0.83	0.83	1.77	1.12
Average	0.89	1.86	2.38	1.45	1.00	1.93	1.32

Fawn density on the study area averaged 1.3/mi^2 during 1968–1978. Yearly averages varied between the low 0.9 recorded for 1974 and a high of 1.8 observed in 1972. Overall averages for individual herds (herd production) varied from 0.9 (Herd I) to 2.4 (Herd IV). The highest fawn density recorded for any herd in any year was 4.6 fawns/mi^2 for Herd IV in 1972, although fawn density among antelope confined to the Iverson pasture reached 8.8/mi^2 in 1971 and 1972.

Herd production more closely reflected the number of productive does in the herd than the number of fawns each doe raised. Fawn density was positively correlated with doe density within herds as well as overall (Table 15), especially during years of population increase (1968–1973), suggesting that successful fawn production causes high density. Conversely, fawn:doe ratios generally were negatively correlated with densities of does within and over all herds. Correlations between fawn density and fawn:doe ratios were varied, but generally negative during 1968–1973 and positive during

1974–1978. Because of this, fawn densities for most herds and the total number of fawns produced in the Yellow Water population continued to increase or remained high into the mid-1970s, while fawn:doe ratios declined.

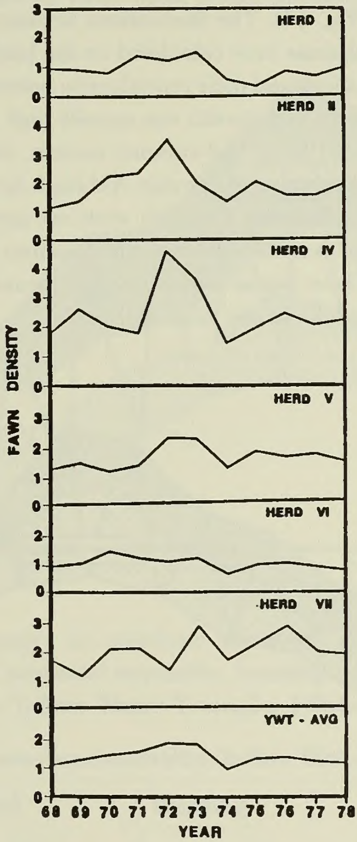


Figure 13. Fawn density trends by antelope herd, Yellow Water Triangle, 1968–1978.

Table 15. Linear correlation coefficients (r) between fawn/doe ratio (F/D), and doe density (DD), and fawn density (FD), Yellow Water Triangle, 1968–1978.

Parameters	Years	I	II	IV	V	VI	VII	YWT
FD:DD	68–73	0.920**	0.952**	0.718	0.530	0.725	0.764	0.953**
	74–78	0.337	0.218	−0.712	0.755	−0.009	0.318	0.241
	68–78	0.588	0.728*	0.457	0.467	0.257	0.590	0.502
F/D:DD	68–73	−0.779	−0.704	−0.602	−0.020	−0.921**	0.341	−0.865*
	74–78	0.060	−0.641	−0.964**	−0.519	−0.528	−0.585	−0.751
	68–78	−0.480	−0.594	−0.723	−0.503	−0.799**	−0.544	−0.772**
F/D:FD	68–73	−0.510	−0.459	0.072	0.564	−0.448	0.329	−0.694
	74–78	0.918*	0.605	0.692	0.163	0.853	0.000	0.456
	68–78	0.378	0.102	0.210	0.453	0.326	0.278	0.105

*$P<0.05$.
**$P<0.01$.

Mortality

Antelope populations on the study area fluctuated greatly between annual highs recorded in July surveys and the lows of spring as indicated by numbers of adults in the surveys the following July (Fig. 14). The fluctuations became even more extreme when potential post-fawning populations were calculated on the basis of numbers of breeding-age females in spring populations and their reproductive potential (Fig. 15). Those calculations assumed that reproductive potential was equally high in all years and that numbers of adult antelope, counted in the mid-summer surveys, were approximately equal to numbers on the area at the beginning of fawning. Although neither assumption may have been entirely correct, the differences probably were not great; except in reproductive potential during 1974 when, as noted earlier, some does may not have conceived or carried fetuses to parturition. There was no evidence of significant late spring–early summer mortality of yearlings and adults in any year.

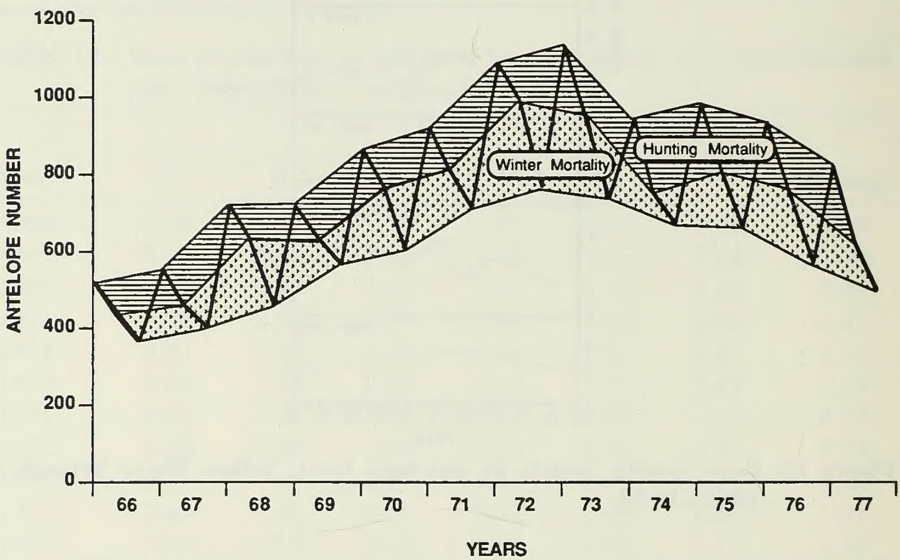


Figure 14. Annual changes in numbers of antelope related to recruitment and hunting and winter mortality in the Yellow Water Triangle, 1966–1977.

Mortality by Seasons

The data indicated that major mortality occurred during late spring-early summer (neonatal fawn mortality), during the fall hunting season (hunting mortality), and over winter (winter mortality) in all years (Table 16).

Neonatal.—Calculated neonatal fawn mortality was high, averaging over half (52%) of potential fawn production and 53% of the total annual mortality (Fig. 15, Table 16). This apparent loss ranged from a low of 18% of potential fawn production in 1968 (the year of highest fawn production in summer surveys) to a high 71% in 1974 (the year of lowest recorded fawn production), and generally increased with total numbers of antelope on the study area. Estimated neonatal mortality averaged 45% during incline years

(1966–1973) and 65% during peak and decline years (1974–1977). This close relationship between survival of young and numbers of adult females could be further evidence of increasing forage competition within doe bands as populations grew. Neonatal mortality apparently was low in 1968 when forage production was very good and the population was low.

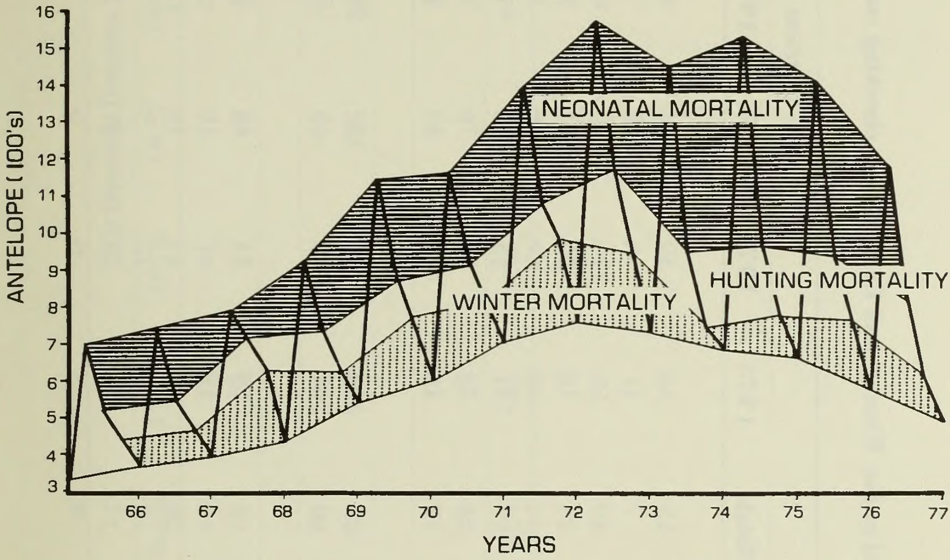


Figure 15. Annual changes in antelope numbers related to potential fawn production, neonatal mortality, hunting mortality, and winter mortality on the Yellow Water Triangle, 1966–1977.

Table 16. Total annual antelope mortality, Yellow Water Triangle, 1966–1977.

	Neonatal		Hunting		Winter		Total
Year	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**
1966	182	55	84	25	65	20	331
1967	197	57	90	26	61	18	348
1968	71	21	85	25	179	53	335
1969	222	59	92	24	65	17	379
1970	303	54	99	18	158	28	560
1971	242	54	106	24	102	23	450
1972	311	49	97	15	227	36	635
1973	444	53	182	22	214	25	840
1974	509	66	198	26	69	9	776
1975	584	65	171	19	150	17	905
1976	472	56	180	21	197	23	849
1977	343	51	206	31	124	18	673
Average	323	53	132	23	134	24	590

Harvest.—Hunting was by permit only due to antelope vulnerability to hunting (Brown, 1953); mortality was correlated with numbers of permits issued and not with numbers of antelope. Hunting removed an average of 16% of summer populations, ranging from

Table 17. Sex and age distribution of hunting mortality as determined at the Winnett and Grass Range checking stations, 1975–1978.

Sex/age		Hunting District 420 1975	1976	1977	1978[1]	Totals	All Hunting Districts 1975	1976	1977	1978	Totals
Males											
1/2	No.	5	2	7	1	15	33	39	60	26	158
	%	9	3	10	8	7	11	9	12	9	10
1-1/2	No.	7	19	19	4	49	53	114	104	69	340
	%	12	30	26	33	24	18	26	21	23	22
2-1/2	No.	15	4	13	2	34	63	60	80	54	257
	%	26	6	18	17	17	21	13	16	18	17
3-1/2	No.	9	5	7	3	24	53	61	76	58	248
	%	16	8	10	25	12	18	14	15	20	16
Subtotal											
	No.	36	30	46	10	122	202	274	320	207	1,003
	%	63	47	64	83	60	67	62	65	70	65
Females											
1/2	No.	4	3	1		8	29	31	48	25	133
	%	7	5	1		4	10	7	10	9	9
1-1/2 No.	3	11	9	1	24	26	53	43	14	136	
	%	5	17	13	8	12	9	12	9	5	9
2-/12	No.	7	7	3		17	16	25	27	19	87
	%	12	11	4		8	5	6	5	6	6

Table 17. *(Continued)*.

Sex/age		Hunting District 420					All Hunting Districts				
		1975	1976	1977	1978[1]	Totals	1975	1976	1977	1978	Totals
3-1/2+	No.	7	13	13	1	34	27	62	57	29	175
	%	12	20	18	8	17	9	14	12	10	11
Subtotal											
	No.	21	34	26 2	83	98	171	175	87	531	
	%	37	53	3617	40	33	38	35	30	35	
Unclassified											
	No.	4	3	11		18	23	41	25	41	130
	%	7	4	13		8	7	8	5	12	8
Total		61	67	83	12	223	323	486	520	335	1664

[1]Winnett station not operated.

9% (1972) to 25% (1977) (Fig. 15). Harvests accounted for 50% of total mortality accruing to summer populations and 23% of the total annual mortality (Table 16). These losses had little effect on population trends because adult males comprised approximately 65% of the harvest (Table 2).

Hunters were highly selective for adult males, and particularly mature males (Tables

Table 18. Relationship between percentage of antelope of various age classes in the population and in annual harvests from the Yellow Water Triangle, 1975–1978.

	1975	1976	1977	1978[1]	Average
Males					
Fawn					
Survey	14	15	16	16	15
Shot:					
All HDs	11	9	12	9	10
HD 420	9	3	10	8	8
Yearling					
Survey	8	9	10	10	9
Shot:					
All HDs	18	26	21	23	22
HD 420	12	30	26	33	25
Mature					
Survey	11	9	10	11	10
Shot:					
All HDs	39	27	31	38	34
HD 420	42	14	28	42	32
Females					
Fawn					
Survey	14	15	16	16	15
Shot:					
All HDs	10	7	10	9	9
HD 420	7	5	1	0	3
Yearling					
Survey	8	9	10	10	9
Shot:					
All HDs	9	12	9	5	9
HD 420	5	17	13	8	12
Mature					
Survey	45	42	38	37	40
Shot:					
All HDs	14	20	17	16	17
HD 420	24	31	22	8	22

[1]Winnett checking station not operated.

16, 17). Yearling females appeared to be more vulnerable to hunters than older females (Tables 17, 18).

Winter.—Some winter mortality apparently occurred on the study area regardless of winter severity. These apparent losses, calculated as the difference between numbers counted in summer surveys and the same sex/age cohorts the following year less hunting mortality, averaged 15% (range 7 - 25%) of summer populations and 12% (range 5 - 23%) of potential total annual populations. Winter losses appeared to comprise about 21% of the annual mortality of adult males, approximately 56% of the mortality of adult females, and 74% of the mortality of fawns.

Mortality By Sex and Age

Adult Males.—The average annual mortality rate for adult males, calculated from summer surveys, was 52% (Table 19). Harvests accounted for an average 41% of summer males and over 80% of the total annual loss of adult males in the area. Winter losses removed another 10% of the males present in summer and accounted for about 20% of the total mortality in males. Winter mortality was highest during the severe winters of 1968–1969 and 1971–1972. After 1972, however, high mortality of adult males occurred regardless of winter severity. This may have been due to increasing numbers of older males subject to higher mortality in the population, increased competition, or both (Fig. 16). High winter mortality indicated that males entered the winter in poor condition following the rut and rapidly became vulnerable to winter stresses. There was some evidence that harvest and winter losses were compensatory; i.e., higher harvests were followed by lower winter mortality.

Table 19. Mortality table for adult male antelope, Yellow Water Triangle, 1966–1977.

	Summer Survey	Hunting Mortality		Fall Survivors		Following Year Mature Males		Other Mortality		Total Mortality	
Year	No. Alive	No.	%	No.	%	No.	%	No.	%	No.	%
1966	89	32	36	57	64	40	45	17	19	49	55
1967[1]	104	47	45	57	55	46	44	11	11	58	56
1968	118	46	39	72	61	48	41	24	20	70	59
1969	123	59	48	64	52	59	48	5	4	64	52
1970	153	59	39	94	61	94	61	0	0	59	39
1971	204	54	26	150	74	110	54	40	20	94	46
1972	230	51	22	179	78	117	51	62	27	113	49
1973	225	98	44	127	56	121	54	6	3	104	46
1974	240	112	47	128	53	95	40	34	14	146	61
1975	187	88	47	99	53	85	45	14	7	102	55
1976	174	88	51	86	49	86	49	0	0	88	51
1977	169	91	54	78	46	78	46	0	0	91	54
Average	168	69	41	99	59	82	48	18	10	86	52

[1]Estimated from a partial 1967 survey plus 1966 and 1968 data.

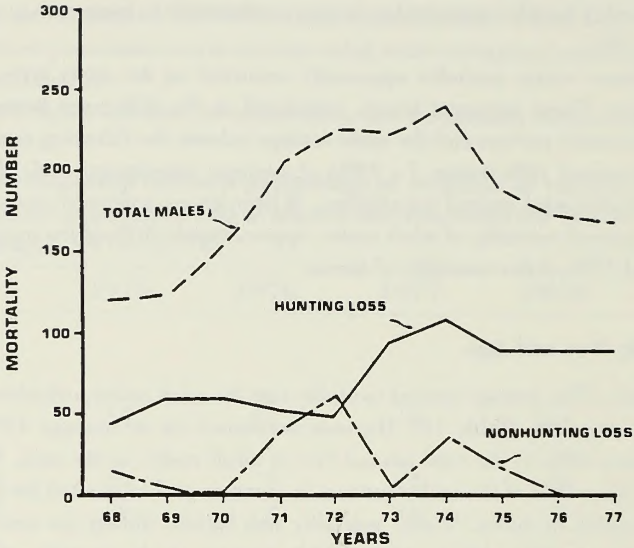


Figure 16. Trends in total numbers of adult males related to hunting and non-hunting mortality in the Yellow Water Triangle, 1968–1977.

Adult Females.—The average annual (summer-summer) mortality rate for adult females was 19% (Table 20). Hunting removals accounted for an average 9% of adult females counted in summer surveys, and winter losses removed another 10%. High non-hunting losses of adult females occurred at 3-year intervals throughout the study (Table 20, Fig. 17).

Table 20. Mortality table for adult female antelope, Yellow Water Triangle, 1966–1977.

	Summer Survey	Hunting Mortality		Fall Survivors		Following Year Mature Females		Other Mortality		Total Mortality	
Year	No. Alive	No.	%	No.	%	No.	%	No.	%	No.	%
1966	246	35	14	211	86	199	81	12	5	47	19
1967[1]	263	25	10	238	90	207	79	31	12	56	21
1968	279	22	8	257	92	257	92	0	0	22	8
1969	332	15	5	317	95	317	95	0	0	15	5
1970	411	20	5	391	95	292	71	99	24	119	29
1971	402	31	8	371	92	361	90	10	2	41	10
1972	481	27	6	454	94	429	89	25	5	52	11
1973	537	48	9	489	91	378	70	111	21	159	30
1974	497	46	9	451	91	441	89	10	2	56	11
1975	518	49	9	469	91	398	77	71	14	120	23
1976	487	56	11	431	89	316	65	115	24	171	35
1977	399	74	19	325	81	271	68	54	14	128	32
Average	404	37	9	367	91	323	81	45	10	81	19

[1]Estimated from a partial 1967 survey, plus 1966 and 1968 data.

