

Ground nesting birds in roadside borders of the Argentine Pampas: habitat use and predation risk of artificial nests

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ABSTRACT: Habitat loss and fragmentation have led to grassland bird declines, with ground nesters particularly vulnerable. Roadsides could provide habitat, although their suitability depends on several roadside and field characteristics. Vegetation structure determines foraging and nesting site availability. In addition, road delimits sharp edges where the activity of nest predators is usually higher, whereas herbaceous vegetation determines ground nest concealment. Trees could provide lookouts to predators, and modified habitat and woodlands in surrounding fields could offer additional resources to predators. Our objective was to assess habitat suitability for ground nester birds in roadsides belonging to one modified grassland of the Argentine Pampas. We surveyed birds (90 plots) and monitored artificial nests (60 plots) in different road types: unpaved, paved of one-lane per side, and paved of two-lanes per side. Within each road type, we evaluated the relationship that ground nesters abundance had with vegetation structure of roadsides and surrounding fields. In addition, we related predation of artificial nests with the proximity to the road, roadside vegetation, and modified land and woodlands of surrounding fields. We made 2832 records of 84 species using roadsides, including 1083 records of 13 ground nesting species. Abundance of ground nesters increased with tall grass cover of roadsides and decreased with the number of native trees within roadsides. Roughly half (31/60) of the artificial nests were predated and 82.6% of the identified egg-marks were of mammal teeth. Nest predation decreased with nest proximity to the road. Our results emphasize the importance of tall grass cover of roadsides for the conservation of ground nesting species, and the necessity of monitoring natural nests in order to clarify the effect of trees, proximity to the road, and other environmental variables on nest success.

KEY-WORDS: corridors, field margins, grassland birds, habitat remnants, survival analysis.

INTRODUCTION

Habitat loss and fragmentation have led to the decline of grassland bird populations worldwide (Askins *et al.* 2007, Zuckerberg *et al.* 2009, Azpiroz *et al.* 2012, Reif 2013). Amongst them, ground nesting birds are particularly vulnerable due to the greater exposure of eggs, chicks and incubating adults to mammalian and bird predators (Pietz *et al.* 2009, Fletcher *et al.* 2010), which increases with habitat fragmentation due to higher amounts of habitat edges with which predators are associated (Evans 2004, Huijser & Clevenger 2006). Thus, conservation researchers have become interested in habitat remnants that could benefit the conservation of these species (Weidman & Litvaitis 2011, Duchardt *et al.* 2016, Port & Schottler 2017). In this context, it has been proposed that roadside networks can provide habitat (Meunier *et al.* 1999, Bergin *et al.* 2000), although their suitability for grassland birds depends on several factors affecting bird abundance and nest predation.

One key factor influencing the abundance of grassland birds in roadsides is vegetation structure, which

determines the availability of shelter, foraging sites and nesting sites (Meunier *et al.* 1999, Kociolek *et al.* 2011). Moreover, habitat availability in the surrounding fields may also promote bird abundance in roadsides (Huijser & Clevenger 2006), while woodlands and modified land (*i.e.*, crops or human settlements) have exhibited a negative association with the abundance of birds inhabiting grassland remnants (Leston 2013, Dotta *et al.* 2016, Pretelli *et al.* 2018). Some grassland birds might avoid these areas since woodlands can increase the abundance of specialist predators (Vickery *et al.* 2009, Ellison *et al.* 2013) and brood parasites (Patten *et al.* 2006, Pietz *et al.* 2009), and modified land may offer resources to generalist predators (Evans 2004, Benítez-López *et al.* 2010).

In addition, roadside characteristics can affect ground nesting bird populations due to their influence on nest predation risk. Nest detectability by predators decreases with greater structural complexity of the vegetation, which contributes to nest concealment (Weidinger 2002, Conover *et al.* 2011). In contrast, detectability may be increased by the proximity to trees, which offer lookouts

to avian predators that use visual cues (Söderström *et al.* 1998, Bergin *et al.* 2000, Flaspohler *et al.* 2001) as well as to brood parasites (Patten *et al.* 2006). Moreover, roads lack structural complexity, and nest proximity to the road could imply the proximity to hard habitat edges where predator activity is higher (Fletcher & Koford 2003, Weldon & Haddad 2005, King *et al.* 2009). Likewise, predation can depend on wider scale factors such as the prevalence of woodlands and modified lands, which offer resources to generalist predators and may enhance their abundance in the landscape (Hogrefe *et al.* 1998, Vickery *et al.* 2009, Ellison *et al.* 2013).

Analyzing factors that affect both abundance and predation risk, therefore, constitutes an appropriate method to assess roadsides' suitability for birds in threatened grasslands. In particular, some of the most important Neotropical grasslands are those of southeastern South America, constituted by a part of Uruguay, southern Brazil and mainly by the Pampas in Argentina (Soriano *et al.* 2001). The conservation status of the Pampas is critical since currently more than 75% of their extent has been converted into croplands (Viglizzo *et al.* 2011). Such habitat loss has caused a decrease in the abundance and distribution of many grassland bird species, including a high proportion of ground nesting birds (Fraga 2003, Di Giacomo & Di Giacomo 2004, Filloy & Bellocq 2007, Azpiroz *et al.* 2012). Roadside conservation and management practices are still uncommon in the region, although it has been reported that ground nesting birds and many other bird species use roadsides more frequently than adjacent pastures and crops (*i.e.*, soy and maize, Leveau & Leveau 2011), and that grassland nesting bird richness increase with the amount of roadside borders in rural areas (Codesido & Bilenca 2011).

