

Nest-predation at the edge: an experimental study contrasting two types of edges in the dry Chaco, Paraguay

Lena M. Eriksson

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Forest fragmentation leads to the creation of isolated forest patches with subsequent impact on forest-interior flora and fauna. Forested corridors have been suggested to alleviate some of the impact by increasing the connectivity between remnant forest patches. However, both fragmentation and corridors increase the ratio of edge to core habitat. We studied nest predation of artificial nests at edges between 1) contiguous forests and pastures and 2) forested corridors and pastures, in a forest-dominated landscape in the dry Chaco, Paraguay. The aim was to determine if nest predation was higher near habitat edges compared to within forests and pastures, with special emphasis on edges at forested corridors. We found that predation rates were similar at edges and in interior habitats. Nest predation was higher for both ground and shrub nests in forested areas than in pastures. Predation rates were also higher for both ground and shrub nests at edges along forested corridors compared to edges neighbouring contiguous forests. Forested corridors connecting contiguous forests may thus act as an ecological sink for some species breeding here. Analysis of predator categories revealed that ground nests in pastures were relatively more depredated by mammals and less by birds, compared to both shrub nests in pastures and ground nests in forests.

Lena M. Eriksson, Swedish Institute for Ecological Sustainability, P. O. Box 7980, SE-907 19 Umeå, SWEDEN. E-mail: Lena.Eriksson@ieb.se

Introduction

As fragmentation of natural habitats continues at an accelerating rate, there is a growing concern for its documented and presumed negative impact on native flora and fauna (Estrada et al. 1993, Robinson et al. 1995, Keyser et al. 1998, Harrison and Bruna 1999). The increased ratio of edge to core area that follows fragmentation may benefit generalist predators at the expense of their prey species and species with narrower niches (Wilcove 1985, Noss and Csuti 1997). Furthermore, the increased isolation of populations might increase risks of extinction (Noss and Csuti 1997). Corridors with natural vegetation have been suggested to alleviate the negative impact of fragmentation to some extent by increasing the connectivity in the landscape and providing shelter, habitat and dispersal routes between patches of natural habitat (Simberloff and Cox 1987, Noss 1987, Saunders and Hobbs 1991). However, corridors may also have negative effects by increasing the ratio of edge to core habitat and by facilitating the spread of invasive alien species, fire and diseases (Noss 1987). Corridors may in addition turn out to be ecological sink habitats for some species, if these suffer higher mortality rates in the corridors than they would in their native habitats (Simberloff and Cox 1987, Saunders and Hobbs 1991). Nicholls and Margules (1991) argue that explicit evidence for the conservation value of corridors is still scarce and in need of scientific verification, if limited economic resources should be diverted from securing the protection and management of large areas of natural habitats.

Nest predation is suggested to be a major cause for the reproductive failure of passerine birds, especially in landscapes fragmented by humans (Wilcove 1985, Robinson et al. 1995). However, natural nests are sometimes difficult to locate and their fates troublesome to determine. They are also not always placed in accordance with required experimental designs. Predation on artificial bird nests has therefore been used as a convenient tool to evaluate the effects of fragmentation and habitat edges (Wilcove 1985, Andrén 1992, see Paton 1994). Even

though predation on artificial nests may not mimic natural predation rates (Storaas 1988, Willebrand and Marcström 1988, King et al 1999), the method is suggested to be suitable when comparisons of relative predation rates are made between local habitats (Reitsma 1992, Roper 1992, but see Martin 1987). We are therefore chosen this approach although we are aware of the ambiguities involved when using artificial nests. The dry Chaco is not well studied ecologically and the use of artificial nests presents a first indication of ecological interactions in the area, that could be followed up with additional studies. Many studies of nest predation in forests adjacent to forest-farmland edges suggest that bird nest predation increases near edges (see Paton 1994, Andrén 1995), but the opposite result has also been found (Nour et al. 1993, Marini et al. 1995, Bayne and Hobson 1997).