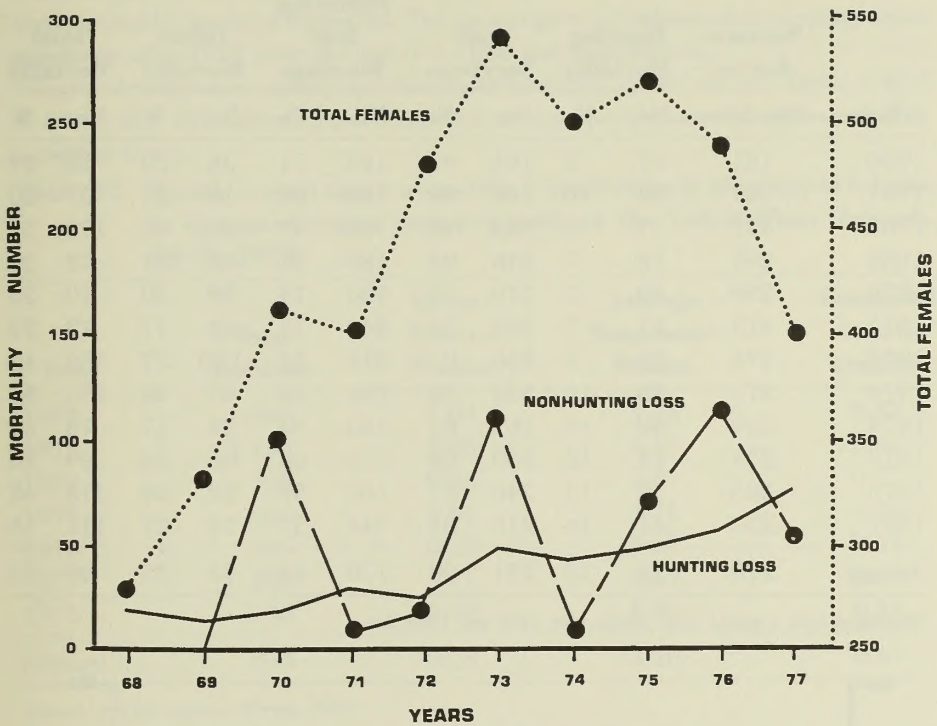


Figure 17. Trends in total numbers of adult females related to hunting and nonhunting mortality in the Yellow Water Triangle, 1968–1977.

Fawns.—Fawn mortality averaged 35%; 10% was due to hunting and 25% to winter (Table 21). Hunting mortality of fawns as a percentage of hunter harvest was underreported by questionnaire (3%) when compared to data from checking stations (20%). Winter mortality was high during severe conditions in 1968–1969 and 1971–1972 but increased as the population increased regardless of winter severity (Fig. 18).

Predation

Excessive predation by coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*) has been considered the cause of low and/or declining antelope populations in several western states. The greatest concern has been high predation on fawns.

The Yellow Water Triangle supported resident populations of all three predators during summer and additionally, migratory golden and bald eagles (*Haliaeetus leucocephalus*) during winter. Empirical evidence of predation was found on several occasions. Twice coyotes were observed chasing fawns; once the chase was unsuccessful and once the outcome was not observed. The feet of 2 fawns and a freshly killed and partially covered fawn were found in the Iverson pasture. Eaten carcasses were found on several occasions. One adult doe may have been killed by a bobcat, judging from the way loose hair was piled over the carcass. Harassment by eagles was often observed during winter.

Table 21. Mortality table for antelope fawns, Yellow Water Triangle, 1966–1977.

	Summer Survey	Hunting Mortality		Fall Survivors		Following Year Yearlings		Other Mortality		Total Mortality	
Year	No. Alive	No.	%	No.	%	No.	%	No.	%	No.	%
1966	181	17	9	164	91	128	71	36	20	53	29
1967[1]	181	18	10	163	90	144	80	19	10	37	20
1968	322	17	5	305	95	150	47	155	48	172	53
1969	266	18	7	248	93	188	71	60	23	78	29
1970	299	20	7	279	93	220	74	59	20	79	26
1971	313	21	7	292	93	240	77	52	17	73	23
1972	375	19	5	356	95	216	58	140	27	159	42
1973	371	36	10	335	90	238	64	97	26	133	36
1974	209	40	19	169	81	134	64	35	17	75	36
1975	273	34	12	239	88	174	64	65	24	99	36
1976	284	36	13	248	87	166	58	82	29	118	42
1977	257	41	16	216	84	146	57	70	27	111	43
Average	278	26	10	251	90	179	65	73	25	99	35

[1]Estimated from a partial 1967 survey, plus 1966 and 1968 data.

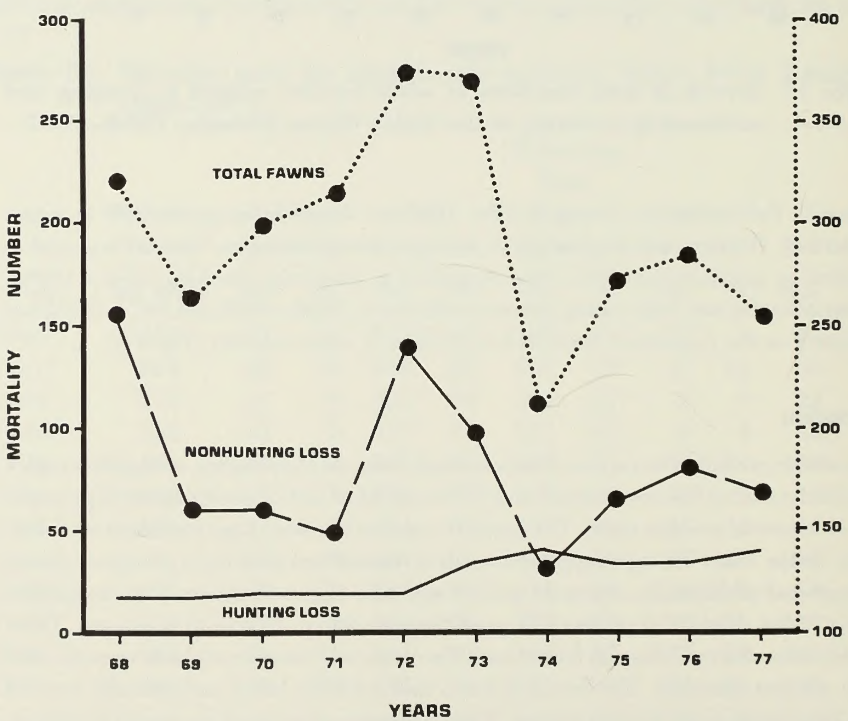


Figure 18. Trends in total numbers of fawns related to hunting and nonhunting mortality in the Yellow Water Triangle, 1968–1977.

The estimated average coyote density in the Yellow Water Triangle during 1972–1978 was 0.7/mi². Yearly densities ranged from 0.5 (1977) to 0.9 (1973) (Table 22). Probably less than half of this density was resident breeders; the others were juveniles, most of which probably dispersed during fall. The surveys gave no evidence of an erupting coyote population after 1972 when the use of C-1080 was discontinued.

Coyote density was positively correlated with antelope populations ($r = 0.88$, 5 df, $P < 0.01$) (Fig. 19), indicating that coyote and antelope populations reacted concurrently to habitat factors.

Table 22. Trends in total numbers and fawn production in antelope in relation to estimated coyote densities (mi²) on the Yellow Water Triangle, 1972–1978.

Year	Total Antelope	Fawns/ Mature Female	Average Responses/ Station	Estimated[1] Coyote Density
1972	1,086	1.04	3.95	0.83
1973	1,133	0.86	4.11	0.87
1974	938	0.56	3.47	0.73
1975	953	0.61	2.76	0.58
1976	941	0.71	3.47	0.73
1977	825	0.81	2.12	0.45
1978	733	0.88	2.50	0.53
Average	944	0.78	3.20	0.67

[1]Based on 67% response (Pyrah 1980).

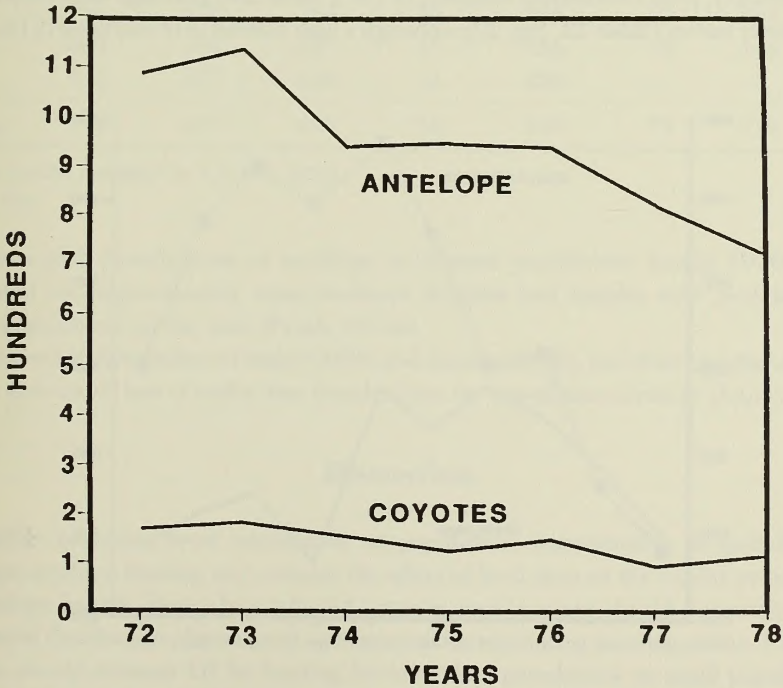


Figure 19. Antelope and coyote population trends, in the Yellow Water Triangle, 1972–1978.

The combined effect of predation by all three major predators may at times contribute to low fawn survival rates. However, antelope populations appear to follow cyclic patterns irrespective of coyote populations. The regularity of the cycles, both in time and magnitude, suggests that predator effects alone were minimal. A possible exception could occur during cyclic lows in antelope populations. The 1978 low of 733 antelope on the study area was higher than the 1966 low of 529, despite extensive antelope losses during the preceding severe winter. Predator control, as practiced during the 1960s with more sheep on the study area, apparently had little effect upon antelope population trends.

Recruitment

Recruitment was measured as the number or proportion of fawns of a given year (or cohort) surviving to 15 months of age; i.e., the second summer population survey after birth. As a proportion of the number of fawns potentially born, recruitment was low, averaging 31% during 1967–1978 (Table 23). The high was 43% in 1971, the low 19% in 1974. The average of 38% for years of general population increase (1967–1972) was significantly higher than the average 21% recorded for the 1973–1978 period of population decline ($t = 6.25$, 10 df, $P < 0.001$).

The low average recruitment rates were influenced largely by the apparent high neonatal mortality discussed earlier. Approximately two-thirds (average 65%) of the fawns counted in summer population surveys were subsequently recruited into adult populations. The range was from 47% (1969) to 80% (1968), the former reflecting high summer fawn survival followed by substantial winter loss during the severe 1968–1969 winter.

Numerically, peak recruitment occurred in 1972 when 240 yearlings were counted in the summer survey (Table 23, Fig. 20); although a high plateau in recruitment (216–240

Figure 20. Trend in numbers of yearlings recruited in relation to total numbers of adult female antelope in the Yellow Water Triangle, 1968–1977.

yearlings per year) extended from 1971 through 1974. It is noteworthy that the 240 yearlings of 1972 were produced by an adult female population of 292 on the area in spring 1971 (Table 23). The addition of up to 137 additional mature females to the population during 1972–1976 did not result in additional numbers of yearlings recruited. The high mature female segment remained in the population through 1976, 2 years after recruitment had dropped 20–30%.

Table 23. Numbers of yearling antelope recruited in relation to number of fawns produced and lost to various causes on the Yellow Water Triangle, 1966–1977.

Year	Potential Repro-duction[1]	Neonatal Mortal-ity	Summer Survey	Hunting Mortal-ity	Fall Survivors	Winter Mortal-ity	Recruit-ment[2] No.	%
1966	363	182	181	17	164	36	128	35
1967	378	197	181	18	163	19	144	38
1968	393	71	322	17	305	155	150	38
1969	488	222	266	18	248	60	188	39
1970	602	303	299	20	279	59	220	37
1971	555	242	313	21	292	52	240	43
1972	686	311	375	19	356	140	216	31
1973	815	444	371	36	335	97	238	29
1974	718	509	209	40	169	35	134	19
1975	857	584	273	34	239	65	174	20
1976	756	472	284	36	248	82	166	22
1977	600	343	257	41	216	70	146	24
1978	515	277	238	18	220	–	–	–
Average	594	320	275	26	249	72	179	31

[1]Mature females multiplied by 1.9 (Ellis 1972).
[2]1 year later

Counts and classifications of yearlings in summer populations during 1970–1973 indicated that approximately equal numbers of males and females were recruited into adult populations on the area (Pyrah 1973a).

The average distribution of males (36%) and females (64%), and their age classes indicate a more rapid loss of males than females from the population structure (Appendix D).

Discussion

Wildlife biologists need information on population characteristics as guidelines to manage antelope hunting and evaluate the effect of land uses on the quality or potential of antelope habitat. Properly conducted summer aerial surveys should accurately measure social distribution plus sex and age composition, including yearling males. A harvest survey should estimate kill by hunting for individual populations or small populations. These two surveys enable the manager to calculate density, production, recruitment, mortality, survival, and population trend.

Observed changes in numbers and densities in the past have been explained as being caused by severe winters and/or droughty summers. Yet the severe winters in 1968–1969 and 1971–1972 did not have catastrophic antelope mortality. However, winter conditions in 1964–1965 and 1977–1978 produced major antelope losses, leading me to conclude that severe winters only cause high mortality to higher declining antelope populations.

Droughts appear to have a similar variable effect. Antelope numbers climbed to high populations during below average rainfall in 7 of 8 years of 1949–1956 and again when 3 of 5 years were below average during 1960–1964. Only during the 1970s has an increasing population accompanied above average annual precipitation. The same generalization might apply to droughts and severe winters alike, they produce major mortality only at high populations.

Although *crude density* (total number and total area) and *ecological density* (total number and occupied habitat) have value for some management analyses, *key density* of specific sex/age classes may be more important for other evaluations. Density of adult females appears to be a key density parameter of antelope herds. Intrasexual competition among females during the summer season appears to have the most effect on reproductive success.

Differences in densities of does and fawns among herd ranges were at least partially related to differences in carrying capacities as influenced by physical and vegetational characteristics and livestock grazing. The most apparent differences involved livestock use and range condition (see Habitat Use).

This antelope study yielded evidence supporting a "cyclic species" designation for antelope. Studies of antelope on other Montana ranges (Wentland 1972, Coop 1975) also suggested cyclic population trends. The recurring cycles appear to bear little relation to trends in vegetation production (as related to annual precipitation), periodic weather influences (wet and dry periods or severe winters), hunting, or predation. Several indicators implicate the antelope themselves, especially density of adult females, as a primary factor in the functioning of the cycle, suggesting a true cyclic behavior, not just a response to some other cyclic factor or phenomenon. Fawn:doe ratio inversity with doe density, higher adult mortality at higher adult density, increasing neonatal losses at high density, and significantly higher survival during "up" years than during "down" years parallel factors identified by Meslow and Kieth (1968) for snowshoe hare cycles in Alberta. These conditions indicate increasing intrasexual competition among adult females at low apparent densities ($< 5/mi^2$). Long term deer surveys in the Missouri River Breaks indicate population fluctuations of similar magnitude and time interval but at higher densities (Mackie 1970, Hamlin 1985).

Low fawn survival, or yearling recruitment, coupled with high adult mortality, in effect bring about the cycle downturn. Thus, antelope populations were apparently controlled by neonatal mortality, recurrent adult female mortality, and mortality of fawns and adult males due to severe winter weather and high populations.

Both fawn:doe ratio and fawn density are useful parameters to assess reproductive success in antelope. The fawn:doe ratio is the more commonly used indicator of annual production; however, this ratio is biased by the inverse relation it shows to doe density. Samples of populations to obtain fawn:doe ratio have been misused to estimate herd production because varying fawn:doe ratios do not reflect herd production, only individual production. Herd production is the basis for determining the harvestable surplus from which hunting season permits are projected. Herd production can be determined by fawn density or by applying fawn:doe ratio to total females or doe density.

The recruitment plateau observed in this study appears to be another important management consideration. Reproduction is not completely successful until young are recruited into the adult population as yearlings. The cyclic highs and lows might be modified if adult females could be harvested at a rate more consistent with their recruitment and/or mortality, which would keep them at a density nearer the level of highest recruitment. This would require expanded use of sex/age-specific hunting permits instead of reliance on either-sex permits.

Another intriguing concept emerged with the evidence of 3-year mortality of adult females. No similar mortality pattern among ungulates was found in the literature. It has not been determined whether this situation occurs as a purely local problem or in other parts of Montana also. Most surveys cannot be reconciled due to either too much time between censuses or inaccurate counts and/or classifications. The regularity of the 3-year female mortality would lead to an assumption that it involves primarily female physiology.