Our objective here was to assess breeding habitat suitability for ground nesting birds in roadsides belonging to one modified grassland of the Argentine Pampas. In particular, we analyzed the effects that roadside and surrounding field characteristics have on bird abundance and nest predation. To achieve that aim, in different road types, we performed bird surveys and evaluated the relationship of bird abundance with vegetation structure of roadsides and surrounding fields. Additionally, we conducted an experiment with artificial nests to identify nest predators, and to evaluate the effects that proximity to the road and vegetation structure of roadsides and surrounding fields have on ground nest predation.

METHODS

Study area and sampling sites

Field work was carried out near General Madariaga

city (37°0'7"S; 57°8'10"W), Buenos Aires province, Argentina, within the flooding Pampa. In the flooding Pampa, mean temperature varies from 23°C in January to 13°C in July with mean annual precipitation of 1000 mm (Soriano *et al.* 2001). The area exhibits subtle topographic variations (most lands are less than 4 m above sea level), with lowlands remaining flooded for long periods. For this reason, the flooding Pampa is the least cropped portion of the Pampas and the distribution of many native bird species is restricted to this area, giving it a high conservation value (Codesido *et al.* 2011). However, since 1990's increasing crop lands and cattle production pose conservation implications (Agra *et al.* 2015). Vegetation in this area is a mosaic of extensive grasslands disrupted by wetlands with a high presence of *Schoenoplectus californicus* (Family Cyperaceae), *Solanum glaucophyllum* (Solanaceae), *Senecio* spp. (Asteraceae), and *Typha* spp. (Typhaceae), and by smaller patches of native woodlands comprised mostly of *Celtis ehrenbergiana* (Cannabaceae) in the higher areas (Vervoorst 1967). About 70% of the area is used for cattle production, with land crops covering 20% (Codesido & Bilenca 2011) and the remaining land consisting in deep water bodies, tree plantations, dunes, salt marshes, and urban areas (Baldi & Paruelo 2008). We conducted our study in October–November 2015, which comprises the peak of the breeding season for most bird species (de la Peña 2015). Within an area of approximately 80,000 ha, we sampled roads representing the three types of roads present in the area. Sampled road types were: unpaved roads of local use (three roads), one paved road of one-lane per side that connects General Madariaga city with Las Armas town, and one paved road of two-lanes per side that connects General Madariaga city with Pinamar city. All these roads could be considered as transects, being the mean distance among transects' midpoints 20.4 km (range: 6.2–26.5 km). Road types have different speed limits (two-lanes per side: 110 km/h, one-lane per side: 100 km/h, unpaved: 60 km/h). In addition, road types could have different traffic intensity in terms of vehicles per unit of time. The two-lanes per side probably has the highest amount of vehicles per unit of time since it connects two cities and leads to one of the most important touristic spots along the coast of Buenos Aires province. We further considered the potential differences among road types from a birds' perspective (see Statistical analysis), since it has been reported that traffic-related factors such as noise can affect bird distribution and behavior (Seiler 2001, Kociolek *et al.* 2011).

Along each road we selected points at random distances from the beginning of the sampling section of the road (one-lane per side: $n = 30$ points, two-lanes per side: $n = 30$, unpaved: $n = 30$), being the minimum distance between neighbour points 400 m. Then, in each point we established one sampling plot, which was a

fragment of roadside borders of 200-m length that was centred in the point and comprised the area between the edge of the road, either right or left, and the fence of its adjacent field. Since the width of our roadside borders had a range of 6.0–45.6 m, the area of our sampling plots varied between 0.12 and 1.08 ha.

Bird sampling

In each sampling plot, we performed bird surveys using 10-min point counts, during the first 4 h after sunrise and in good weather conditions (Bibby 2000). Sampling plots were divided in two 100-m length subplots, and each of two observers recorded every bird seen or heard in one subplot, disregarding those birds flying above the plot. We considered that there was minimal need to account for detection probability given the high visibility in these roadside borders mainly constituted by grassland, and because each observer recorded individuals at a maximum distance of 50 m (Smucker *et al.* 2005). To increase the accuracy of abundance estimations, we surveyed each plot twice (one visit during October and the other one during November), and the maximum number of individuals recorded for each species was considered the species' abundance. Later, we classified species by their nesting sites (de la Peña 2015). We only considered in further analyses the abundance of those grassland birds that build their nests directly on the ground, or very close to the ground on clumps of grasses (de la Peña 2015), hereafter designated as "ground nesting birds". We also noted which of these ground nesting bird species are considered as grassland obligates (Azpiroz & Blake 2009). Scientific nomenclature was in accordance with South American Classification Committee (SACC–American Ornithologists' Union, Remsen-Jr. *et al.* 2019).

Vegetation sampling

In each sampling plot, we estimated local vegetation cover based on three transects perpendicular to the road, separated by 75 m. One observer (D. Depalma) measured the length of intersection of each vegetation type (see below) on each transect, by walking along the transect using a measuring tape (Matteucci & Colma 1982). When there was no accessibility (*e.g.*, wetlands), the length of intersection of vegetation types was measured with a rangefinder (Redfield® Raider™ 550). Then we expressed the lengths of intersection as percentages. Finally, in every plot, for each vegetation type we used the average of the three transects. The perpendicular orientation of transects allowed us to account for the vegetation gradient present in roadside borders.