We performed a nest-predation study in a forest-dominated landscape in the dry Chaco, Paraguay, that has been exposed to clear-cuttings during the last 20 - 25 years following the establishment of cattle-ranches. The legislation of Paraguay states that buffer zones of natural vegetation (henceforth forested corridors), at least 100 m wide, must be left between pastures in order to prevent soil erosion and spread of pests and fire (Anon. 1986). Corridor use as habitat and dispersal routes for the native fauna has just recently begun to be studied (Areskoug, unpubl.). By carrying out the study in a forest-dominated landscape, the effects of edges and corridors may not be confounded by differences in forest patch-size and in differential isolation of these.

We used artificial nests to experimentally evaluate the relative level of nest predation at forest-pasture edges and forested corridors in this landscape. We addressed three connected aspects: 1) Does the level of predation differ between forest and pasture, the two major habitats at this study-site? 2) Does the level of predation differ between edges at forested corridors and edges neighbouring contiguous forest? 3) Does an edge effect exist, i.e. increased pre-

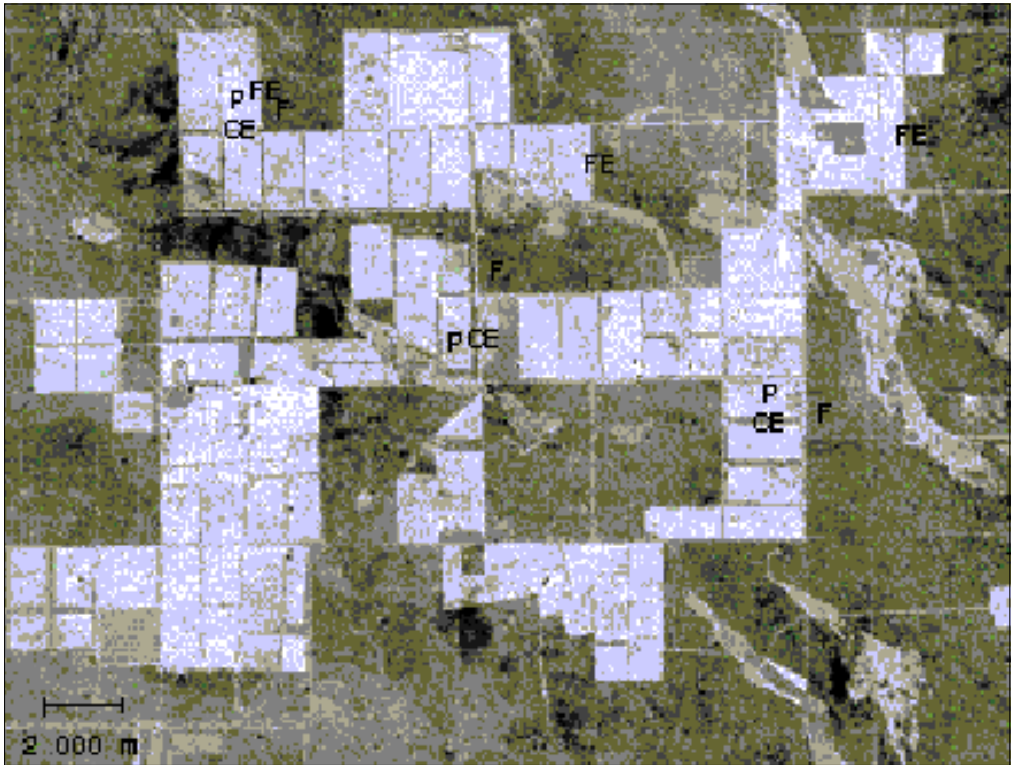


Fig. 1. Satellite image of the study area. FE = Forest edges, CE = Corridor edges, F = Interior forests, P = Interior pastures.

dation near edges, and if so, how far from the edge does it extend? In addition we aimed at identifying categories of predators in forests and pastures by marks left in clay-eggs.

Nomenclature for birds follow Hayes (1995), for mammals Wilson and Reeder (1993) and for trees Lopez et al. (1987).