The 3-year female mortality exerts a major effect on dynamics of does. Because the event does not happen every year, doe/fawn hunting permits may have to be issued in anticipation of the 3-year female mortality in order to avoid excess additive mortality after high natural mortality. Several times in the past high hunting mortality has added to already high natural mortality and reduced populations below desired levels. Compensatory mortality should be the attempted goal of doe/fawn harvests.

Wildlife management has traditionally supported removal of nonproducing males and protection of females to produce more young; a different philosophy is needed for antelope management in this area. Males compete less with females during summer than do females with each other. Some protection of males might increase the number of larger mature males available to either-sex permit holders without reducing the total harvest, and without increasing summer competition with females.

Although predators kill antelope, and especially fawns, their effect upon population trends appears to be negligible in this study area. Predation effects appeared to be secondary to density and habitat quality because antelope forage and possibly abundance of alternate prey were related to weather/vegetation and livestock grazing.

HABITAT RELATIONSHIPS

Habitat relationships of antelope involve food habits and range use. They are related to habitat requirements of the species, and to availability as influenced by natural environmental factors (e.g., topography, vegetation, weather, and climate) as well as land use (e.g., livestock grazing) and management practices (e.g., sagebrush control). The following discussions summarize findings in the Yellow Water Triangle and their possible implications with respect to theoretical concepts about habitat selection, habitat requirements, carrying capacity, and habitat continuum.

Food Habits

The food habits of antelope in the Yellow Water Triangle have been intensively studied through field observation, by recording plant use at feeding sites, and by analysis of ruminal contents (Cole 1956, Bayless 1967, Wentland 1968, Roberts 1970, and Becker 1972). Data from these studies show great variation in the kinds and amounts of different food plants eaten between years and periods of years.

Collectively, antelope use has been recorded on 124 plant species, including 96 forbs, 14 shrubs, and 14 grasses (Appendix E). By eating such a wide variety of plants, antelope are able to occupy and utilize nearly all of the habitat available. They also have been able to adapt to a wide range of vegetational changes and differences in availability associated with natural environmental variations, as well as livestock grazing and other land uses. Generally, forbs are eaten where and when they are available, especially during wet years; shrubs receive higher use when forbs are not available and during dry years.

Seasonal changes in diet are shown in Figure 21. Shrubs (primarily sagebrush) are used almost exclusively from November through March and moderately through the other months. Grass has its highest use during April with minor amounts eaten during most other months.

Forbs comprise the primary summer forage and are the "production" plants for antelope in the Yellow Water Triangle. As noted earlier, fawn survival was highest in years when forbs were abundant and remained green throughout the summer. Leaves, buds, flowers, and young stems of these plants are succulent, have high protein content, and are easily digested during the growing season. Important species in summer food habits include alfalfa (*Medicago sativa*), sweetclover (*Melilotus* spp.), three-leaved milkvetch (*Astragalus gilviflorus*), western yarrow (*Achillea millefolium*), American vetch (*Vicia americana*), goatsbeard (*Tragopogon dubius*), prickly lettuce (Lactuca serriola), dandelion (*Taraxacum officinale*), prairie clover (*Petalostemon* spp.), and asters (*Aster* spp.). Most of these occur in relative abundance in some localities.

The low average amounts of forage taken from many forb species results from low availability and short preference period, giving biased appraisal of their importance. Flowering stages of phenology usually cover short time periods and this appears to be the stage when they are most palatable. Perennial forbs as a class make up less of the plant commu-

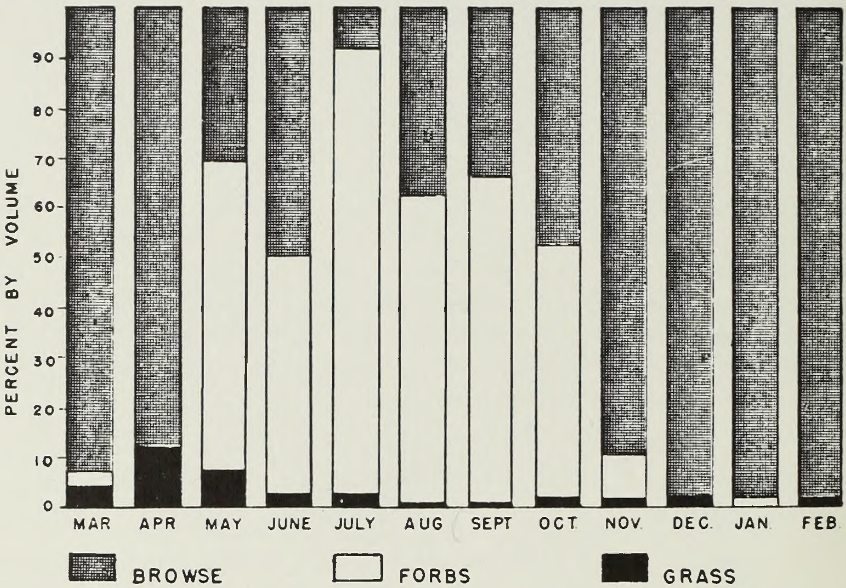


Figure 21. Forage class use by months as indicated by volume percentages of antelope rumen samples (from Cole 1956).

nity than either shrubs or grasses; yet, many more species occur, each flowering for a short time during the spring-summer-fall period. Figure 21 could indicate that forbs have low palatability during dormant stages. There is much more to learn about antelope summer food habits because of the great diversity of species eaten and their low densities. Annual forbs, other than those listed, appear to receive little use by antelope or their life cycle is short and use on these plants has been missed.

Shrubs and half-shrubs are "survival" plants and the primary winter forage for antelope in central Montana. Production in shrubs varies less with annual precipitation. They remain green throughout summer and contain more woody fiber than forbs, but they are not grazed heavily by livestock. Wyoming big sagebrush is the most widely used forage during 8 fall-spring months. Rabbitbrush (*Chrysothamnus nauseosus*) and silver sagebrush (*A. cana*) are less abundant but are used consistently during fall and winter. Rose (*Rosa* spp.) and snowberry (*Symphoricarpus* spp.) are important summer forages.

Several half-shrubs have also been identified as important antelope foods. Cudweed sagewort (*A. ludoviciana*) was important during the mid-1950s (Cole 1956) but received less use in all recent studies. It may have been more prevalent on the area during the 1950s as a result of previous grazing practices (i.e., more sheep grazing). Cudweed sagewort is a nonlegume with nitrogen-fixing bacterial root nodules (Farnsworth and Hammond 1968). Fringed sage (*A. frigida*) received heavier use during recent studies than during Cole's study. Longleaf sage (*A. longifolia*) and prickly pear cactus (*Opuntia polycantha*) were eaten occasionally during each study period.

Grasses, especially bluegrass (*Poa* spp.), provide important spring and fall forage during green-up (Roberts 1970, Becker 1972). However, they consistently comprise a small part of the total antelope diet, except during early spring before vernal forbs emerge. Cole (1956) found major changes in diets from shrubs in March to grass in April to forbs during May. The degree of fall green-up (plus livestock competition) determines the extent of grass use during the change from forbs to grass to shrubs. During dry years the fall transition is predominantly from forbs to half-shrubs to shrubs.

Range Use

Summer and Winter Habitats

Sagebrush types made up the main winter and summer habitat for antelope in the Yellow Water Triangle (Fig. 22). Selection for ARTR types was indicated by Use Index (UI) values over 1.0. Collectively, ARTR habitat groups (ARTR/AGSP, ARTR/AGDA, ARTR/SAVE) had a UI of 1.33 for summer and 1.51 for winter, representing 84% of all summer observations and 95% of all winter observations on 63% of the habitat area.

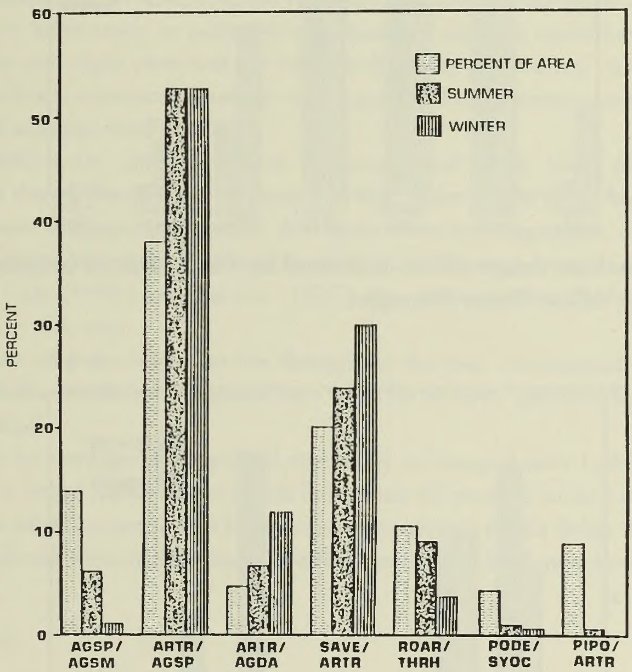


Figure 22. Percentages of total antelope observed seasonally using various habitat groups relative to percentage of the total area covered by each type in the Yellow Water Triangle.

The ARTR/AGSP habitat group provided primary habitat for antelope, covering 38% of the study area and accounting for 53% of the observed use (UI = 1.40) (Figs. 22, 23). Within this group, antelope used ARTR/BOGR and ARTR/AGDE at higher UIs than the ARTR/AGSP type (Fig. 24); ARTR/BOGR and ARTR/AGDE prevailed on areas of level topography, which antelope may prefer for high security (i.e., easier to run). These types also included disturbed communities in which some preferred antelope forages (e.g., sweetclover) commonly occurred. The ARTR/AGSP type characteristically occurred on steeper topography where disturbance or grazing impact was minimal.

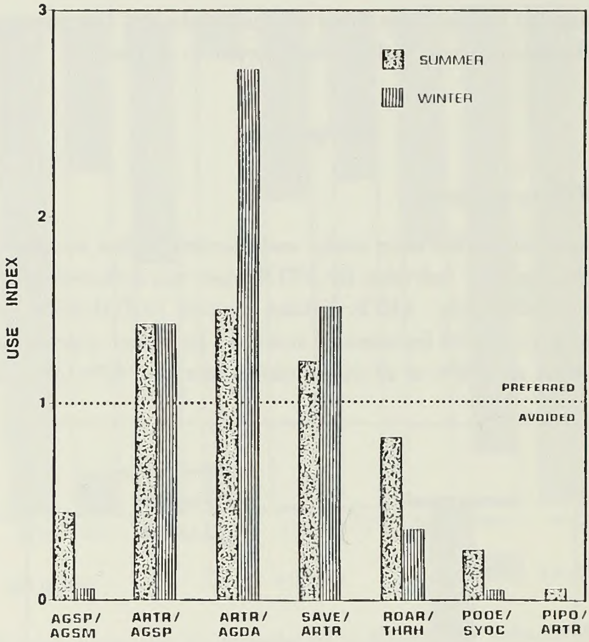


Figure 23. Antelope range use, as indicated by Use Index, of habitat groups in the Yellow Water Triangle.

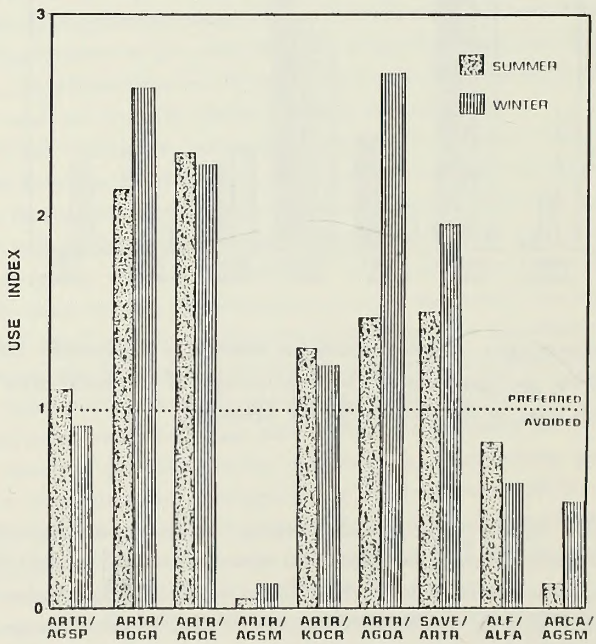


Figure 24. Antelope range use, as indicated by Use Index, of various habitats in the Yellow Water Triangle.

ARTR/AGDA type had the highest UI, with highest preference indicated during winter (Fig. 24). This type occurred on only 5% of the area and other factors may have been responsible for the apparent preference.

ARTR/SAVE typically occurs on level terrain in valley bottoms. It is usually adjacent to mesic vegetation (including alfalfa) during summer-fall and to ARCA/AGSM during winter. Both inclusions provide preferred antelope forages that may bias the use attributed to ARTR/SAVE.

The higher UIs for ARTR/AGDA and ARTR/SAVE do not appear to be related to better food and cover within these types; however, both have higher bare ground coverages than other types (Jorgensen 1979). This, together with level terrain, may function in providing high security during summer by having low cover and open visibility, and during winter by wind-blown, snow-free areas.

The ARTR/AGSM and ARCA/AGSM types covered small areas (each 2% of the area). However, their importance or potential importance to antelope could have been greater than their size and slight observed use would indicate. Both occurred on mesic meadows and swales, where consistently heavy livestock grazing during summer may have reduced or prevented antelope feeding.

Use of alfalfa fields, although low on a seasonal and yearly basis, fulfills important forage needs during the dry late summer and fall. Many alfalfa fields are on mesic bottomlands where antelope traditionally find more succulent vegetation; others are artificially mesic due to irrigation. Antelope feeding on alfalfa seed crops cause conflict with landowners. Cole (1956) and Bayless (1967) also noted late summer-early fall use of alfalfa fields in this area.

Antelope use of grain fields was low throughout the year. Occasionally antelope were observed in fallow fields but this could have been for security provided by the surrounding bare ground.

Habitat use by antelope has remained essentially unchanged since Cole's (1956) study. Although Cole found higher use of alfalfa fields than the present study, his study focused on damage to alfalfa crops and included only areas around alfalfa fields. The differences could also indicate some improvement in upland vegetation leading to lower use of alfalfa fields.

Key Pastures

Pastures that received high seasonal antelope use were classified as "key pastures" (Fig. 25). Several additional pastures used predominantly during late summer were also identified as key pastures. Though used less heavily on a full season basis, the latter were critical to the continued existence of herds or herd segments.

Sixty-five percent of all pastures on the study area were used by antelope during summer (Table 24). Only about one-third of those (23% of the total) received use exceeding 10% of the total observations of antelope during summer. The remainder received only minor or occasional use.

Winter use of pastures by antelope was restricted; only 25% of all pastures on the area were used and 14% had use exceeding 10% of all antelope observed in winter. Use of the other 11% of the pastures was relatively minor or occasional (Table 24).

The average doe band area included 3 pastures (63 pastures/22 doe bands) on which the band was observed most often during summer. In winter, high use occurred on an average of 2 pastures per doe band (39 pastures/22 doe bands) (Table 24). Some key pastures were important for more than one doe band. For example, some pastures

Table 24. Observed antelope use of key pastures[1], Yellow Water Triangle, 1968–1973.

			Summer Use					Winter Use				
			Pastures	Antelope	Percent of Use			Pastures	Antelope	Percent of Use		
Herd	Band	Pastures	Used	Observed	>10	<10	0	Used	Observed	>10	<10	0
I	A	22	8	154	5	3	14	2	44	2		20
	B	19	3	53	3		16	1	24	1		18
	C	25	10	85	3	7	15	1	5		1	24
	Subtotal	66	21	292	11	10	45	4	73	4		62
II	A	11	10	988	3	7	1	2	192	2		9
	B	16	14	1,891	3	1	2	1	571	4	7	5
	C	8	7	616	3	4	1	4	333	2	2	4
	Subtotal	35	31	3,495	9	22	4	17	1,096	8	9	18
IV	A	10	7	1,240	3	4	3	4	970	1	3	6
V	A	12	9	820	3	6	3	6	151	3	3	6
	B	21	19	867	3	16	2	7	702	3	4	14
	C	27	14	1,155	2	12	13	1	147	1		26
	D	11	11	388	3	8	0	5	176	3	2	6
	Subtotal	71	53	3,230	11	42	18	19	1,176	10	9	52

Table 24. *(Continued).*

Herd	Band	Pastures	Summer Use					Winter Use				
			Pastures Used	Antelope Observed	Percent of Use			Pastures Used	Antelope Observed	Percent of Use		
					>10	<10	0			>10	<10	0
VI	A	6	6	1,025	3	3		6	1,342	2	4	
	B	7	5	670	2	3	2	1	1,003	1		6
	C	8	8	909	2	6		3	453	2	1	5
	D	4	1	207	1		3	1	461	1		3
	E	14	11	538	2	9	3	4	151	2	2	10
	F	15	13	217	3	10	2					15
	G	21	6	103	4	2	15					21
	Subtotal	75	50	3,669	17	33	25	15	2,410	8	7	60
VII	A	4	3	570	3		1	3	1,233	3		1
	B	6	5	314	3	2	1	3	61	2	1	3
	C	9	9	415	3	6		1	22	1		8
	D	3	3	839	3			3	629	2	1	
	Subtotal	22	20	2,138	12	8	2	10	1,945	8	2	12
Totals		279	182	14,064	63	119	97	69	8,670	39	30	210
			65%		23%	43%	35%	25%		14%	11%	75%

[1]Pastures with >80 acres in the doe band area.

included 2 parcels of rangeland separated by a drainage and used by separate doe bands or herds.