Vegetation types consisted of short grass (areas consisting mainly in grasses shorter than 30 cm), tall grass (grassland of 30–80 cm height dominated by the

exotic pasture *Festuca arundinacea* –with low presence of *Bromus catharticus*, *Dactylis glomerata*, *Triticum aestivum*, *Nassella neesiana*, *Avena sativa* and *Phalaris minor*), Pampa grass (individuals of the native grass *Cortaderia selloana* of 0.7–2 m height), dicotyledoneous (grassland of 30–80 cm height dominated by exotic flowering plants with non-negligible presence of native flowering plants), wetland vegetation (*S. californicus* and *Typha* spp.), water, native trees (*C. ehrenbergiana* and *Scutia buxifolia*) and exotic trees (mainly *Populus* spp.). All flowering plants were classified into the finest level possible, and thus we determined that exotic flowering plants belonging to the family Brassicaceae represented 55% of the total flowering plants, and plants belonging to the native species *Matricaria chamomila* represented 32%. We also counted individual trees within the entire area of each sampling plot. In all statistical analyses, the number of trees was incorporated instead of tree cover, since it may be a more accurate variable to measure in linear fragments (McDonald & Johnson 1995; Table 1). The number of trees has been also mentioned as one of the major factors influencing bird richness and abundance in field borders (Hinsley & Bellamy 2000).

In addition, while measuring vegetation cover at plot scale, we described the cover of surrounding fields. Later, we estimated the cover of surrounding fields in satellite images of November 2015 (Image® 2017 Digital Globe, source: Google® Earth™) with Google Earth Pro Software (Sullivan 2009). Validating the images with our observations recorded in the field, we measured the percentage of short grassland, seminatural grassland, native woodland, exotic woodland, and modified land within a 200-m radius circular area around each plot (Table 1). Short grassland consisted in extremely short grass intensively grazed or mowed. Seminatural grassland consisted in tall grass often moderately disturbed by grazing. Modified land consisted in crops (mainly maize and soy), stubble, and human settlements. Finally, native woodland consisted in groups of trees mainly composed by *C. ehrenbergiana* and *S. buxifolia*, and exotic woodland were composed by at least 80% of exotic trees (mostly *Eucalyptus* spp., Table 1). We considered the percentage of seminatural grasslands as available habitat for grassland birds, and the percentage of native and exotic woodlands and modified land as potential sources of predators.

Artificial nests experiment

Artificial nests carry a certain bias since their visual signals (absence of parental activity) and chemical signals differ from those of natural nests, and thus they may underestimate or overestimate the actual predation risk, according to nest type and predator community composition (Thompson & Burhans 2004). However, they provided us a possibility to evaluate the relationship

Table 1. Characteristics of roadside borders of the Argentine Pampas. Frequencies of occurrence and mean value \pm standard deviation per sampling plot are shown. Ranges are in parentheses.

Vegetation type	Frequency of occurrence (%)	Value per plot
Roadsides		
Short grass (%)	86.6	10.8 \pm 10.5 (0–39.5)
Tall grass (%)	70	32.7 \pm 28.5 (0–95.8)
Pampa grass (%)	47.7	5.7 \pm 10.1 (0–48.5)
Dicotyledonous (%)	82.2	5.4 \pm 6.9 (0–32.9)
Wetland (%)	72.2	21.4 \pm 21.8 (0–87)
Native trees (<i>n</i>)	55.5	7.4 \pm 14.5 (0–71)
Exotic trees (<i>n</i>)	5.5	1.4 \pm 7.6 (0–50)
Total trees (<i>n</i>)	58.8	8.8 \pm 17.4 (0–89)
Surrounding fields		
Seminal grassland (%)	46.6	12.3 \pm 17.2 (0–72.1)
Short grass (%)	60	2.7 \pm 23.9 (0–81.2)
Wetland (%)	76.6	14.4 \pm 15.1 (0–52.8)
Modified land (%)	44.4	8.6 \pm 14.3 (0–55.4)
Native woodland (%)	43.3	1.3 \pm 2.6 (0–11.5)
Exotic woodland (%)	22.2	0.6 \pm 1.4 (0–6.5)
Total woodland (%)	66.6	2.5 \pm 3.8 (0–24.19)

between predation risk and environmental variables through a field experiment, controlling for nest location, clutch size and differences in parental activity around the nest (Thompson & Burhans 2004). In addition, we were able to identify types of predators by the marks left on artificial eggs (Zanette & Jenkins 2000). Within a representative subsample of 60 plots (*i.e.*, one-lane per side: $n = 20$, two-lanes per side: $n = 20$, unpaved: $n = 20$), we placed one artificial nest made of hemp on the ground. To resemble the nesting sites of ground nesting birds, all nests were located beneath a clump of tall grass, therefore equally sheltered. Monitoring was performed every four days until predation occurred or during 16 days, which encompassed the approximate duration of laying plus incubation periods of most ground nesting passerines (de la Peña 2015). The artificial nest (10.5 cm diameter \times 5.5 cm depth) was always placed in the center of the 200 m of the plot, beneath the first clump of tall grass encountered by walking from the road into the roadside border. We used this method instead of selecting fixed locations because, due to the presence of wetlands within most roadsides, many locations were unsuitable for nest placement (Table 1). In each nest, we put two quail eggs (*Coturnix coturnix*): one natural egg and the other filled with paraffin and tied to the nest by a nylon thread (Svagej *et al.* 2003). We considered the removal and/or break of at least one of the eggs as a predation event. When predation was detected, nests were immediately removed and no longer monitored. After monitoring,