Methods

Study Site

The study was carried out at Gran Siete in the dry Chaco, Paraguay (S 22(31', W 060(36'). Gran Siete encompasses five cattle-ranches that cover a total of 35 000 ha of which 17 000 ha have been cleared for pastures since the 1970's (Fig. 1). Mean annual temperature is around 24(C, reaching above 40(C during the austral summer months (November to Januari), and occasionally dropping below freezing during winter nights (Hayes 1995). Precipitation is low, reaching aro-

und 800 mm per year, and is highly seasonal and concentrated to the summer months (Hayes 1995). No precipitation was recorded during this study (July and August 1999), but drinking water for animals is available at human-made water holes.

The dominant natural vegetation in the area is dry thorn scrub forest with a 3-4 m high canopy. Dominating species are *Ruprechtia triflora*, *Acacia* spp. and *Prosopis* spp., together with some *Cereus stenogonus* and *Cereus coryne*. The canopy is interspersed with 10-12 m high trees of predominantly *Aspidosperma quebracho-blanco*, *Schinopsis quebracho-colorado*, *Bulnesia sarmientoi*, *Chorisia insignis*, and in lower areas also *Calycophyllum multiflorum*. Bromeliaceae and Cactaceae are major components of the ground vegetation. Vegetation composition in natural habitats has been described in detail by Short (1975). Almost all of the natural grasslands have been turned into pastu-

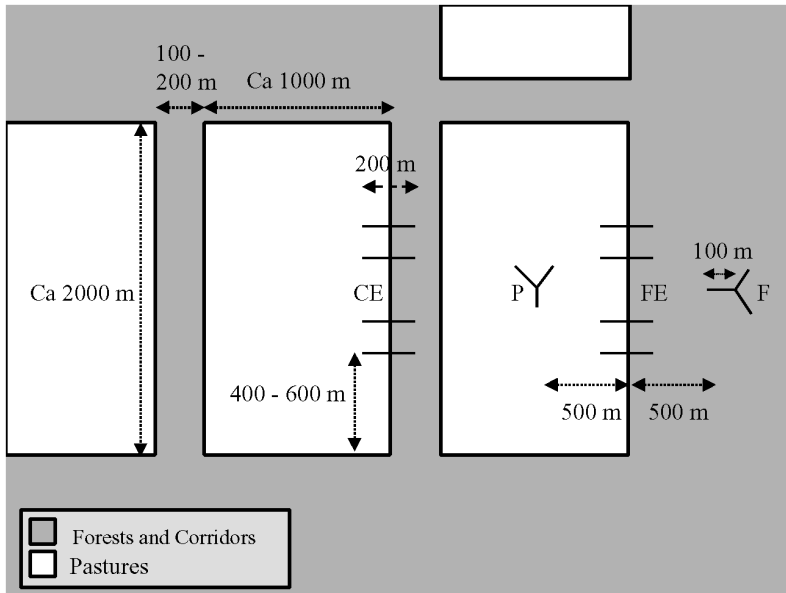


Fig. 2. A schematic view showing an approximate set-up for a forest edge (FE), a corridor edge (CE), an interior forest (F) and an interior pasture (P).

res or cultivated fields and planted with introduced, more palatable, grasses or crops.

The pastures at Gran Siete are normally around 200 ha (1000 x 2000 m) with forested corridors 70 - 200 m wide in between, connecting areas of contiguous forests (Fig. 1). The pastures are planted with Buffalo grass *Pennisetum ciliare* and Gatom panic *Panicum maximum* var. gatom panic, and varies much in grass height, shrub height and in percentage cover of grass, shrub and bare ground, depending on their management history. *Acacia* spp. and *Ruprechtia triflora* dominate among shrubs.