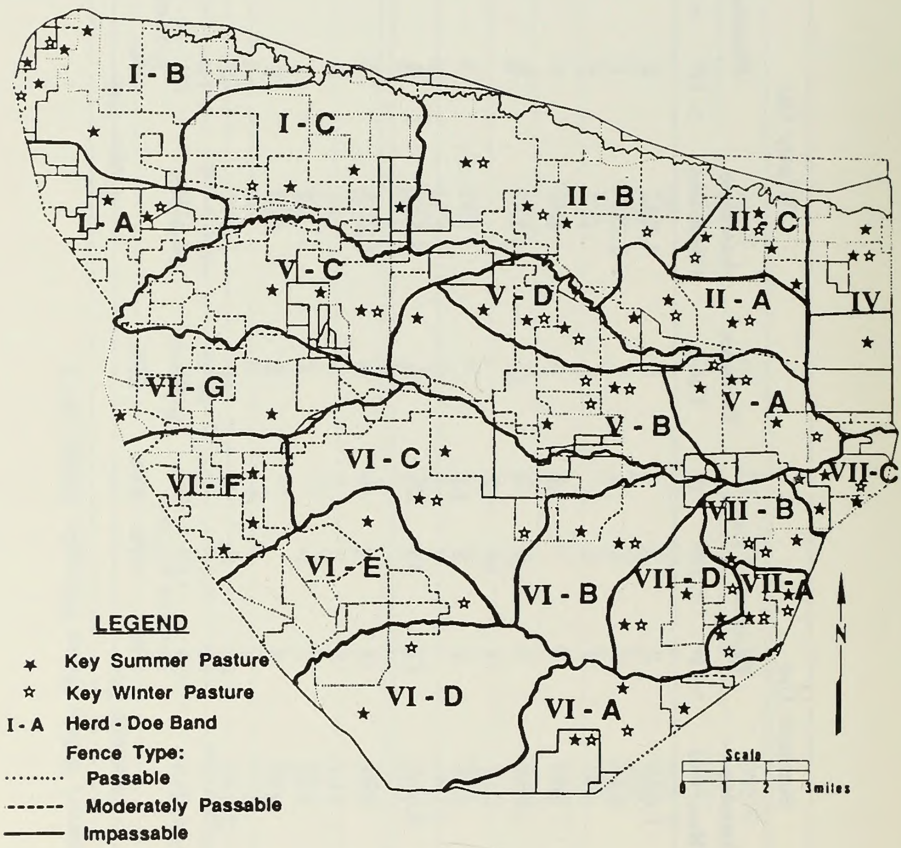


Figure 25. Key summer and winter pasture for use by antelope on Yellow Water Triangle.

Fawn Bedding Cover

General observations indicated: 1) pregnant does tended to select dense sagebrush during isolation and fawn bearing (Fig. 26); 2) sagebrush, or minor topographic relief, provided good concealment of fawns < 3 weeks old; and 3) lactating does frequented sagebrush stands having good cover during the early fawn-rearing period.

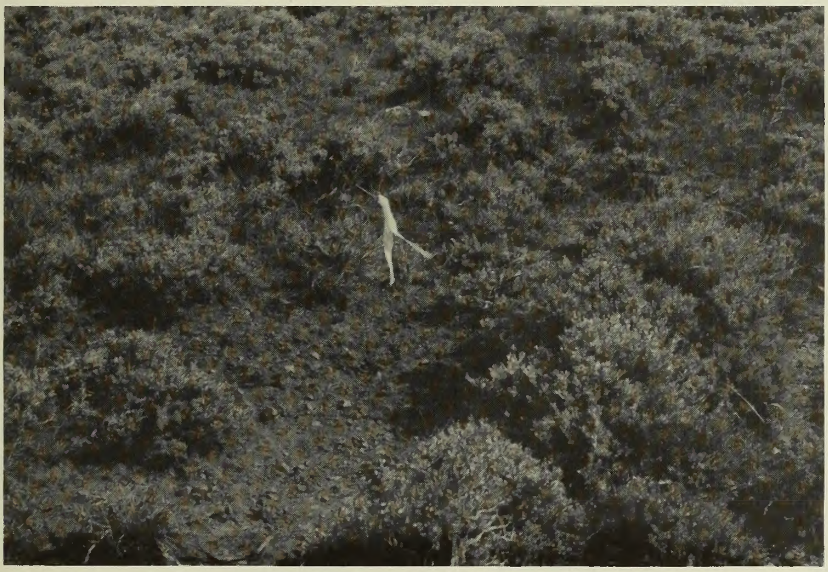


Figure 26-A. Aspect of fawn birth site in ARTR/BOGR type in the Iverson treatment area, 31 May 1973. Canopy coverage: live sagebrush 39%, dead sagebrush 2%, grass 28%, forbs 4%, and total 71%. Cover volume: sagebrush 25 ft^3-, grass 8, forbs 1, and total 34.

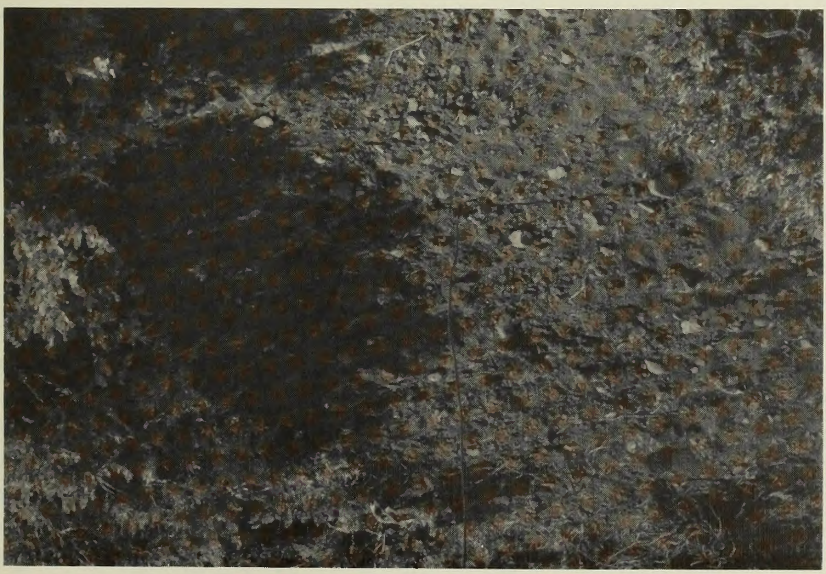


Figure 26-B. Close-up view of Figure 26-A.

Vegetational cover was measured near 85 fawn bedding sites during the 1972 and 1973 fawning seasons. Average canopy coverage was 21% sagebrush, 32% grass, 14% forbs, and 67% total. Average cover volume was 16 ft^3 sagebrush, 14 ft^3 grass, 4 ft^3 forbs, and 34 ft^3 total (Table 25). Vegetation classes, particularly sagebrush and grass, apparently were complementary in providing fawning cover; decreases in one class at a bedding site were often compensated by increases in the other, making average total cover relatively more uniform.

Table 25. Canopy coverage (%) and cover volume (%) at 85[1] fawn bedding sites, Yellow Water Triangle, 1972–1973.

Vegetation Cover Class	Height Class	Canopy Coverage X[2]	Canopy Coverage SD[2]	Cover Volume X[2]	Cover Volume SD[2]
Sagebrush-Live	1	4.6	3.8	1.2	0.8
	2	12.4	7.0	9.4	5.4
	3	3.8	3.5	4.8	4.3
	4	0.3	0.9	0.8	2.2
	Subtotal	21.2	10.1[3]	16.1	9.0[3]
Grass	1	20.7	12.5	5.2	2.8
	2	10.4	8.1	7.9	6.0
	3	0.9	1.6	1.1	1.8
	Subtotal	32.0	11.7[3]	14.1	6.5[3]
Forbs	1	11.3	7.3	2.8	1.8
	2	2.1	3.5	1.6	2.6
	3	T	–	T	–
	Subtotal	13.5	8.2[3]	4.4	3.3[3]
Total		66.7	17.6[3]	34.6	10.4[3]

[1]Grass and forb cover not measured on 12 ARTR/BOGR sites

[2]X = mean, SD = standard deviation

[3]Average of 2 years, calculated separately

Sagebrush was the most stable year-to-year cover element. Shrubs and grasses were used over a fairly wide range of coverage values, indicating flexibility in habitat use by antelope. The ranges in canopy coverage and cover volume that appeared suitable for fawning were, canopy cover: sagebrush 5-35%, grass 15-40%, forbs 0-30%, and total 50% or greater; and cover volumes: sagebrush 5-25 ft^3, grass 5-25 ft^3, forbs 0-10 ft^3, and total 15-50 ft^3 (Table 26).

The ARTR/AGSP habitat group accounted for 82% of the bedding sites observed. Within this group, ARTR/BOGR cover type (UI = 3.6) was preferred (Table 27), although part of the preference may be related to level topography. Little ground cover occurred in the ARTR/SAVE and ROAR/THRH cover types, which might explain their light use.

Significantly greater canopy coverage ($P < 0.05$) and cover volume of sagebrush ($P < 0.05$) was measured at bedding sites in the ARTR/BOGR type than in ARTR/AGSP (Table 28). Significantly greater cover volume ($P < 0.05$), but not canopy coverage, of grass and forbs occurred at bedding sites in the ARTR/AGSP type. Total canopy coverage and cover volume did not differ significantly between types, reflecting some compensation among the sagebrush, grass, and forb classes.

Table 26. Percent frequency distribution of canopy coverage and cover volume (ft^3) at 85 fawn bedding sites, Yellow Water Triangle, 1972–1973.

	Canopy Coverage				Cover Volume			
Class[1]	Sage	Grass	Forbs	Total	Sage	Grass	Forbs	Total
0 - 5	2	0	10	0	9	3	71	0
5 - 10	10	3	31	0	21	38	23	0
10 - 15	22	3	10	0	22	27	5	2
15 - 20	24	7	17	0	13	19	1	7
20 - 25	12	17	14	0	24	5		12
25 - 30	15	14	14	0	5	3		12
30 - 35	10	17	3	4	4	3		26
35 - 40	2	7	4	1	1			14
40 - 45	2	10		4				13
45 - 50	14		7	1				10
50 - 55		7		14				0
55+				68				2

[1]Classes are from 5.1 - 10, 10.1 - 15, etc.

Table 27. Distribution of 85 fawn bedding sites by habitat or cover type as related to availability, Yellow Water Triangle, 1972–1973.

	Availability	Bedding Sites		Use
Type	(%)[1]	No.	%	Index
ARTR/BOGR	12.5	40	47	3.8
ARTR/AGDE	3.0	3	4	1.3
ARTR/AGSP	28.0	26	31	1.1
ARTR/AGDA	6.0	7	8	1.0
ARTR/SAVE	17.0	7	8	0.6
ROAR/THRH	13.0	2	2	0.2

[1]Percentage of antelope habitat (138,071 acres)

Table 28. Comparison of ARTR/AGSP and ARTR/BOGR fawn bedding sites by canopy coverage (%) and cover volume (ft^3) of cover classes, Yellow Water Triangle, 1972–1973.

Method	Type	No. Sites	Sage	Grass	Forbs	Total
Canopy Coverage						
	ARTR/AGSP	26	18.2	31.5	13.7	63.6
	ARTR/BOGR	40	24.4	31.0	10.7	66.4
	Both	66	21.9	31.3	12.2	65.0
Cover Volume	ARTR/AGSP	26	13.5	16.7	4.8	35.2
	ARTR/BOGR	40	18.6	9.8	2.8	30.1
	Both	66	16.6	13.2	3.8	33.0

Year-to-year differences in cover volume indicated significantly less grass, forbs, and total vegetation in 1973 than 1972 ($P < 0.05$). Canopy coverages of all classes and cover volume of sagebrush were not significantly different between years.

Collectively, the data indicated that antelope fawns selected more strongly for sagebrush than for other cover classes in the Yellow Water Triangle. Regarding habitat selection by birds, Thorpe (1949:86, in Hochbaum 1955:40) stated, "One can safely assume that quite apart from the recognition of a particular locality, birds can recognize the right *type* of environment for themselves. If this were not so, every year would find birds trying unsuccessfully to breed in all sorts of unsuitable places. This recognition of an environmental *type* may be very largely the result of experience, but it is in line with the modern concepts of instinctive behavior to assume that there may be an innate hereditary, primarily visual recognition of the right type of environment." This might also infer that the observed habitat of antelope fawns was the result of that innate ability to select the better bedding sites.

Grasslands made up approximately 22% of the total antelope habitat; however, grasslands and the ARTR/AGSP or ARTR/BOGR cover types without sagebrush were used only infrequently by young fawns. Older fawns, like adults, commonly used open grassland areas.

Older fawns were less selective for good bedding cover than younger fawns.
(Photo by: Montana Department of Fish, Wildlife and Parks)

Although vegetation measurement indicated that vegetation classes were somewhat complementary in providing fawn bedding cover, grass probably could not substitute totally for sagebrush. Sagebrush plants are better cover because they are taller, stronger, and carry dense foliage to higher levels than grasses. In many areas, residual grass cover is limited or absent due to the degree of previous season grazing by domestic livestock. New grass growth is in initial growth stages when fawns are being born. In the absence of sagebrush, fawns would be more vulnerable to losses by predation and unfavorable weather. Reductions in total cover would probably result in similar losses of fawns.

Effects of Sagebrush Control

Only two of the four sagebrush treatment areas, the King and Iverson areas (Fig. 27), received sufficient antelope use during the study to measure responses to sagebrush manipulation.

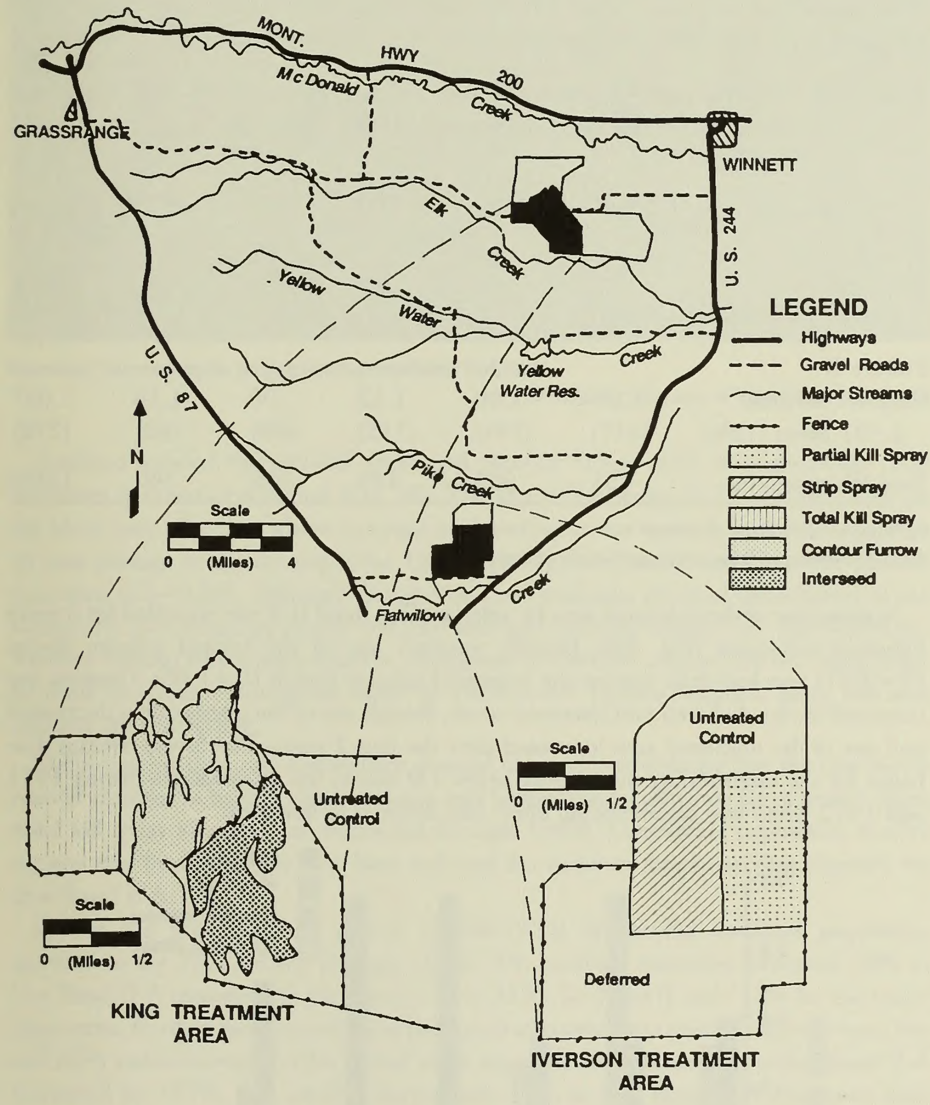


Figure 27. Locations of sagebrush treatment areas in the Yellow Water Triangle.

King Treatment Area

The treatment pasture was heavily used as winter range by Herd II prior to treatment during 1967–1968. It also comprised an important part of the summer range of Doe Band II-A.

Observations during the winter of 1966–1967 indicated over four times more antelope use in the pasture scheduled for treatment than in the untreated (grazed) control pasture (Bayless 1967). Following treatment, winter use of the treated pasture declined significantly (UI=2.21 to 0.97), while antelope use of the untreated pasture continued at or above the 1966–1967 level (UI=0.53 to 0.99). Overall, the untreated, grazed pasture was used more than the treatment pasture (Table 29). Winter antelope use in the treatment pasture was limited to areas with the least effect: deferred and interseeded. Total kill block spray and contour furrow treatments had negligible winter use.