we observed the natural and the paraffin-filled eggs and looked for marks. We interpreted the marks based on the criteria used by Cozzani & Zalba (2012) to identify ground nest predators in Buenos Aires province. Thus, we considered incisor marks on the paraffin-filled egg as predation by small mammals, while bigger and deeper teeth marks, and horseshoe shape marks on the natural egg were considered as predation by medium-sized mammals. Likewise, unique, deep marks on the paraffin-filled egg were considered as predation by birds, and the presence of two marks separated by a distance of 0.9 cm was considered predation by ophidians.

Statistical analysis

All statistical analyses were conducted using the R environment (R Core Team 2019). We evaluated the relationship between total abundance of ground nesting birds and environmental variables using a Generalized Linear Mixed Model (GLMM) with the “glmmadmb” function of the “glmmADMB” package (Bolker *et al.* 2012). Since overdispersion occurred when adjusting the model to a Poisson distribution, we solved this problem by using a Negative Binomial distribution. We accounted for potential interdependencies among plots belonging to the same road type by incorporating “road type” as a random factor. Furthermore, since plots along unpaved roads were grouped in three different roads, we incorporated the random factor “road identity”

nested within road type. The dependent variable in the model was total abundance of ground nesting birds. We considered nine candidate independent variables measured at plot scale: the percentage (%) of short grass, tall grass, dicotyledonous, Pampa grass, wetland vegetation and water, the number of native trees, the number of exotic trees, and the number of total trees. We also considered five candidate independent variables of surrounding fields (200-m radius): available habitat for grassland birds (percentage of seminatural grassland), and sources of predators (percentage of native woodland, percentage of exotic woodland, percentage of total woodland and percentage modified land). Since sampling plots had different widths, we incorporated plot area as an offset, which specifies an *a priori* known component to be included in the linear predictor during fitting (Crawley 2012).

We evaluated the support for predictor variables by information theoretic procedures (Burham & Anderson 2002), using the “MuMIn” package (Bartoń 2013). We used Akaike's information criterion corrected for small sample size (AIC_c). In order to improve the parsimony (in terms of model parameters) of the global model, and to avoid generating an excessively large set of models based on sample size which could lead to spurious results (Grueber *et al.* 2011), we only incorporated relevant parameters. In order to define relevant parameters, we first built 14 univariate models, each of them having one candidate independent variable as the only predictor. We incorporated to the global model only those variables that lowered the AIC_c in more than 2 units relative to the null model. Those variables were the percentage of tall grass within roadsides and the number of native trees within roadsides (the correlation between these two variables was not significant). In addition, we also included the interaction between both variables. We considered models with all possible combinations of the three final predictor variables and ranked them by their AIC_c. Finally, we obtained parameter estimates by averaging models with a $\Delta AIC_c < 4$ from the best model, and calculated 95% confidence interval limits of parameter estimates (Grueber *et al.* 2011).

To test the effects of environmental variables on artificial nests' survival we used a mixed Cox proportional hazards model (Cox 1972) with the “coxme” package (Therneau & Therneau 2018). This model is an extension of survival analysis similar to a logistic regression, and is able to evaluate the relationship between independent variables and the rate of occurrence of predation (Santabárbara *et al.* 2016). As with the model of bird abundance, we accounted for potential interdependencies among plots belonging to the same road and road type by incorporating the random factor “road identity” nested within the random factor “road type”. The dependent variable was composed of the survival time (days) and

the occurrence of predation (0 or 1). The coefficient of an independent variable indicates its relationship with the occurrence of predation: a positive coefficient means that the variable is positive associated with the occurrence of predation. Coefficients were calculated by the partial maximum likelihood method. Likewise, for every independent variable the model estimates a Hazard Ratio (HR). A HR > 1 indicates that the variable is positively associated with the probability of predation, while a HR < 1 indicates the opposite. We considered nine candidate independent variables measured at plot scale: the percentage (%) of short grass, tall grass, dicotyledonous, Pampa grass, wetland vegetation and water, the number of native trees, the number of exotic trees, and the number of total trees. We also considered four candidate independent variables of surrounding fields (sources of predators within the 200-m radius): percentage of native woodland, percentage of exotic woodland, percentage of total woodland, and percentage of modified land.

To improve the parsimony of a potential global model, we first built one univariate mixed model to test the effect of each independent variable on survival separately, in order to further incorporate relevant parameters only. The only independent variable that had a significant effect on survival was “distance to road”. We checked the assumptions about the linear functional form of the independent variables and hazards proportionality (*i.e.*, the ratio of the survival rates remaining constant through time; Santabárbara *et al.* 2016). To accomplish this, we deleted two nests belonging to the two-lanes per side road that impeded the linear functional form of the variable “distance to road”. These nests (*i.e.*, outliers) were removed from all the analyses.