The edges between forests and pastures are straight and sharp, at most creating a limited visual edge-zone with denser vegetation, although effects of abiotic factors such as wind, light and temperature are likely to extend some distance into the forests. Wire-fencing separates different pastures and are located in the middle of corridors and 35 - 50 m into the forest at edges between contiguous forests and pastures. Grazing has therefore had an impact on ground vegetation to a varied extent at edges. The fences are not a hinder for the passage of the native fauna.

Some open cup nesters in this region are cinereous tyrant *Knipolegus striaticeps*, red-crested

finch *Coryphospingus cucullatus*, greater wagtail-tyrant *Stigmatura budytoides*, many-coloured chaco-finch *Saltatricula multicolor* and grassland sparrow *Ammodramus humeralis*; see de la Peña (1988, 1989). Of 65 species of the Order Passeriformes mist netted or seen at Gran Siete during the course of this study, 16 species are open cup nesters; 26 are closed cup; 8 are cavity nesters; 5 use hanging cups; 2 utilise mud or dirt; there is 1 platform and 1 ground depression nester, and there is 1 brood parasite. Five species have nest types which are unknown/not described (de la Peña 1988, 1989, Isler and Isler 1999, Sick 1993). Potential mammal nest predators in the area are Azara's fox *Pseudalopex gymnocercus*, crab-eating fox *Cerdocyon thous*, Geoffroy's cat *Oncifelis geoffroyi*, tayra *Eira barbara*, lesser grison *Galictis cuja*, white-eared opossum *Didelphis albiventris* and several rodents. Potential nest predators among birds are great antshrike *Taraba major*, rufous-browed peppershrike *Cyclarhis gujanensis*, plush-crested jay *Cyanocorax chrysops*, golden-billed saltator *Saltator aurantiirostris*, white-banded mockingbird *Mimus triurus*, red-legged seriema *Cariama cristata* and crested caracara *Polyborus plancus*. The dry Chaco also has a prolific reptile fauna where some species could be potential nest predators.

Nest Predation

The study was carried out in August 1999, just before the onset of the main breeding season for birds. We selected edges between contiguous forest and pasture (FE) and edges between forested corridors (100 - 200 m wide) and pasture (CE) (Fig. 1). Edges were for some analysis further divided into a forested part (FE-F and CE-F respectively) and a pasture part (FE-P and CE-P respectively). We used interior forests (F) and interior pastures (P) as controls and these were located at least 400 m from the nearest edge (Fig. 1). Three replicates of each type (for simplicity henceforth habitats) were used, separated by 7 500 - 9 500 m.

Four transects were set up at each edge running perpendicular to the edge, reaching 100 m into the forest/corridor and 100 m into the pasture (Fig 2). The distances between transects at an edge were 200 - 400 m and the minimum distance from a transect to another edge was 400 - 600 m (Fig. 2). We used a thin, dark green nylon thread along transects in forested areas so they could be located without clearing conspicuous trails. The thread was placed through the dense canopy and was thus well hidden and not possible to follow for predators. It was high enough (approximately 140 - 160 cm) for most animals to pass under, rheas (*Rhea americana*) excluded, and low enough to be reached by a hand and followed. A nest-station was marked every 25 m, (9 nest-stations per transect, 36 per edge), with one station being placed exactly at the border between forest and pasture, using knots on the nylon thread in forested areas and flagging tape in pastures. The flagging tape was tied to shrubs at least 10 m from nest-stations, a distance suggested not to affect predation rates by predators using visual cues (see Major and Kendall 1996).

The experiment was run for four consecutive trials, each lasting four days. Four days was chosen since it mimics egg-laying patterns of some passerines in the area, and is thus a period where the nests are left unattended by the parent birds for longer periods of time. In each trial, nine ground nests and nine shrub nests were

randomly placed among the 36 nest-stations at each edge, so that one ground and one shrub nest was placed at each distance from the edge. All nests were relocated to other nest-stations along the transects for every new trial. A design with varied distances between nests at each trial was used to lower the risk that predators would develop a search-pattern over the trials (Yahner and Mahan 1996). Areas approximately 400 m into the forests and 400 m into the pastures were used as controls. Three 100 m transects were set up in each area extending from a centre-point, with nest-stations every 25 m (Fig. 2). During each trial, one ground and one shrub nest were placed on each transect at one of the marked nest-stations. A ground and a shrub nest were never placed at the same nest-station at the same trial, and each nest-station only received one ground and one shrub nest during the experiment. No studies on natural nest densities have been made in the area but are in progress (Meritt, unpubl.). We used on average one nest/ha/trial during the experiment.