Table 29. Comparison of antelope use indexes for treated and untreated pastures on the King Treatment Area, 1969–1972.

Treatment	1968	1969	1970	1971	1972	Use Index
Pasture A						
Treated	.88	1.00	.69	1.25	.55	.87*
1,057 acres(28%)	(104)	(74)	(27)	(37)	(15)	(257)
Pasture B						
Grazed Untreated	1.05	1.00	1.12	.90	1.18	1.05*
2,691 acres (72%)	(317)	(191)	(112)	(69)	(83)	(772)
Total Observations	421	265	139	106	98	1,029

( ) Number of antelope observed
*92% probability of these being significantly different.

Summer use of the treatment area by antelope Doe Band II-A was recorded for 5 years following treatment (Fig. 28). Overall, summer use of the treated pasture (mean UI=0.87) was less than that on the untreated pasture (mean UI=1.05). Greatest use occurred on the deferred and interseed areas, though use of the interseeding decreased and use of the ungrazed area increased after the first 2 years. The 5-year average Use Index for the interseeding was slightly below 1.0 due to few observations during 1971 and 1972 when less observational effort was directed to that area.

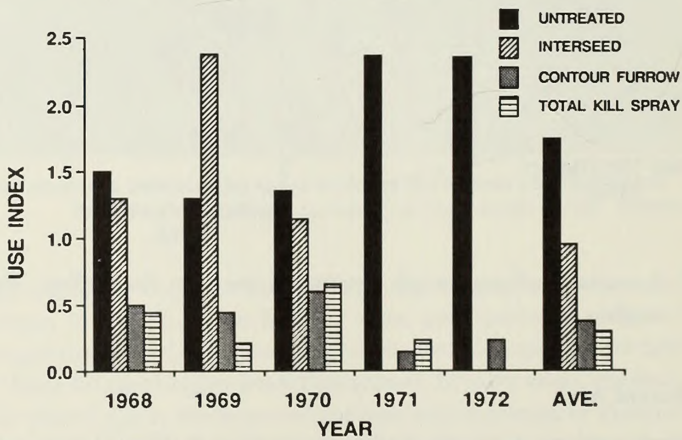
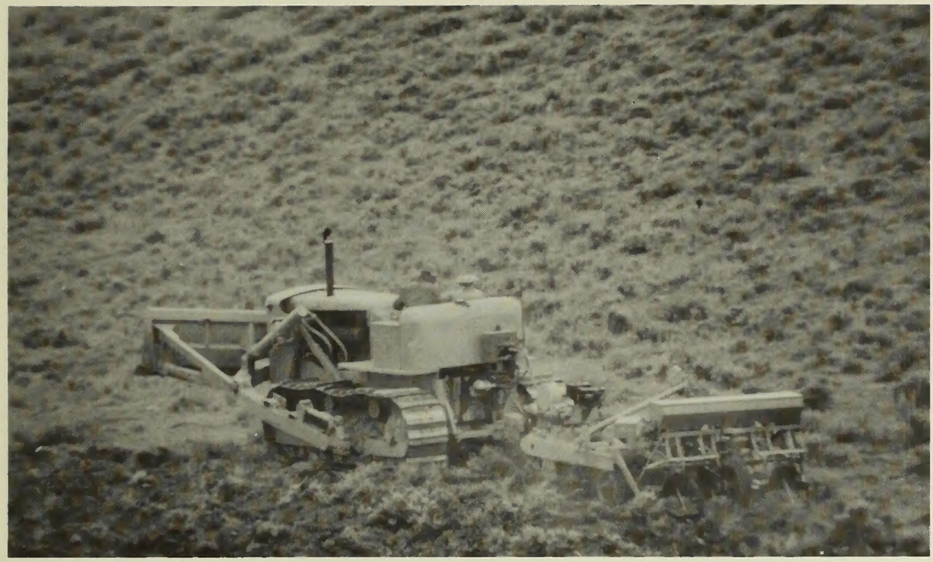


Figure 28. Annual and 5-year (1968–1972) average antelope use of various sagebrush treatments on the King Treatment Area.



Contour furrowing in Sagebrush-grassland habitat.
(Photo by: Bureau of Land Management)

Antelope avoided the total-kill spray and contour furrow areas throughout the post-treatment observational period (Fig. 28). The lowest Use Index (0.32) was recorded for the block total kill spray, where antelope food and cover was severely reduced by mortality and damage to shrubs and forbs. Only slightly greater use occurred on the contour furrowing (UI=0.38). Although forage remained available, physical disturbance of the surface by furrowing apparently reduced antelope mobility/security on that treatment. Another contour furrowing treatment, completed in 1968 on an area that had been heavily used by antelope during the winter of 1966–1967 (Bayless unpubl. data), was also avoided after treatment.

The foregoing data and subsequent general observations indicate that the treatments caused changes in habitat characteristics and habitat use by antelope for at least 7 years (total kill spray area had not recovered through 1985). Concurrent population studies suggest that these changes may have reduced the summer range carrying capacity for Doe Band II-A.

During the post-treatment period (1968–1973) of general antelope population increase in the Yellow-Water Triangle (Table 30), antelope numbers increased 58% in Doe Band II-A compared to increases of up to 313% for Herd II and 113% for the entire study area. Further, numbers of fawns produced or surviving to summer surveys were low and fairly stable throughout the period when numbers of adult females in Doe Band II-A increased by 107%. The average fawn:female ratio in Doe Band II-A was lower than ratios for Herd II and the Triangle as a whole.

It was noted earlier that fawn production was inversely correlated with density of adults; the highest correlations occurred on areas of lowest carrying capacity. The correlation coefficient for Doe Band II-A ($r = -0.83$) was significant ($P < 0.05$) and higher than coefficients for Herd II and the Triangle (Table 30). These data suggest that numbers of adult antelope in Doe Band II-A were above carrying capacity for the band area during most of the period. Although this does not clearly establish the treatments as the cause of population decline, it appears that some factor(s) had reduced the amount or quality of summer range within the band area as compared with Herd Range II and other areas.

Table 30. Aerial survey results for the Yellow Water Triangle, Herd II, and Doe Band 11-A in Summer, 1968–1974.

	Year	Numbers of Antelope Counted				Adult	Fawns per
		Males	Females	Fawns	Total	Density	Female
YWT	1968	118	202	233	533	1.50	1.15
212.9	1969	123	316	253	692	2.06	.80
mi²	1970	150	411	299	860	2.64	.73
	1971	203	382	291	876	2.75	.76
	1972	230	481	375	1,086	3.34	.78
	1973	225	537	371	1,133	3.58	.69
	1974	240	474	199	913	3.35	.42
				Fawns/female:adult density r = −.7820*			
Herd II	1968	9	31	29	69	1.48	.94
27.0	1969	26	38	35	99	2.37	.92
mi²	1970	35	72	59	166	3.96	.82
	1971	40	60	41	141	3.70	.68
	1972	67	124	94	285[1]	7.07	.76
	1973	53	89	52	194	5.26	.58
	1974	65	91	36	192	5.77	.40
				Fawns/female:adult density r = −.6668			
Doe Band II-A							
5.7	1968	5	14	12	31	2.18	.86
mi²	1969	9	4	4	17	1.49	1.00
	1970	12	19	13	44	3.56	.68
	1971	2	17	9	28	2.18	.53
	1972	10	26	12	48	4.14	.46
	1973	10	29	10	49	4.48	.46
	1974	21	11	6	38	3.56	.54
				Fawns/female:adult density r = −.8269*			

*Correlation coefficient (r) significant at 95%.

[1]Possibly an overcount; 233 total count on a separate flight.

The comparatively large increase in Herd II during 1968–1972 indicated that habitat changes or losses in the treatment pasture did not seriously affect winter range characteristics and relationships of antelope in the area. This implied that the amount of area treated, to the extent that winter forage or forage use was reduced, comprised only a small part of the total winter range of the herd, and perhaps minimal losses were readily compensated. It could also imply that the amount and quality of winter habitat and forage available were less limiting to antelope on the area than summer range and forage. Given the forage and other habitat requirements of antelope on the area, however, it seems unlikely that loss or severe alteration of any great amount of winter range in a favored location would not reduce carrying capacity.

Iverson Treatment Pasture

Post-treatment (1968–1972) observations of habitat selection and use by antelope confined to this pasture indicated that the untreated area and strip partial kill spray area were preferred. Antelope Use Indexes for the partial kill strip treatment were consistently higher than those for the partial kill block treatment, indicating the former was preferred. Antelope Use Indexes were highest on the untreated area during 3 of the 5 years (Fig. 29), including the last 2 years of observation. This suggested a general shift to greater use of the untreated area after 1970; however, high antelope Use Indexes recorded for 1968 and 1970 were attributed largely to antelope behavior and attempts to return to previously-used habitat adjacent to the treatment pasture.

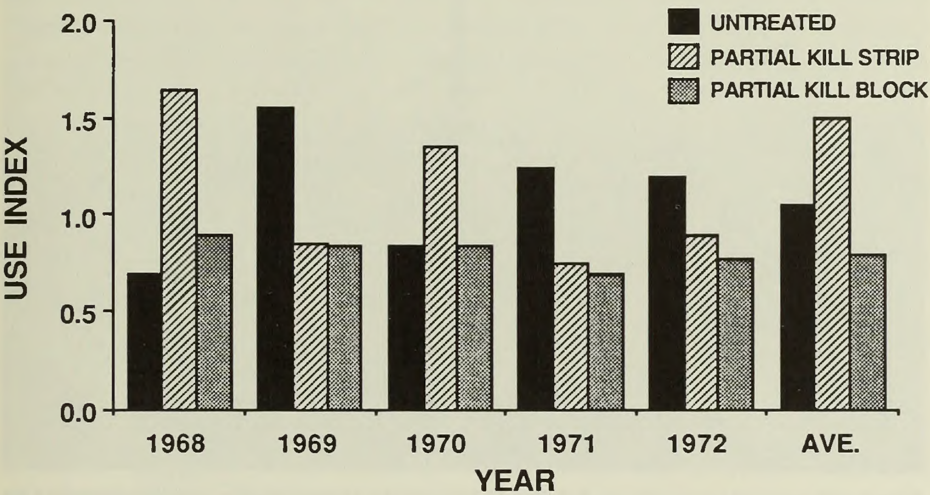
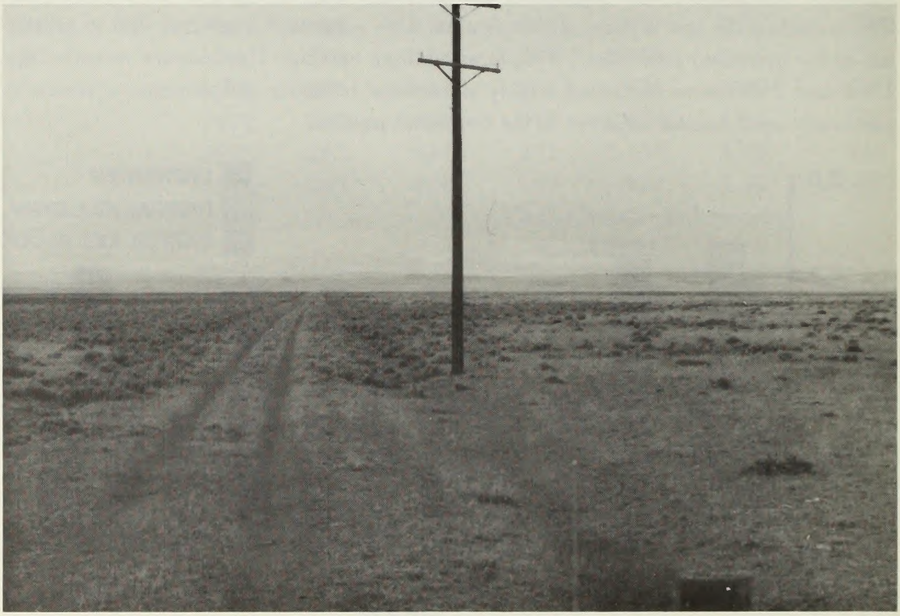


Figure 29. Annual and 5-year (1968–1972) average antelope use of various treatments on the Iverson Treatment Area.

Data for the Iverson pasture suggest that strip spraying for partial kill of big sagebrush would be less detrimental to antelope habitat values and use than partial kill in blocks. Strip spraying for partial kill is generally considered impractical or uneconomical because of less increase in livestock forage (less area treated) in relation to investment (costs of spraying, deferment of grazing). However, this treatment left one-half of the habitat in essentially the original condition and did not significantly reduce the total amount of sagebrush-grassland habitat available to antelope. When applied with proper grazing management, it could be useful for speeding recovery of rangeland forage species with less impact on wildlife than other spray treatments. Both partial kill treatments were less detrimental to antelope habitat characteristics and use than the total kill spray and contour furrowing treatments on the King Treatment Area.

Effects of Fire

Reduction in the use of herbicides for sagebrush control has increased interest in other methods, notably controlled burning. Although the effects of fire were not specifically studied, observations of sagebrush reinvasion of old burns on the study area indicated that fire has a devastating and enduring effect on antelope wintering and fawning habitat. Rangeland burned in the Carey Act Fire of 1936 (Sibbert treatment area) continues to have only limited sagebrush coverage, and the Winnett Railroad Fire of 1940 includes large expanses of grassland where sagebrush has not reinvaded. More recent burns, including the Sibbert Fire (1960) and the Bratten Fire (1971) also show little reinvasion of sagebrush. Eichhorn and Watts (1984) reported slow sagebrush reinvasion on burns in other areas of central Montana.



Sagebrush burned by the Carey Act Fire of 1936 (right of trail) shows sparse reinvasion by that species 50 years later. *(Photo by: Author)*

These observations indicate that fire removes most sagebrush from extensive areas and reinvasion is a lengthy process, probably due to winter drought coinciding with sagebrush germination (Thomas pers. comm.) With 20% average canopy coverage of sagebrush required at fawn bedding sites, most burns on the area do not offer suitable habitat at this time, and may not for many years. The use of fire, therefore, must be viewed very critically from a wildlife standpoint. If burning is used in sagebrush control, it should be applied carefully in scattered locations or under conditions where complete kill of sagebrush over extensive areas is unlikely. Fire removes the antelope forage supply (sagebrush) over the burn area. Antelope were observed on recent burns (e.g. Bratten Fire in 1971); however, this selection may have indicated a security choice because most foraging occurred in unburned adjacent sagebrush.

Effects of Livestock Grazing

Livestock grazing in the Yellow Water Triangle in recent years has consisted mainly of cow-calf, cattle operations, with some yearlings and 2-year-old steers. Sheep grazing, which historically dominated, began to decline during the early 1940s, with most of the remaining sheep herds sold during 1968 and 1970. The latter allowed antelope in Herd II to expand their range into Herd Range I. Current summer grazing by sheep has been restricted to areas with low antelope use throughout the study; sheep grazing could be a cause of the low antelope use. Antelope avoided areas grazed by sheep during summer as has been reported by Buechner (1950), Campbell (1970), and Freeman (1971). However, winter sheep grazing with no summer grazing permitted the highest density and production by Doe Band IV-A.

Throughout the year antelope generally avoided concurrent pasture use with cattle. For the 3 years of study, an average of 71% of 9,530 antelope distribution sightings occurred in pastures without cattle present at the time of the observation (Fig. 30). The yearly averages ranged from 64% in 1970 to 73% in 1972; this variation probably reflected annual changes in the abundance of favored antelope foods within grazed pastures. The extent of association between antelope and cattle in pastures varied monthly through spring and summer (Fig. 30). Antelope shared pastures with cattle at the lowest level (5%) during April. Presumably, this low association level prevailed from November to April when livestock were absent from public lands and private summer pastures. By April, antelope had dispersed from winter herds but continued to use largely the same public land habitats as used during winter. Livestock were largely confined to winter-spring pastures on private land until May, when cattle were transferred to spring and/or summer pastures and the extent of concurrent use of pastures increased sharply. By then, antelope had become established on certain feeding/fawning areas, and fawning usually occurred before competition forced them to move. Antelope were also most widely dispersed, seeking isolation for fawning, during mid May to early June.

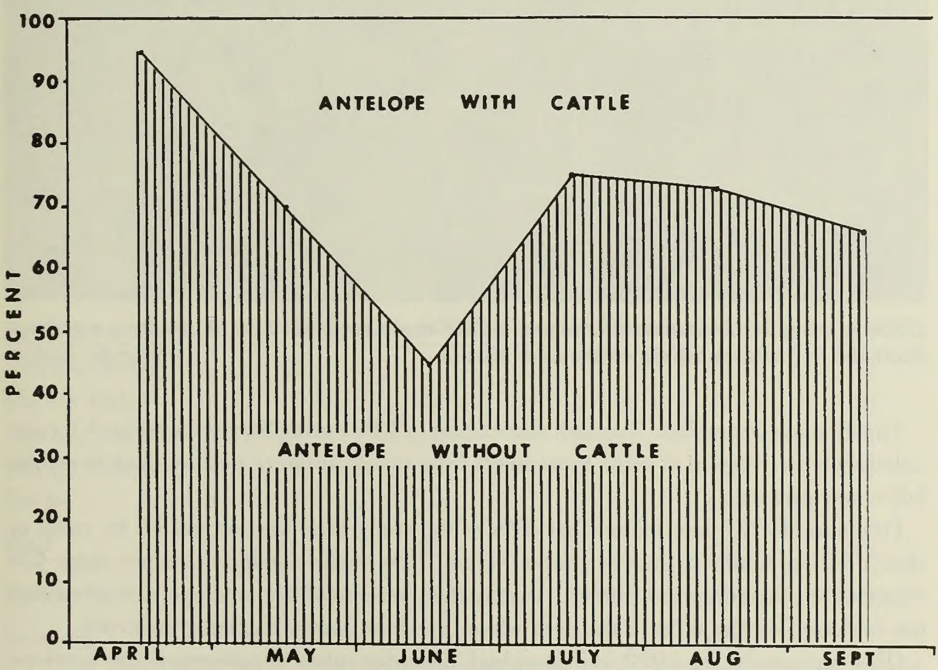


Figure 30. Percentages of total antelope observed monthly in pastures with and without cattle on the Yellow Water Triangle. Data are for 9,530 antelope observed during 1970–1972.