RESULTS

Bird abundance

We made 2832 records of 84 species using roadside borders. Amongst them, 1083 individuals (38.2%) belonging to 13 species (15.5%) were ground nesting species (Appendix I). Seven of these species are considered grassland obligates (*Leistes superciliaris*, *Anthus correndera*, *Sicalis luteola*, *Embernagra platensis*, *Vanellus chilensis*, *Nothura maculosa* and *Rynchotus rufescens*; Appendix I). As shown by the GLMM, ground nesting birds' abundance was positively associated with the percentage of tall grass within roadsides, and negatively associated with the number of native trees within roadsides (Table 2).

Survival of artificial ground nests

Of the 60 artificial nests we set out, 31 were predated within the 16-day period (one-lane per side: $n = 10$, two-

lanes per side: $n = 10$, unpaved: $n = 11$). Thus, artificial nest survival was 48.3%. According to the criteria used by Cozzani & Zalba (2012), 43.7% of predated nests (14 nests) exhibited small mammal marks, 15.6% (5 nests) were predated by medium sized-mammals, 9.4% (3 nests) were predated by birds and 3.1% (1 nest), by ophidians (Fig. 1). In 25% of nests (8 nests), we could not identify the predator, since in five cases the artificial egg had non identifiable marks (Fig. 1), and in three cases it had been removed. In such situations, we could not identify the predator using the natural egg either, since it had been removed in four nests, and it exhibited unidentifiable marks in the remaining nests.

Moreover, during field work we detected potential mammalian predators: *Galictis cuja* (Order Carnivora), *Conepatus chinga* (Order Carnivora), *Cavia aperea* (Order Rodentia) and *Didelphis albiventris* (Order Didelphimorphia). We also detected potential ophidian predators: *Liophis poecilogyrus* and *Liophis anomalus* (Order Squamata). Likewise, we recorded potential avian predators during bird surveys: *Caracara plancus*, *Milvago chimango*, *Chroicocephalus maculipennis*, *Circus buffoni* and *Guirra guirra* (Appendix I).

As shown by the results of mixed univariate Cox regressions, only distance to road had a significant effect on nest survival. The probability of nest predation was

Table 2. Candidate Generalized Linear Mixed Models with factors influencing the abundance of grassland ground nesting bird species in roadside borders of the Argentine Pampas, listed in decreasing order of importance. Only those models with a $\Delta AIC_c < 4$ from the best model and the null model are included. Averaged estimates of parameters are shown in the second part of the table. Those parameters whose 95% Confidence Intervals excluded 0 are in bold. K: number of parameters. TGR: tall grass of roadsides; NTR: native trees of roadsides; TGR*NTR: interaction term. SE: unconditional Standard Error. CI: 95% Confidence Interval.

Candidate models	K	Log-likelihood	AIC _c	ΔAIC_c	Weight
TGR + NTR	6	-262.22	537.5	0	0.58
TGR	5	-264.39	539.5	2.04	0.21
TGR + NTR + TGR*NTR (Global model)	7	-262.1	539.6	2.13	0.2
Null model	4	-268.91	546.3	8.83	0.01

Model averaging	Estimate	SE	CI	Relative importance
TGR	0.247	0.07	0.097, 0.397	1
NTR	-0.092	0.07	-0.229, -0.005	0.79
TGR*NTR	0.001	0.02	-0.073, 0.119	0.2

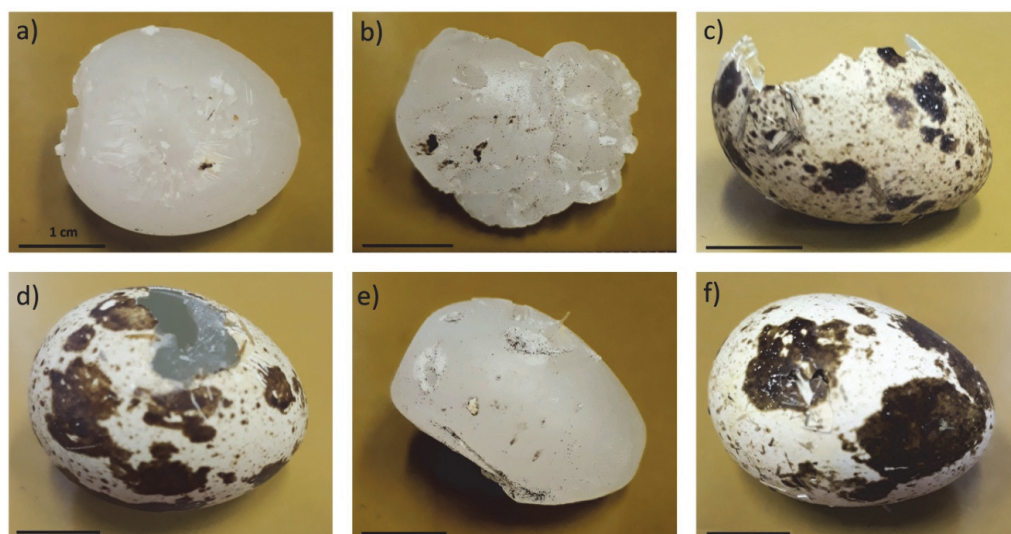


Figure 1. Predated natural and paraffin-filled *Coturnix coturnix* eggs on roadside borders of the Argentine Pampas. Examples of marks produced by small-sized mammals' incisors (A), medium-sized mammals' teeth marks (B), a horseshoe-shaped mark produced by a medium-sized mammal (C), one unique bird's beak mark (D), two marks produced by an ophidian predator (E) and one unidentifiable mark (F).

positively associated with the distance to road ($P < 0.05$; Table 3, Fig. 2). Nevertheless, the probability of nest predation also exhibited a marginal positive association with the number of native trees within roadsides ($P = 0.05$, Table 3).