During June, antelope mixed with cattle at the highest rate (56%) due both to continuous widespread distribution of antelope in fawning/fawn rearing and the general availability of preferred summer forage (Pyrah 1972).

The primary growing season for upland plants in the Yellow Water Triangle extended typically from 1 May to 15 June. Plant succulence on uplands after 15 June depended upon timing and amount of spring-summer rainfall as well as lateral sub-surface movement of moisture to lowland sites. Grasses and shrubs remained green longer than forbs. Gravitational movement of subsurface soil moisture into lower sites kept vegetation green in swales and coulee bottoms which became increasingly important food sources for cattle. Mesic rangeland sites exposed to continuous cattle grazing rapidly became unusable by antelope. Kitchen (1974) found wet weight of forage correlated best with antelope use areas during late summer indicating their dependence on mesic sites on the National Bison Range. Out-competed in the swales and with upland vegetation desiccated, antelope moved into adjoining pastures (or hayfields if present) not occupied by cattle during summer. Antelope-livestock association declined sharply to 25% in July and 27% in August.

Cattle grazing is the dominant land use on the study area, yet 71% of antelope sightings occurred in pastures where cattle were absent. *(Photo by: Author)*

The increase in antelope-livestock association to 33% during September (Fig. 30) coincided with the reversal of cattle movements from public summer pasture back to private fall-winter pasture.

Freeman (1973) determined that 39% of the study area was not grazed by cattle or sheep during summer; thus in general terms, 71% of the antelope summer range use occurred on this ungrazed portion. Twenty-nine percent of the antelope summer range use occurred on the 61% of the area where livestock summer grazing occurred.

Observations during 1970 indicated high fawn:doe ratios in pastures where antelope were not currently competing for forage with cattle. For 1,406 antelope observations, there were 0.82 fawns/doe in pastures occupied by antelope and cattle and 0.92 fawns/doe in pastures occupied by antelope alone (Table 31).

Table 31. Numbers of antelope counted and sex and age ratios in pastures with and without concurrent cattle use in the Yellow Water Triangle, 1970.

Date:	No. Obs.	Male No.	Male %[1]	Female No.	Female %[1]	Fawn No.	Fawn %[1]	Uncl.	Total No.	Total %	Males: Female	Fawns: Female
1 July–22 September												
W/Cattle	64	108	28	151	39	124	32	38	421	30	.72	.82
WO/Cattle	117	178	19	385	42	356	39	66	985	70	.46	.92
Subtotal	181	286	22	536	41	480	37	104	1,406		.53	.90
9 June–22 September												
W/Cattle	152	212	30	334	47	170	24	38	754	35	.63	.51
WO/Cattle	236	314	23	602	44	443	33	66	1,425	65	.52	.74
Total	388	526	25	936	45	613	30	104	2,179		.56	.65

[1]Percent of animals classified.

These limited data indicate that much of the cattle grazing, as it exists in the Yellow Water Triangle, lowers the habitat quality for antelope and decreases antelope carrying capacity.

Manipulation of livestock grazing in the Iverson pasture provided some exceptional observations of antelope response to rotated livestock grazing with proper forage utilization. The following management strategy provided for the recovery of the herbaceous vegetation in the pasture: 1) no use in 1968 following partial kill spray treatment, 2) fall use in 1969 and 1970 at 83% of calculated proper use, 3) light spring use (<50%) during 15 May-June, 1971, followed by 4) utilization of the remaining forage during November.

Table 32. Numbers and composition of the antelope doe band confined in the Iverson treatment area, 1968–1972.

	1968	1969	1970	1971	1972
Yearling Males	3			3	4
Mature Males	1	4	1	1	0
Yearling Females	3	0	2	3	7
Mature Females	4	7	7	9	9
Fawns	1	10	7	17	17
Total	12	21	17	33	37
Density[1]	0.34	11.10	8.98	17.44	19.55
Removal	1	11[2]	1	13[3]	–

[1]Antelope per square mile.

[2]Eight fawns collected by Roberts; three adult males left the pasture.

[3]Killed or chased out by poachers.

Fawn production and total number of antelope in the Iverson pasture (Table 32), as indicators of habitat suitability, improved very rapidly in response to vegetational improvements brought about by the changes in livestock management. Reproduction flourished (17 fawns/9 mature does in 1970 and 1971). Density of antelope (19.6/mi^2) was much higher than anywhere else in the Yellow water Triangle. Antelope increased while livestock grazing was maintained at or near the surveyed carrying capacity, whereas the grazed untreated area outside of the pasture continued to be unused during summer. The two important changes in livestock management for the benefit of the antelope were: reduction of spring livestock grazing, and grazing only the allowable forage. Under these conditions, Becker (1972) found livestock grazing to be compatible with antelope use of the area. This management also benefited livestock because major grasses increased. Late cyclic increases in herds V and VII (Fig. 10) indicated that a change from continuous spring-fall use to rotated pastures increased antelope carrying capacity. Dual use at the same season appears to be a problem that was resolved by a grazing rotation.

These effects and others make livestock grazing the most important factor in the functioning of the ecosystem which includes the Yellow Water Triangle. In those areas where erosion continues to remove topsoil and reduce site potential, its influence surpasses the combined effects of weather and soils.

Livestock grazing involves two direct effects on antelope: annual herbage removal and long term changes in species composition, successional phases, and soil erosion in plant communities. There may be other, more subtle direct effects if antelope avoid the presence of cattle or sheep.

Habitat Concepts

Habitat Selection

Animals have an innate ability to choose their habitat in the environmental niche or niches where they are best adapted to live (Thorpe 1949). Offspring of antelope are introduced into the dam's habitat and, to some extent, are habituated by their gregarious behavior to the habitat used by adult social groups. Autenrieth and Fichter (1975) suggest that some habitat selection by fawns (bedding cover) may be due to neonatal imprinting at the birth site. Habitat selection may also arise from behavior of genetic, investigative, or traditional origin.

It is axiomatic that normal wild animals select and use the best habitat niches available to them. Thus, antelope use the areas that are best for them under conditions prevailing at any given time. Often, however, some of the better habitat components of an area may not be available due to limited access, incompatible land uses, undeveloped or lost habitat use traditions, or behavioral constraints. Fences, disturbances, major vegetation type changes, highway construction, and cultivation illustrate such habitat losses.

Habitat Requirements

"Attempts to describe and enumerate the habitats of the earth in a quantitative fashion have generally proven less than useful; one of the major reasons is that descriptions of the environment, if they are to be used to predict the occurrence and abundance of animals, must be related to the environment as actually perceived by an animal (its *Umwelt*)" (Klopfer 1969). "The distinguishing features of habitat niches for a species are often too elusive for human perception" (Errington 1956).

Wildlife habitat needs are often described as food, cover, and water, with space a recent consideration. These requirements overlook the security needs of nonhiding species and the selection of microhabitats to reduce stresses of weather. Antelope living requirements are better expressed as sustenance, security, and comfort.

Sustenance includes all things essential to sustain the animal's body: unpolluted food, moisture, and minerals needed for all seasons, proper climate (temperature and precipitation), and freedom of movement for forage selection.

Good habitat provides security. For hiding species, security means good hiding cover. Hiding cover has limited value for antelope security except for newborn fawns. Obviously, security for antelope means something else. It appears that their security involves two of their outstanding defense attributes: extraordinarily acute vision and fast running speed. Thus level ground and areas of light cover probably provide security through better visibility of approaching predators and easier running for escape.

Cryptic coloration blends into the pristine landscape of grass and shrubs giving antelope their first line of passive defense. The ability to see and outrun mammalian predators (e.g., coyotes and bobcats) is the antelope's first line of active defense. They also have other defense behaviors. Antelope often select resting sites on raised elevations and/or in open grassy areas, both of which they may choose for security value against these predators rather than for other habitat values. Security and cover for special activities include shallow draws and ridges for concealment, dense shrubs for parturition and fawn bedding cover, tall shrubs and trees or sheltered terrain for unusually extreme winter conditions, and windswept ridges for "running room" during winter when deep snow limits movements (Telfer and Kelsal 1984).

Space untenanted by other antelope social units may also be classed as a security requirement. The function of space becomes more complex when one considers the role of social organization and social distribution. Space occupied by cohort members differs from that occupied by foreign cohorts at both the doe band and herd levels.

Winter is a period of stress for antelope, and accounts for 15% of total annual mortality in central Montana. *(Photo by: Montana Department of Fish, Wildlife and Parks)*

Because antelope are highly visible during daylight, their escape flight must take them beyond the distance that predators would normally pursue. Suitable foraging habitat must be available in widely dispersed parts of their summer and winter habitat. Movement restrictions like fences and deep snow, especially during winter, facilitate predation when antelope cannot flee from the area or must return to it. Flight to an area already occupied by a foreign social unit places the doe band or herd too low on the habitat continuum (see later) and/or subjects them to more severe food competition. Large herds of antelope converge during winter; in coming together to better cope with predators (and heat/energy loss?), they also become involved in greater forage competition.

Comfort is generally ignored by habitat analysts, probably because we know so little about it. Antelope during winter seek comfort on south-facing slopes where wind protection and heat radiation combine to provide a warmer and more comfortable microclimate. Similarly, antelope lie down in protected sites (swales, lee slopes, or tall brush) during periods of raw, cold winds during spring, fall, and winter. Antelope in central Montana seldom lie in shade; often they lie on a south exposure in full sunlight, even during summer.

Temperature regulation physiology may be similar between antelope and African ungulates. Oryx (*Oryx* sp.) and eland (*Taurotragus* sp.) employ unique moisture conservation strategies; their body temperature increases during the day and decreases during the night to conserve moisture used in body cooling (Taylor 1969). Antelope appear to be better adapted to live in dry habitats than most other wild ungulates of North America.

Antelope seem to be less well adapted to northern winters than are mule deer. On the other hand, antelope appear to be better adapted to sagebrush forage which is more nutritious for them than for deer in winter. The antelope's light color, thin skin, low fat accumulations, and the above possible temperature regulation mechanism suggests that antelope are better able to cope with warm temperature than with cold, which would agree with their apparent evolutionary roots. It would be highly unlikely for an animal to be equally adapted for coping with heat and cold stresses. Inability to cope with extreme cold could also help to explain some of their unusual behaviors during prolonged stress of that kind.

Carrying Capacity

Widespread use of the term and concept of carrying capacity (Leopold 1933:51) indicates acceptance of this idea for expressing wildlife stocking guidelines. Carrying capacity is defined by Smith (1966:35) as, "the maximum number that can be supported in a given habitat. " Allen's (1954:44) definition is, "what it (an area or habitat) actually is supporting." Other authors give varying definitions when referring to different species or purposes but the term means or implies a forage limitation. Seasonally limited forage during winter or drought is considered by Wing (1951) to determine carrying capacity. None of these definitions provide a measurable base in vegetation or animal density by which a species might be managed. Klopfer (1969:12) states: " . . . organisms generally prove to be too diverse and too complex with regard to the conditions they can tolerate to allow for a classification of habitat on the basis of some manageable number of parameters."

In range management, however, carrying capacity measurements are of vegetation composition and production and assume a specified level of animal use of the vegetation. This use is ambiguous and misleading when applied to wildlife at densities so sparse as to exert little influence on forage production. Forage utilization guides mostly reflect livestock use which is different than wildlife use. Antelope are neither cows nor sheep and cannot be managed by the same standards as domestic livestock.

Carrying capacity measurements, as used by range managers, have little meaning in areas of sparse antelope densities because of the slight influence of antelope on available vegetation. *(Photo by: Author)*

Antelope experience migrations and seasonal movements that cloud defining carrying capacity for them. These movements permit antelope to use a greater variety of habitats, including those with seasonal forage resources. Winter ranges frequently have shallow snow depths, but are too dry for summer occupancy; by contrast, deep snow during winter contributes to production of succulent vegetation on mesic summer ranges. Migration corridors provide important connectors between these seasonal habitats. Blockage of these corridors has resulted in some antelope herds living entirely on their winter or summer range with much reduced populations, probably lost migration traditions, and potentially larger fluctuations in populations.

The occurrence of apparently cyclic fluctuations in antelope populations in the Yellow Water Triangle indicates that factors other than vegetation are inherent in determining carrying capacity. Those may include animal density. Involvement of intrinsic population regulation mechanisms tends to further confuse application of the concept of forage carrying capacity to antelope.

Results of this study suggested that carrying capacity for antelope might be best defined as *the density of adult females that yields the highest sustainable recruitment.* Where antelope are managed primarily to produce a huntable annual surplus, carrying capacity can be expressed as the number of adult females that produces the highest sustainable production surplus (recruitment above natural mortality), which is the basis for legal hunting. This might also be called the *optimum production density.* When the production surplus exceeds all mortality losses, the population increases; conversely, the population decreases during periods of production deficit.

Determining animal density for some species is nearly impossible, but many, if not most, antelope populations can be counted with reasonable precision. In many areas, sufficient antelope population data are already available to make average density estimates, plot trends and dynamics, and thus also establish approximate carrying capacity.

Carrying capacity of adult females occurred at near-average density.
(Photo by: Frank R. Martin)

Obviously, we do not know enough about measuring and interpreting the factors of habitat quality that control density and production. We know even less about interacting and compensating influences. If carrying capacity explains the potential of the habitat to support a species, then to what does one assign cyclic, genetic, physiologic, and behavioral effects that may in part determine the animal's ability to utilize the habitat? How do we compromise the variable influence of livestock grazing?

Cycles in density may be as much a population function as they are related to weather and/or vegetation production. Thus, continuing studies of the populations in the Yellow Water Triangle are aimed at determining the feasibility of interrupting the cycle or reducing the magnitude of its fluctuations and holding the population near the optimum production density.

Carrying capacity of adult females in the Yellow Water Triangle occurred at near-average density derived from either the 10-year average or the average between maximum and minimum numbers of adult females on the area. Carrying capacity was about 400 adult females (300 mature, 100 yearling) between a minimum of 246 and a maximum of 537; or a density of 2/mi². The high numbers and densities may actually represent Leopold's (1933:51) saturation point for cyclic species. Differences in carrying capacity usually indicate differences in the quality of the basic factors, thus the density of a species often expresses the adequacy of the area's resources. Carrying capacity assumes that animals living on an area are the product of all habitat factors, known and unknown.

Because density is seldom the same between areas, it is evident that a continuum in habitat quality exists, both within and between all doe band areas and herd ranges (Fig. 11). Population parameters (density, fawn survival, total number) also vary between social units due to the variable nature of the habitat each unit utilizes yearlong. Thus, those parameters would also appear to reflect or be the product of interaction between inherent characteristics of the animals and inherent characteristics of each habitat occupied.

Antelope are able to utilize key forage species over a wide amplitude of availability. When antelope are restricted to small areas of suitable range, forage plants may become overused. Antelope, however, ordinarily do not completely utilize all of the plants at their disposal.

Sometimes habitat quality is related to density or canopy coverage of important species, such as dense sagebrush used during parturition and fawn bedding, open grassy areas used for resting during late summer, a wide range of sage density used during winter, and a wide range in food plant density. Antelope eat substantial amounts of plants that are so rare as to be unsampled by usual vegetation measurements.

Evaluating habitat quality on the basis of density of key plant species has not been attempted seriously for antelope; indeed, it may not be possible or feasible. Seasonal preferences exist for different plants and plant densities, often within the same part of the home range. Until adequate research correlating antelope distribution, habitat use, and population parameters with meaningful habitat measurements is completed, there will be continued controversy regarding specific amounts of various plant species needed for good antelope habitat.

Recruitment to an antelope population is related to habitat quality, and also to antelope density. When more adult antelope are carried in the population than necessary for maximum productivity, surplus animals are forced to use habitat lower on the habitat quality continuum, and total herd productivity is reduced. Adult antelope can live and survive through normally adverse conditions in habitat of low quality, but their productivity is typically low in proportion to the quality continuum level of their habitat. In poor habitat, many adult females are unable to produce survivors and they may not survive themselves under the most adverse environmental conditions as severe winters or extreme drought may create.

Discussion

Pronghorn antelope appear to have evolved in the "subtropical xerophytic flora" of plains regions and extended their range north as grass and low shrubs replaced tree formations. Periods of mild climate (Oosting 1948:300) could have facilitated their northward range extension. Specific adaptations to utilize shrubby *Artemisia* species as winter forage in the northern plains probably occurred later during periods of colder climate and winter snow cover.

Today, antelope occur in three major habitat zones in western North America. These include: 1) the northwest, west of the Continental Divide and northward from northern Utah, Nevada, and California; 2) the northeast, east of the Continental Divide from Colorado to southern Canada; and 3) the southern, including the southwestern states and Mexico. Buechner (1960) proposed only two zones of occurrence, the eastern and western. Three zones would seem more consistent with difference in floristic components associated with geologic and climatic characteristics across western North America. Those differences also appear to be reflected in differences in habitat selection and use by antelope between zones as well as between specific habitats within zones.

Daubenmire (1968:262) described the genesis of some of the present vegetation on antelope range as follows:

Antelope are strongly dependent on sagebrush for food and cover (above) on the Northern Plains, but some will subsist in less satisfactory habitats where sagebrush is absent (below). *(Photos by: Richard J. Mackie)*

"The geologic histories of floras are clearly imprinted in vegetation patterns. This historic aspect of vegetation can be conveniently emphasized in the . . . vegetation province.

"As a specific illustration, the group of nine steppe zones recognized in eastern Washington belong to a different province than the steppe zones east of the Rockies in the same latitude. the chief dominants of the former (*Agropyron spicatum*, *Festuca idahoensis*, *Poa secunda*, *Artemisia tridentata*, *A. tripartita*) are derivatives of a boreal flora (arctotertiary geoflora) and are adapted to grow in cool spring weather and endure a dry summer, while most the characteristic dominants of the latter (*Bouteloua gracilis*, *Buchloe dactyloides*, *Aristida*, *Sporobolus*, *Stipa*) are derived from an ancient subtropical xerophytic flora (madrotertiary geoflora) and stay dormant until high temperatures arrive and so require rainfall to prosper."

Axelrod (1940, from Beetle 1960) addressed shrub, and specifically sagebrush, distribution as "Many species related to those of the present chaparral, sagebrush, and desert shrub formations of the western United States occupied a seral stage in the middle and later Tertiary woodland flora. With the restriction of woodland in the late Cenozoic, these more xeric communities gradually became climax over areas formerly dominated by woodland."

As indicated by the results of this and other studies in the northern great plains, antelope are strongly dependent on the *Artemisia* complex for food and cover in northern plains habitats. Where *Artemisia* is not present, some antelope eat *Juniperus* or other less satisfactory winter food. Summer habitats usually involve non-sagebrush types only if they occur near or have migratory access to sagebrush for winter forage during severe winters. Even in predominantly grassland areas, scattered or localized sages (*A. tridentata*, *A. cana*, or *A. frigida*) provide the major food resource during winter (Sundstrom et al. 1974).

Antelope presently occupy habitats throughout much of their historical range. Four major factors appear to make that possible. First, intensive agriculture did not permanently preempt large areas of native dry plains vegetation, some of which have improved during the past few decades. Second, antelope adapted to life on the dry plains by utilizing large areas and evolving flexible habitat use behaviors, including migration. Third, hunting, that once contributed to the antelope's near demise in many areas, has been controlled. And fourth, some vacant parts of historic distribution range were restocked by the innate pioneering behavior of the species or by transplanting programs. Antelope now occupy most of their historical habitat in the Yellow Water Triangle. Much of the cultivated land of the homestead era has reverted to native rangeland. Most of the people and many of the fences are gone.

Nonetheless, important habitat changes affecting antelope have occurred and continue to occur in the Yellow Water Triangle. Landowners fenced some cultivated lands with woven wire when high antelope populations during the 1940s and 1950s resulted in crop depredations. Other netting-wire fences were built to control sheep movements. These fences limited antelope access to much potential habitat, including key late summer succulent forage sources and more fertile lands. Livestock grazing changed the composition of pristine plant communities resulting in less cover and forage. Livestock out-compete antelope on most rangelands because they can effectively utilize less nutritious forage and because they are removed at the end of each grazing season. New highways have restricted antelope movements and reduced the size of herd ranges and doe band areas. In addition, over 6,000 acres of sagebrush-grassland in private ownership have been plowed for cultivated crops in the study area during recent years and several thousand more acres are expected to be converted to agricultural croplands in the future.

MANAGEMENT RECOMMENDATIONS

Since 1960 Montana's antelope management strategy has been: complete population aerial surveys of one-third of all antelope hunting districts each year and harvest by either-sex hunting permits issued at conservative rates. Although this strategy has been modified somewhat in recent years (e.g., additional doe-fawn hunting permits in some districts), even more efficient resource utilization is possible.

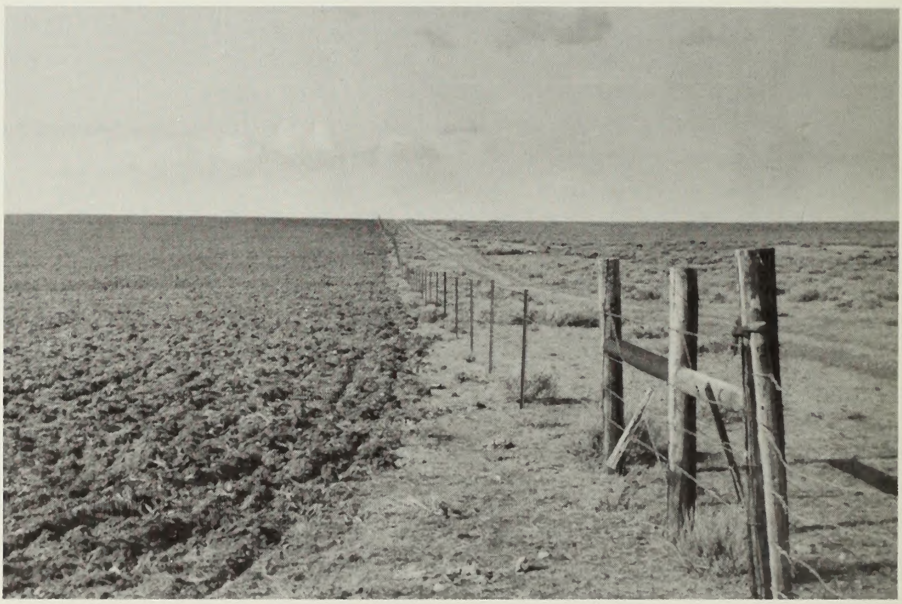
This study suggested the following as a basic framework for management:

1. Manage on the basis of population characteristics. Population data can be obtained with sufficient accuracy for relatively precise management of hunting mortality, and there are no singular habitat/forage characteristics that can be readily and accurately measured to indicate population status and habitat relationships.
2. The essential first step in management should be definition of social distribution and population/habitat units. This should delineation of populations in contiguous habitat between apparent barriers, as well as doe band areas within the herd range. Key pastures or range use areas should also be identified. Integrity of these habitat units should be protected.
3. Each population should be characterized by density/production parameters through intensive aerial population surveys, preferably on an annual basis. Classification of animals by sex and age classes, as well as of yearling and mature males, provides the basic population data. Density and distribution of adult females and fawns, the two critical management beacons, can be determined from those data.
4. Harvest should be by sex-specific permits, issued on the basis of a) increasing or decreasing populations, and b) proportion of annual recruitment to be harvested. Additional harvest of adult females should be attempted prior to high natural mortality years.
5. A system of habitat monitoring is needed even though habitat surveys to determine population status are not practical. The habitat area used by social units provides the essential land area for density determinations. Changes in the basic habitat area might change herd potential. Habitat management might include:
   a. protection from massive habitat conversions
   b. improvements in livestock management to control utilization and provide ungrazed pastures in each doe band area via a livestock rotation grazing system
   c. improvements in density of key forage species can be achieved by manipulating season of use by livestock to favor important forbs
   d. planting summer forage may be practical in some areas, especially inclusion of nitrogen-fixing legumes in seeding mixtures.
6. Population-habitat modeling may have application in management after sufficient base data have been obtained to ensure reliability in model projections.

Some important theories have been advanced in this bulletin, but they are still in the hypothesis stage. This was only one study, covering a small area compared to all of the antelope range over the state; the results may be artifacts of short-term or otherwise limited data coverage. The importance of developing long-term monitoring of representative populations throughout the state cannot be overemphasized.

Although use of herbicides to eliminate sagebrush has subsided, burning (above-right) and plowouts (below-left) continue to threaten antelope habitats in Montana.

(Photos by: Author)



EPILOGUE

This study was generated because of concern for the welfare of one of North America's unique big game species—the pronghorn antelope. It was prompted by a perceived threat to the basic ingedient for survival of every wildlife species—its habitat!

The results of the study, which covered the period 1966 to 1978, included several new concepts and scientific hypotheses to be tested by management and research. Continued surveys and other studies on the Yellow Water Triangle since 1978 (C.R. Watts pers. comm.) have now provided additional information and insight about antelope population ecology, habitat trends, and management. That information and management/research implications are presented in the following discussions. Tables updating earlier data summarizing antelope population surveys, seasonal mortality, and harvests from 1978–1979 through 1985–1986 are presented in the Appendix (Tables F-J).

Populations

The social organization and distribution of antelope in herds and bands continues as originally observed and interpreted. Recent studies, however, have identified dispersal (emigration) as a possible factor influencing numbers of adult females in herds and bands. Movements of adult females captured and marked with radio collars in summer 1985 have been much greater than those recorded during the core study, and included several instances of dispersal from herd and band ranges in which they were marked. These differences could reflect antelope response to different capture and/or monitoring techniques. The recent studies included capture using a helicopter and net gun (Firehow et al. 1986) and frequent relocation from an airplane, while earlier captures were effected by hazing antelope into net traps and monitoring was primarily from the ground.

Population parameters followed previous patterns, and remained within earlier documented extremes, from 1978 to 1986. Extreme cold and deep snow during the 1977–1978 winter resulted in movement to emergency winter range and higher-than-average mortality. The antelope population on the study area, which had already declined by summer 1977 to approximately 76% of that at the cyclic-high in 1973, decreased further by the summer of 1978 to 66% of 1973 numbers. Although even more severe temperatures and snow conditions prevailed during the following (1978–1979) winter, the combination of reduced antelope numbers and possibly the occurrence of high winds that exposed food plants and facilitated travel by antelope allowed high overwinter survival. This information confirmed earlier observations about the role and importance of winter weather in the ecology of antelope on the study area, but indicated that effects of severe winters may be variable, depending upon many population and other environmental factors.

The high survival through the 1978–1979 winter and high fawn production in 1979 marked the beginning of another upswing in the population that continued for 5 years, through 1983. Coincident with this increase, harvest strategies were changed to increase hunter take and reduce populations to landowner tolerance. An average of 356 permits was issued for the study area and an average of 222 antelope was harvested from the 213 mi^2 of habitat each year from 1979 to 1983. At the same time, an average of 288 yearlings was recruited into the population each year; more than 300 were recruited in "high" years of 1979, 1982, and 1983. Earlier recruitment plateaus were recorded as 200–240 yearlings in association with the previous cyclic high in 1973.

Trends during 1978–1986 continued to support the occurrence of "cyclic" changes in antelope abundance, with "highs" occurring at approximately 10-year intervals. Following a population "low" of about 750 antelope during 1974–1978, numbers increased to a high of slightly over 1,100 antelope during 1982–1983. This was approximately the same number as occurred on the area at the previous peak in 1973. Fawn production and total numbers declined once again, beginning in 1984, with the population dropping to a new low of about 700 antelope in summer 1986.

The pattern of periodically (3-year) high female mortality also appeared to continue, though less regularly. Previously, high female mortality had occurred in 1967, 1970, 1973, and 1976. The next highs occurred in 1980 (a 4-year gap) and 1982 (a 2-year gap). It is possible that either high mortality associated with the severe 1977–1978 winter or the liberalized harvest strategy may have interrupted or altered the periodicity. However, data on adult mortlaity were complicated by the high yearling counts recorded in several years.

Little reestablishment of big sagebrush (left) has occurred 18 years after spraying for total kill on the King Treatment Area. *(Photo by: Author)*

Habitat

In 1986, 18 years after treatment, there was little evidence of reinvasion of sagebrush into areas of total kill. Conversely, big sagebrush has returned to pre-treatment densities on partial kill sites as well as on those strip-sprayed areas where partial kill of sagebrush occurred.

Only limited information is available for trends in other plants and vegetational characteristics. Although bluebunch wheatgrass plants continue to survive on areas of total sagebrush kill, where they were once protected by the sagebrush, the apparent lower vigor of many plants attests to grazing stress and only additional time will tell whether they will survive.

That antelope use of all treatments, including the total kill spray and contour furrows, has increased slightly from the levels observed during the core study, suggests that vegetation and site conditions are slowing being restored. It will likely be many years, however, before areas sprayed for total kill of sagebrush will have habitat conditions entirely suitable for sagebrush-dependent species. Fifty years have now passed since the Carey Act Fire of 1936, and the area still does not have sufficient sagebrush cover for antelope bedding or sage grouse nesting.

Management

Use and consideration of population data in management of antelope has increased since the initial study was completed. With this, public recreational hunting has increased and conflicts with agriculture have decreased in some areas. Nonetheless, the primary emphasis in management remains on summer population counts with corresponding alteration of harvest quotas. The continuing studies with marked antelope suggest that summer aerial surveys may underestimate populations in this area. Additional monitoring and assessments are required to improve survey techniques and accurately interpret observed population parameters. Such assessments, as well as population studies, need to be conducted concurrently in several different habitats for comparative, interpretive reliability.

Significant advancements in agricultural technology have occurred since the 1940s. The advent and widespread economical use of herbicides to control undesirable vegetation led this advance. Today, landowners can quickly and effectively alter their operations such that habitat alterations can occur without opportunity for adaptation by most wildlife species. Because of this, habitat-specialized species, like antelope and sage grouse, can be threatened more quickly than ever before.

Although the use of herbicides to control sagebrush on public lands in Montana had subsided by the time the initial study was completed in the mid-1970s, efforts to otherwise control agriculturally undesirable plants and modify rangeland vegetation have continued. There has been and now is growing support for burning, chaining, and ripping sagebrush communities and for chisel plowing of many rangelands considered less productive than they could be.

In the early 1980s, government incentives encouraged private entrepreneurs to plow and convert large acreages of prairie rangeland to agriculture cropland. Within days, blocks of 5,000 to 30,000 or more acres of sagebrush range were plowed, overriding all of the past efforts of wildlife managers and others, as well as the results of studies such as this one, to provide for maintenance of wildlife habitats on those or adjacent public lands.

The preservation of beneficial wildlife species remains one goal of society. Coincident with that goal must be another to preserve wildlife habitats and their unique as well as common components. Pressure to remove individual components or to obliterate some habitats continues. Public vigilance, backed by information about the status and trends of wildlife species and their habitat needs, is necessary if desirable species and their habitats are to remain part of prairie ecosystems on public lands. Similar preservation of wildlife habitats and populations on private lands may ultimately be addressed in the marketplace. However, economic incentives to maintain these species should be developed and made available to private land managers.

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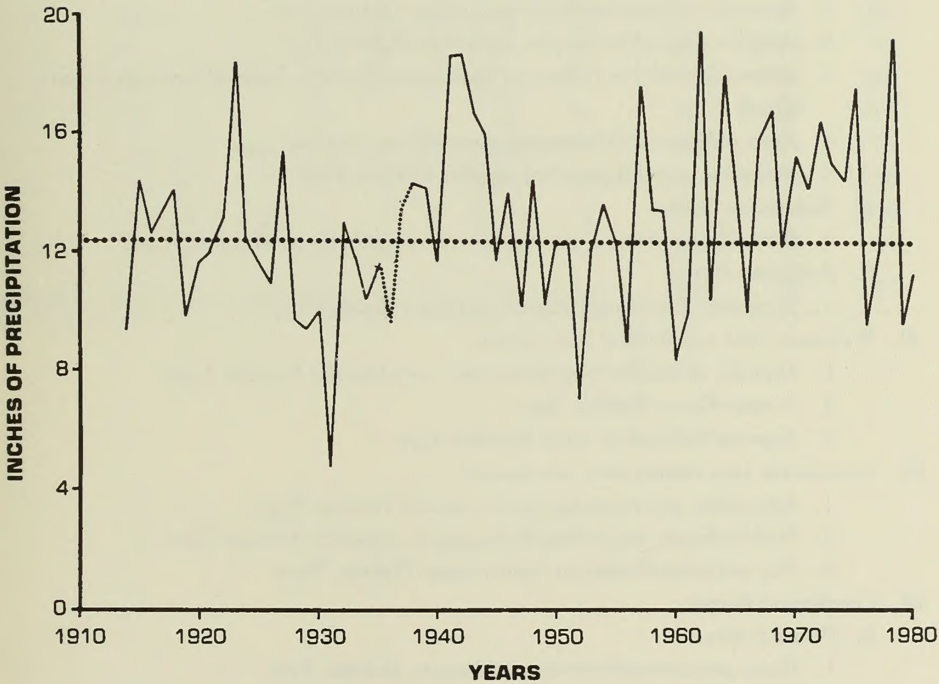
APPENDICES

Appendix A

Annual precipitation at Flatwillow Station 1913–1980.



Appendix B

Habitat type classification of vegetation in the Yellow Water Triangle (Jorgensen 1979).