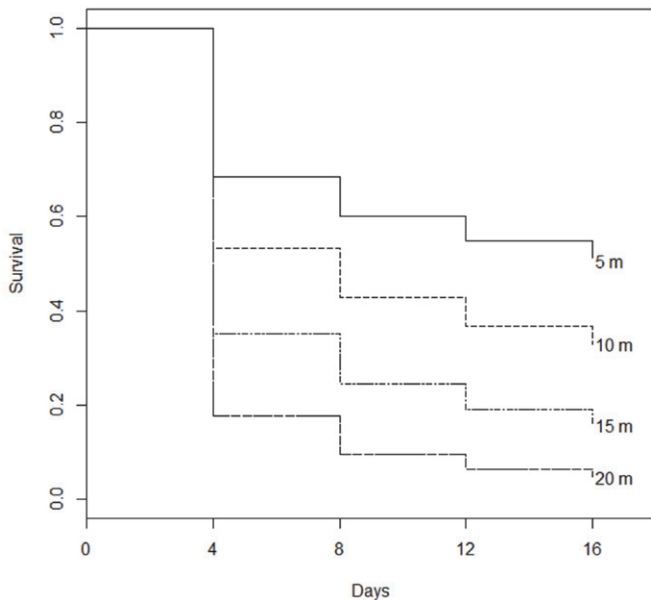


Figure 2. Expected survival curves for artificial nests located at different distances to the road in roadside borders of Argentine Pampas. Survival curves were built by fitting a mixed Cox proportional hazards model with distance to the road as the predictor variable. Predicted survival for nests located at 5, 10, 15 and 20 m from the road are shown.

DISCUSSION

In order to assess the suitability of roadsides for ground nesting birds in one modified grassland of the Argentine Pampas, we evaluated the influence of roadside factors and surrounding field factors on bird abundance, and on the predation of artificial nests. We found that bird abundance was positively associated with tall grass cover of roadsides and negatively associated with the number of native trees of roadsides, while evidence of predation decreased with proximity of nests to the road.

Regarding bird abundance, our results indicate that tall grass cover of roadsides favors their use by ground nesting birds, while the number of native trees reduces it. Similarly, it has been previously reported that ground nesting birds of the Pampas such as *Sicalis luteola* use grassy field margins more frequently than margins with trees (Leveau & Leveau 2011). In another study of birds inhabiting field margins of the Argentine Espinal region, authors found that while total bird density increased with the number of trees, the density of some ground nesters decreased (Di Giacomo & Lopez-de-Casenave 2010). In this sense, it is possible that tall grass increase the amount of escape cover and nest concealment for most ground nesters considered in our study (Isacch & Martínez 2001, Davis 2005), while native trees in the proximities imply higher rates of nest predation and parasitism (Flaspohler *et al.* 2001, Patten *et al.* 2006, Pietz *et al.* 2009). It is not clear why only native trees, rather than total trees,

Table 3. Factors influencing predation of artificial nests in roadside borders of Argentine Pampas, tested by Mixed Cox Logistic Regression models. Regression coefficient and hazard ratio for the predictor variable of each of the univariate models are shown. Significant predictor variables ($P < 0.05$) are in bold.

Univariate model	Coefficient	P-value	Hazard ratio
Short grass	0.005	0.57	1.01
Tall grass	-0.005	0.41	0.99
Pampa grass	0.014	0.5	1.01
Dicotyledonous	-0.036	0.27	0.96
Wetland vegetation	0.007	0.43	1.01
Water	-0.005	0.73	0.99
Native trees	0.02	0.05	1.02
Exotic trees	-0.02	0.37	0.97
Total trees	0.006	0.41	1.01
Distance to road	0.102*	0.02	1.11
Modified land	< -0.001	0.21	0.99
Native woodland	0.028	0.71	1.02
Exotic woodland	0.105	0.37	1.11
Total woodland	< -0.001	0.97	0.99

* $P < 0.05$

. $P < 0.1$

were negatively associated with bird abundance. One explanation is that native trees attract more predators than exotic trees. For example, in the Pampas, insectivorous birds usually prefer to forage on native trees than on exotic ones (Cueto & Lopez-de-Casenave 2002). Therefore, native trees could attract some insectivorous birds that predate nests opportunistically, and thus represent an additional predation pressure. Another explanation is that native trees were more abundant than exotic ones in roadsides (Table 1) and formed continuous lines along field fences, which could provide more shelter to predators, and be perceived by sharp edges by birds (Fletcher & Koford 2003, Weldon & Haddad 2005).

Unlike local vegetation of roadsides, the cover of surrounding fields did not relate with bird abundance. On the one hand, the lack of associations between bird abundance and the cover of seminatural grasslands in the landscape could suggest that during the breeding season birds travel short distances to fulfill their requirements, and forage within nest proximities rather than using surrounding alternative habitats (Robinson *et al.* 2004, Vickery *et al.* 2009). On the other hand, the lack of associations between abundance and sources of predation such as woodlands and modified lands could be related to the characteristics of our study area. Also in the flooding Pampa, Pretelli *et al.* (2018) found no negative effect of agriculture on the abundance of grassland specialist birds inhabiting grassland remnants, probably because in this region agriculture is often mixed with short grasses and pastures. In contrast, they did report a negative effect of a continuous forest matrix around grassland remnants on bird abundance, although our study area did not exhibit a forest matrix but rather small scattered patches of woodland, which could be perceived differently by birds.

Regarding nest predation, most marks left on artificial nests belonged to mammals. A high frequency of predation by mammals in our nests is consistent with other studies, which compared nest predation at different heights and reported that mammals were the most frequent predators of ground nests (Söderström *et al.* 1998, Colombelli-Négrel & Kleindorfer 2009). As proposed for other habitat strips within modified landscapes, these roadsides could serve as corridors for mammals, which could predate nests in an opportunistic manner as they travel (Meunier *et al.* 1999, Conover *et al.* 2011).

Additionally, predation mostly due to mammals could explain the striking negative relationship between proximity to the road and the probability of predation. These animals are usually affected by the presence of roads (Seiler 2001, Benítez-López *et al.* 2010). Moreover, recent researches about animals killed by collisions in Argentine roads found dead individuals of some of the mammalian predators we detected during this study such

as *Didelphis albiventris*, *Galictis cuja* and *Cavia aperea* (Attademo *et al.* 2011, Bauni *et al.* 2017). Therefore, it is possible that mammals do not prefer to forage in road proximities, but rather move along the road, parallel to it (Forman & Alexander 1998, Meunier *et al.* 1999).

Nevertheless, the success of real nests may be influenced by additional factors. Real nests might not be exposed to the same predation pressures as artificial nests (Thompson & Burhans 2004), and artificial nests can underestimate predation by birds due to the lack of parental activity (Söderström *et al.* 1998, Flaspohler *et al.* 2001). Thus we cannot reject based on our results the possibility that nest predation may be causing the negative relationship between bird abundance and native trees, and that native trees may have a significant, rather than marginal, positive effect on nest predation. During bird surveys, we detected avian predators perching on trees in roadsides (Appendix I), and trees could offer them lookouts during the predation of real nests (Flaspohler *et al.* 2001).

Another explanation, although not excluding, would be that the negative association between grassland birds and native trees is actually the result of a higher risk of nest parasitism near trees (Patten *et al.* 2006, Pietz *et al.* 2009). Within the Pampas, nest parasitism by the generalist brood parasite *Molothrus bonariensis* is one of the major causes of egg losses for nesting birds, due to the punctures performed on the host's eggs during inspection visits (Massoni & Reboreda 2002). However, this icterid might not be able to break the thick shell of quail eggs (Svagej *et al.* 2003). Likewise, it might not visit artificial nests frequently, since parasites' behavior is usually based on parental activity around the nest (Wilson *et al.* 1998). The monitoring of real nests would be necessary in order to test the potential implications of native trees for nest predation and parasitism. In addition, real nest monitoring could also clarify the effect of road proximity on ground nest success. Although our artificial nests were less likely to be predated in road proximities, chicks of natural nests that hatch and fledge closer to roads may be more exposed to collisions (Kociolek *et al.* 2011).

In summary, this paper highlights that roadside borders of the flooding Pampas are inhabited by a wide range of grassland bird species, including several grassland obligates, and their conservation value could be increased with the application of appropriate managements. Such managements should consider the importance of tall grass for ground nesting birds, as well as the negative effects of native trees on their abundance. Future studies that involve the monitoring of real nests are necessary in order to elucidate the potential effects of native trees, distance to the road, and other environmental variables on ground nest success.

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APPENDIX I

Birds recorded using roadside borders of the Argentine Pampas ($n = 90$ sampling plots). In every plot, the maximum abundance of each species recorded across samplings (October and November) was used. Total individuals of each species summed those detected over the 90 sampling plots. (*) Grassland ground nesting species. (**) Grassland obligates.

Order, Family, Species	Total individuals	Presence (%)	Mean abundance
TINAMIFORMES			
Tinamidae			
<i>Rhynchotus rufescens</i> * **	27	22.22	0.03
<i>Nothura maculosa</i> * **	7	7.77	0.07
ANSERIFORMES			
Anhimidae			
<i>Chauna torquata</i>	1	1.11	0.01
Anatidae			
<i>Dendrocygna viduata</i>	1	1.11	0.01
<i>Callonetta leucophrys</i>	4	2.22	0.04
<i>Spatula versicolor</i>	15	7.77	0.16
<i>Anas georgica</i>	2	1.11	0.02
<i>Anas flavirostris</i>	4	3.33	0.04
<i>Netta peposaca</i>	3	2.22	0.03
PODICIPEDIFORMES			
Podicipedidae			
<i>Rollandia rolland</i>	4	2.22	0.04
<i>Podilymbus podiceps</i>	2	2.22	0.02
<i>Podiceps major</i>	1	1.11	0.01
COLUMBIFORMES			
Columbidae			
<i>Patagioenas picazuro</i>	10	8.88	0.11
<i>Zenaida auriculata</i>	63	36.66	0.7
<i>Columbina picui</i>	3	2.22	0.03
CUCULIFORMES			
Cuculidae			
<i>Guira guira</i>	25	5.55	0.27
GRUIFORMES			
Aramidae			
<i>Aramus guarauna</i>	1	1.11	0.01
Rallidae			
<i>Pardirallus maculatus</i>	1	1.11	0.01
<i>Pardirallus sanguinolentus</i>	15	13.33	0.16
<i>Porphyriops melanops</i>	2	2.22	0.01
<i>Fulica ruffrons</i>	3	2.22	0.03
<i>Fulica armillata</i>	6	2.22	0.06
<i>Fulica leucoptera</i>	4	4.44	0.04
APODIFORMES			
Trochilidae			
<i>Chlorostilbon lucidus</i>	8	3.33	0.08