- I. Shrub-grasslands
  - A. *Artemisia* Series
    1. *Artemisia tridentata/Agropyron spicatum* Habitat Type, *Bouteloua gracilis* Phase
    2. *Artemisa tridentata/Agropyron spicatum* Habitat Type, *Agropyron smithii* Phase
    3. *Artemisia tridentata/Agropyron dasystachyum* Habitat Type, *Agropyron spicatum* Phase
    4. *Artemisia tridentata/Agropyron dasystachyum* Habitat Type, *Sarcobatus vermiculatus* Phase
    5. *Artemisia tridentata/Koeleria cristata* Habitat Type
    6. *Atriplex dioica/Gutierrezia sarothrae* Habitat Type
    7. *Artemisia tridentata/Festuca idahoensis* Habitat Type, *Bouteloua gracilis* Phase
    8. *Rosa arkansana/Thermopsis rhombifolia* Habitat Type
    9. *Artemisia cana/Agropyron smithii* Habitat Type
  - B. *Sarcobatus* Series
    1. *Sarcobatus vermiculatus/Agropyron dasystachyum* Habitat Type
  - C. *Juniperus* Series
    1. *Juniperus horizontalis/Carex parryana* Habitat Type
- II. Wetlands (not subdivided into series)
    1. *Populus deltoides/Symphoricarpus occidentalis* Habitat Type
    2. *Scirpus/Carex* Habitat Type
    3. *Suaeda/Salicornia rubra* Habitat Type
- III. Grasslands (not subdivided into series)
    1. *Agropyron spicatum/Agropyron smithii* Habitat Type
    2. *Muhlenbergia cuspidata/Andropogon scoparius* Habitat Type
    3. *Poa pratensis/Artemisia ludoviciana* Habitat Type
- IV. Coniferous Forest
  - A. *Pinus* Series
    1. *Pinus ponderosa/Artemisia tridentata* Habitat Type
    2. *Pinus ponderosa/Agropyron spicatum* Habitat Type

Appendix C

Hunting mortality estimates from hunter questionnaires, HD 420, and Yellow Water Triangle, 1966–1978

	H.D. 420							Yellow Water Triangle			
	Adult Males		Adult Females		Fawns		Total	Adult Males	Adult Females	Fawns	Total
Year	No.	%	No.	%	No.	%	No.	No.	No.	No.	No.
1966	50	47	56	53	6	5	112	32	35	17	84
1967	74	65	40	35	6	5	120	47	25	18	90
1968	75	68	35	32	3	3	113	46	22	17	85
1969	89	79	23	21	11	9	123	59	15	18	92
1970	97	75	33	25	2	2	132	59	20	20	99
1971	90	63	52	37	0	0	142	54	31	21	106
1972	81	65	44	35	4	3	129	51	27	19	97
1973	149	67	74	33	19	8	242	98	48	36	182
1974	183	71	75	29	7	3	112	46	46	40	198
1975	135	65	74	35	18	8	228	88	49	34	171
1976	144	61	91	39	5	2	240	88	56	36	180
1977	148	55	120	45	6	2	274	91	74	41	206
1978	51	58	37	42	1	1	89	31	23	13	67
Average	105	65	58	35	7	4	170	66	36	25	127

Appendix D

Distribution of sex and age classes during summer, Yellow Water Triangle, 1966–1978.

		Males				Females				Total
Year		1/2	1-1/2	2-1/2+	Total	1/2	1-1/2	2-1/2+	Total	Antelope
1966[1]	No.	93	56	35	184	93	56	196	343	529
	%	18	11	7	35	18	11	37	65	
1967[1,2]	No.	90	64	40	194	91	64	199	354	548
	%	16	12	7	35	17	12	36	65	
1968[1]	No.	161	72	46	279	161	72	207	440	719
	%	22	10	6	39	22	10	29	61	
1969[1]	No.	133	75	48	256	133	75	257	465	721
	%	18	10	7	36	18	10	36	64	
1970	No.	149	94	59	302	150	94	317	561	863
	%	17	11	7	35	17	11	37	65	
1971	No.	161	110	94	365	161	110	292	563	928
	%	17	12	10	39	17	12	31	61	
1972	No.	187	120	110	417	188	120	361	669	1,086
	%	17	11	10	38	17	11	33	62	
1973	No.	185	108	117	410	186	108	427	723	1,133
	%	16	10	10	36	16	10	38	64	
1974	No.	104	119	121	344	105	119	378	602	946
	%	11	13	13	36	11	13	40	64	
1975	No.	136	77	110	323	137	77	441	655	978
	%	14	8	11	33	14	8	45	67	
1976	No.	142	89	85	316	142	89	398	629	945
	%	15	9	9	33	15	9	42	67	
1977	No.	128	83	86	297	129	83	316	528	825
	%	16	10	10	36	16	10	38	64	
1978	No.	119	73	78	270	119	73	271	463	733
	%	16	10	11	37	16	10	37	63	
Average	No.	137	88	79	304	138	88	312	538	842
	%	16	11	9	36	16	11	37	64	

[1]Yearlings estimated from 1970 ground survey.

[2]Partial aerial survey, totals estimated.

Appendix E

Plant species eaten by antelope in the Yellow Water Triangle by season: spring = 1, summer = 2, fall = 3, and winter = 4. Seasons are tabulated in descending order of importance.

	Investigator				
Species	Cole 1953–54 (1,2,3,4)	Bayless 1966–67 (4,1)	Wentland 1966–67 (2,1,3)	Roberts 1968–69 (2,1,3)	Becker 1971 (2,3,4)
Shrubs					
Artemisia cana	4,3,1,2	4,1	2	2	
A. tridentata	1,4,2,3	4,1	2,1	1,2,3	4,3
Atriplex confertifolia	1	4,1			3
Chrysothamnus nauseosus	2,3,4,1	1,4	2	2,3	
C. viscidiflorus	2				
Eurotia lanata	1	4			
Guiterrezia sarothrae	2		2	2,3	3,2
Juniperus horizontalis	1,4	1			
Rhus trilobata	2				
Rosa arkansana	2,3,1		2	2	
Salix spp.	2				2,3
Sarcobatus vermiculatus	1,2,3		2	2	
Shepherdia argentea	2				
Symphoricarpos occidentalis	3,2,4	1			
Forbs					
Achillea millefolium	1,2,3		2	2,1	2
Agoseris cuspidata	3				
Allium textile	1	1			
Amaranthus retroflexus				2	
Antennaria rosea		4,1			
Apocynum cannabium	2				
Arenaria hookeri	1		2		
Arnica soraria			2		
Artemisia campestris	2				
A. frigida		4,1	2	3,2,1	3,2,4
A. longifolia		1	2	2	
A. ludoviciana	2,3,1				2,3
Aster spp.	2,3,1,4	4	2		2
Astragalus agrestis	2				
A. bisulcatus	3,2		2	2	2
A. drummondii				2	
A. flexuosus	2				
A. gilviflorus	3,1,2		2	2,3	

Appendix E. *(Continued).*

	Investigator				
Species	Cole 1953–54 (1,2,3,4)	Bayless 1966–67 (4,1)	Wentland 1966–67 (2,1,3)	Roberts 1968–69 (2,1,3)	Becker 1971 (2,3,4)
Forbs *(continued)*					
A. gracilis				2	
A. missouriensis	3,2		2	2	
A. spatulatus				2,3	
A. striatus	3				
Atriplex argentea	2				
A. dioica				3,2	
Bahia oppositifolia	2,3			2,3	3
Besseya cinerea	1				
Chenopodium album				2	
C. glaucum					3
Chrysopsis villosa	2				
Cirsium vulgare				2	3
Commandra umbellata	2,1,3		2		
Conringia orientalis	2				
Crepis occidentalis			2		
Descuriana richardsoni	3				
Erigeron caespitosus	3,2				
E. ochroleucus			2		
E. pumilus	2		2	2	2
Eriogonum flavum	2				
E. multiceps	2,3		2	3,2	
Gaura coccinea	2,3		2	2	2
Glycyrrhiza lepidota	2,3		2		2
Grindellia squarrosa	2		4	2	2
Haplopappus acaulis	1				
H. nuttallii	2,3,1,4		2	2	
H. spinulosus	3				
Helianthus spp.	3,2,4				2
Hymenopappus filifolius	2			2	
Hymenoxys acaulis	1,2,3,4				
H. richardsonii			2		
Hyoseyamus niger				2	
Iva xanthifolia				2	
Kochia scoparia					3,2
Lactuca seriola	2,3				2
Lepidium densiflorum				2	
Leptodactylon pungens		4,1			
Liatris punctata	3,2				
Linum rigidum	2			2	

Appendix E. *(Continued).*

	Investigator				
Species	Cole 1953–54 (1,2,3,4)	Bayless 1966–67 (4,1)	Wentland 1966–67 (2,1,3)	Roberts 1968–69 (2,1,3)	Becker 1971 (2,3,4)
Forbs *(continued)*					
Lomatium foeniculatum	1				
Lygodesmia juncea				2	2
Medicago lupulina				2	2
M. sativa	3,2,4		2	2	2,3
Melilotus alba	3,2		2	2	
M. officinalis			2	2,3,1	2,3
Microseris cuspidata			2		
M. nutans	1				
Musineon divaricatum	1		2		
Oenothera caespitosa					2
Opuntia polycantha	4,1	4,1	2		
Oxytropis sericea		4	2		
Penstemon albidus	2				
P. nitidus	1		2		
Petalostemon spp.	2,3		2	2	2
Phlox hoodii	1	4		1,2	3
Plantago spinulosa	3			2	
Polygonum spp.	3,2		2	2	
Potentilla gracilis	2			2	
Psoralea argophylla	2				2
P. tenuiflora	2,3		2	2	2
Ratibida columnaris	2,3		2		
Rorippa spp.					2
Rumex spp.	2,3				3,2
Salsola kali	2				
Sisymbrium loeselii				2	
Solidago missouriensis	2,3,1			2	
Sonchus arvensis	3				
Spharalcea coccinea	3,2,1		2	2	3
Taraxacum officinale	3,2		2	1,2	
Thelasperma marginatum	1,2		2	2	
Thermopsis rhombifolia			2	2	
Tragopogon dubius	2,4		2	2	
Trifolium spp.	2,3				
Verbena bracteata	2			2	3,2
Vicia americana	1,2,3		2	2,3,1	1
Lichen	1	1	2		

Appendix E. ***(Continued).***

Species	Investigator: Cole 1953–54 (1,2,3,4)	Bayless 1966–67 (4,1)	Wentland 1966–67 (2,1,3)	Roberts 1968–69 (2,1,3)	Becker 1971 (2,3,4)
Grass					
Agropyron desertorum				2	3,2
A. smithii				1,2	3,2,4
A. spicatum		4	2		
Bouteloua gracilis					3
Bromus japonicus					2
B. tectorum					3
Carex eleocharis					3
C. filifolia	1,4				
Koeleria cristata				1,2	2,3
Poa spp.		4		1,2	3
Scheddonardus paniculatus					3
Stipa viridula				2	2,3
Triticum aestivum	3				

Appendix F

Antelope aerial surveys, Yellow Water Triangle, 1978–1986.

	Adult Males						
Year	Yrlg.	Mat.	Total	Adult Females	Total Adults	Fawns	Total Antelope
1978	73	80	153	353	506	246	752
	(79)	(87)	(166)		(519)		(765)
1979	87	64	151	374	525	379	904
	(105)	(77)	(182)	(404)	(586)	(409)	(995)
1980	150	68	218	502	720	325	1,045
1981	120	67	187	419	606	270	876
	(123)	(68)	(191)	(476)	(667)	(307)	(974)
1982	125	86	211	498	709	378	1,087
	(135)	(93)	(228)		(726)		(1,104)
1983	156	90	246	467	713	402	1,115
1984	156	72	228	461	689	136	825
				(471)	(699)	(139)	(838)
1985	22	94	116	435	551	151	702
1986	40	51	91	385	476	183	700[1]

[1]Includes 41 unclassified

( ) Survey adjustments

Appendix G

Antelope harvest statistics, 1978–1985.

	H.D. 420[1]							Estimated Antelope Harvest, Yellow Water Triangle			
			Antelope Harvested								
Year	No. Permits	No. Hunters	Males	Females	Fawns	Total	Percent Success	75% Total	Fawns (20%)	Adult Males	Adult Females
1978	150	120	51	37	1	89	74	67	13	31	23
1979	400	354	142	90	41	277	78	208	42	114	52
1980	500	437	192	85	8	285	65	214	43	119	52
1981	400	320	167	68	12	247	77	185	37	105	43
1982	550	460	216	123	21	360	78	270	54	138	78
1983	475	398	187	61	9	308	75	231	46	139	46
1984	425	353	125	96	0	221	63	166	33	75	58
1985	200	140	74	25	0	99	71	105	21	63	21

[1]From the Statewide Hunter Questionnaire survey for H.D. 420.

Appendix H

Mortality table for adult male antelope, Yellow Water Triangle, 1966–1985.

	Summer Survey	Hunting Mortality		Fall Survivors		Following Year Mature Males		Other Mortality		Total Mortality	
Year	No.	No.	%	No.	%	No.	%	No.	%	No.	%
1966	89	32	36	57	64	40	45	17	19	49	55
1967	(104)[1]	(47)	(45)	(57)	(55)	(46)	(44)	(11)	(11)	(58)	(56)
1968	118	46	39	72	61	48	41	24	20	70	59
1969	123	59	48	64	52	59	48	5	4	64	52
1970	153	59	39	94	61	94	61	0	0	59	39
1971	204	54	26	150	74	110	54	40	20	94	46
1972	230	51	22	179	78	117	51	62	27	113	49
1973	225	98	44	127	56	121	54	6	3	104	46
1974	240	112	47	128	53	95	40	34	14	146	61
1975	187	88	47	99	53	85	45	14	7	102	55
1976	174	88	51	86	49	86	49	0	0	88	51
1977	169	91	54	78	46	78	46	0	0	91	54
1978	153	31	20	122	80	64	42	58	35	89	54
	(166)		(19)	(135)	(81)	(77)	(52)				
1979	151	114	63	37	37	68	37	0	0	114	63
	(182)			(68)							
1980	218	119	55	99	45	67	31	32	15	151	69
1981	181	105	55	82	45	86	45	0	0	105	55
	(191)			(86)		(86)					
1982	211	138	61	73	39	90	39	0	0	138	61
	(228)			(90)							
1983	246	139	57	107	43	72	29	35	14	174	71
1984	228	75	33	153	67	94	41	59	26	134	59
1985	116	63	54	53	46	51	44	2	17	65	56

[1]Calculated survey adjustments based on previous year and succeeding year data.

Appendix I

Mortality table for adult female antelope, Yellow Water Triangle, 1966–1985.

	Summer Survey	Hunting Mortality		Fall Survivors		Following Year Mature Females		Other Mortality		Total Mortality	
Year	No.	No.	%	No.	%	No.	%	No.	%	No.	%
1966	246	35	14	211	86	199	81	12	5	47	19
1967	(263)[1]	(25)	(10)	(238)	(90)	(207)	(79)	(31)	(12)	(56)	(21)
1968	279	22	8	257	92	257	92	0	0	22	8
1969	332	15	5	317	95	317	95	0	0	15	5
1970	411	20	5	391	95	292	71	99	24	119	29
1971	402	31	8	371	92	361	90	10	2	41	10
1972	481	27	6	454	94	429	89	25	5	52	11
1973	537	48	9	489	91	378	70	111	21	159	30
1974	497	46	9	451	91	441	89	10	2	56	11
1975	518	49	9	469	91	398	77	71	14	120	23
1976	487	56	11	431	89	316	65	115	24	171	35
1977	399	74	19	325	81	271	68	54	14	128	32
1978	353	23	7	330	93	287	81	43	12	66	19
1979	374 (404)	52	13	322 (352)	87	352	87	0	0	52	13
1980	502	52	10	450	90	299	60	151	30	203	40
1981	419	43	10	376	90	373	89	3	1	46	11
1982	498	78	16	420	84	311	62	109	22	187	38
1983	467	46	10	421	90	305	65	116	25	162	35
1984	461 (471)	58	12	403 (413)	88	413	88	0	0	58	12
1985	435	21	5	414	95	345	79	69	16	90	21

[1]Calculated survey adjustments based on previous year and succeeding year data.

Appendix J

Mortality table for antelope fawns, Yellow Water Triangle, 1966–1985.

	Summer Survey	Hunting Mortality		Fall Survivors		Following Year Yearlings		Other Mortality		Total Mortality	
Year	No.	No.	%	No.	%	No.	%	No.	%	No.	%
1966	181	17	9	164	91	128	71	36	20	53	29
1967	(181)[1]	(18)	(10)	(163)	(90)	(144)	(80)	(19)	(10)	(37)	(20)
1968	322	17	5	305	95	150	47	155	48	172	53
1969	266	18	7	248	93	188	71	60	23	78	29
1970	299	20	7	279	93	220	74	59	20	79	26
1971	313	21	7	292	93	240	77	52	17	73	23
1972	375	19	5	356	95	216	58	140	27	159	42
1973	371	36	10	335	90	238	64	97	26	133	36
1974	209	40	19	169	81	134	64	35	17	75	36
1975	273	34	12	239	88	174	64	65	24	99	36
1976	284	36	13	248	87	166	58	82	29	118	42
1977	257	41	16	216	84	146	57	70	27	111	43
1978	246	13	5	233	95	210	85	23	9	36	15
1979	409	42	10	367	90	300	93	67	16	109	27
1980	325	43	13	282	87	246	76	36	11	79	24
1981	270	37	12	233	88	270	88	0	0	37	12
	(307)			(270)							
1982	378	54	14	324	86	312	83	12	3	66	17
1983	402	46	11	356	89	312	78	44	11	90	22
1984	139	33	24	106	76	44	32	62	45	95	68
1985	151	21	14	130	86	80	53	50	33	71	47

[1]Calculated survey adjustments based on previous year and succeeding year data.

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