Order, Family, Species	Total individuals	Presence (%)	Mean abundance
CHARADRIIFORMES			
Charadriidae			
<i>Vanellus chilensis</i> * **	2	1.11	0.02
Recurvirostridae			
<i>Himantopus mexicanus</i>	2	1.11	0.02
Laridae			
<i>Chroicocephalus maculipennis</i>	29	5.55	0.32
<i>Gelochelidon nilotica</i>	1	1.11	0.01
SULIFORMES			
Phalacrocoracidae			
<i>Phalacrocorax brasilianus</i>	1	1.11	0.01
PELECANIFORMES			
Ardeidae			
<i>Ardea alba</i>	2	2.22	0.02
<i>Egretta thula</i>	1	1.11	0.01
ACCIPITRIFORMES			
Accipitridae			
<i>Elanus leucurus</i>	1	1.11	0.01
<i>Rostrhamus sociabilis</i>	21	14.44	0.23
<i>Circus buffoni</i>	5	3.33	0.05
<i>Rupornis magnirostris</i>	1	1.11	0.01
PICIFORMES			
Picidae			
<i>Colaptes melanochloros</i>	1	1.11	0.01
<i>Colaptes campestris</i>	2	2.22	0.02
FALCONIFORMES			
Falconidae			
<i>Caracara plancus</i>	24	16.66	0.26
<i>Milvago chimango</i>	27	24.44	0.3
PSITTACIFORMES			
Psittacidae			
<i>Myiopsitta monachus</i>	62	18.88	0.68
PASSERIFORMES			
Furnariidae			
<i>Furnarius rufus</i>	32	25.55	0.35
<i>Phleocryptes melanops</i>	90	37.77	1
<i>Leptasthenura platensis</i>	2	2.22	0.02
<i>Phacellodomus striaticollis</i>	23	2.22	0.25
<i>Anumbius annumbi</i>	25	21.11	0.31
<i>Limnortyx sulphiferus</i>	35	24.44	0.38
<i>Synallaxis albescens</i>	3	1.11	0.03

Order, Family, Species	Total individuals	Presence (%)	Mean abundance
Tyrannidae			
<i>Serpophaga nigricans</i>	8	7.77	0.08
<i>Serpophaga subcristata</i>	1	1.11	0.01
<i>Pseudocolopteryx flaviventris</i>	61	38.88	0.67
<i>Tachuris rubrigastra</i>	8	5.55	0.08
<i>Pyrocephalus rubinus</i>	14	10	0.15
<i>Hymenops perspicillatus</i>	144	74.44	1.6
<i>Satrapa icterophrys</i>	7	6.66	0.07
<i>Machetornis rixosa</i>	2	2.22	0.02
<i>Pitangus sulphuratus</i>	57	35.55	0.63
<i>Tyrannus melancholicus</i>	17	13.33	0.18
<i>Tyrannus savana</i>	64	37.77	0.71
Hirundinidae			
<i>Progne tapera</i>	9	6.66	0.1
<i>Progne chalybea</i>	3	3.33	0.03
<i>Tachycineta leucorrhoa</i>	24	20	0.26
<i>Hirundo rustica</i>	128	28.88	1.42
Troglodytidae			
<i>Troglodytes aedon</i>	25	22.22	0.27
<i>Cistothorus platensis</i>	1	1.11	0.01
Poliophtilidae			
<i>Poliophtila dumicola</i>	5	4.44	0.05
Turdidae			
<i>Turdus rufiventris</i>	5	5.55	0.05
Mimidae			
<i>Mimus saturninus</i>	14	10	0.15
Motacillidae			
<i>Anthus correndera</i> * **	3	3.33	0.03
Fringillidae			
<i>Spinus magellanicus</i>	9	6.66	0.1
Passerellidae			
<i>Zonotrichia capensis</i> *	378	96.66	4.2
Icteridae			
<i>Leistes superciliaris</i> * **	1	1.11	0.01
<i>Molothrus bonariensis</i>	219	73.33	2.43
<i>Amblyramphus holosericeus</i>	19	12.22	0.21
<i>Agelaioides badius</i>	58	16.66	0.64
<i>Agelasticus thilius</i>	152	56.66	1.68
<i>Pseudoleistes virescens</i>	222	72.22	2.46
Thraupidae			
<i>Sicalis flaveola</i>	28	15.55	0.31
<i>Sicalis luteola</i> * **	526	85.55	5.84
<i>Sporophila caerulescens</i>	8	5.55	0.08

Order, Family, Species	Total individuals	Presence (%)	Mean abundance
<i>Embernagra platensis</i> * **	111	65.55	1.23
<i>Poospiza nigrorufa</i>	64	45.55	0.71
<i>Donacospiza albifrons</i> *	6	5.55	0.06
<i>Paroaria coronata</i>	1	1.11	0.01
<i>Pipraeidea bonariensis</i>	5	3.33	0.05