The artificial nests were open cup canary nests of rattan woven through with millet (Vo-Toys Inc., Harrison, NJ 07029, USA). They measured 103 mm ((3 mm, 1 SD, N = 10) in outer diameter and 44 mm ((3 mm, N = 10)) in outer height. The same type of nest was used in all habitats and for both ground and shrub nests. Shrub nests were wired to forked branches, using a light gauge steel wire, at a mean height of 140 cm ((12 cm, 1 SD, N = 156) in forested areas and 71 cm ((23 cm, N = 132) in pastures, depending on available vegetation. Ground nests were wired to bases of canopy trees in forested areas and bases of shrubs in pastures. Dominating plant species used as substrates were *Ruprechtia triflora* and *Acacia* spp. We used three types of eggs in this study; Quail eggs (length 35 mm, (1 mm, 1 SD; width 27 mm, (0.8 mm; weight 11 g, (0.9 g, N = 30); Clay eggs, made of non-hardening and non-toxic light-grey modelling clay (length 22 mm, (0.6 mm; width 15 mm, (0.5 mm; weight 3 g, (0.1 g, N = 30; AMACO Inc.), that were secured in the nest by a thin gauge steel wire (Darice Inc.); Light-blue hard plastic eggs

(length 19.5 mm; width 12.5 mm; weight 1,5 g, $N = 30$). One egg of each type was placed in each nest during the experiment. Depredated eggs and nests were collected for later identification of predators. No attempts were made to conceal nests or mimic nests and/or eggs of a specific bird species. Rubber gloves and rubber boots were used to reduce human scent.

We classified a nest as depredated when one or more eggs were removed, broken or when the clay or plastic egg had marks on them. Twenty-two shrub nests that were disturbed by wind in pastures (the quail and the plastic egg was found beneath the nest after several days of strong winds) were classified as not depredated for the following reasons: The nests were still baited with the egg that performed best during the study; There were no signs of predation and the quail egg and plastic egg were found below the nest; Including these nests as not depredated in analysis may have introduced a bias and underestimated the predation rate in pastures since the clay egg did not capture 100 % of the predation in the study. However, excluding these nests would have increased the calculated predation rate for pastures and therefore, in our opinion, introduced a larger bias than if these nests were included in analyses.

Data Analysis

Ground nests and shrub nests were analysed separately. Two-tailed probabilities and a p -value of 0.05 were used in all statistical tests. Bonferroni correction for multiple comparisons was used when appropriate. There were no significant differences in nest predation between the three replicates so data was pooled for analysis.

We used two methods to test if nest predation events were independent, that is not influenced by the fate of neighbouring nests. The first method (modified from Hannon and Cotterill 1998) treated ground nests and shrub nests separately and looked at neighbouring nests on each transect and recorded in how many instances they were a) both depredated, b) one depredated and one not depredated or c) both not depredated, to get observed values for each

event. Expected frequencies were calculated from the observed overall probability of predation for shrub (0.42) and ground nests (0.44) using a binomial distribution ($p^2 + 2pq + q^2$). p is the probability of a nest being depredated and q the probability of the nest escaping predation. p^2 is thus the expected frequency of two neighbouring nests both being depredated, $2pq$ is the expected frequency of one nest being depredated, the other not, and q^2 is the expected frequency of two neighbouring nests escaping predation. Expected frequencies were multiplied by the total number of depredated nests to give expected values for each event.

Secondly, if the fate of a nest is influenced by the fate of its neighbour, then the mean distance between nests experiencing the same fate should be shorter than between neighbouring nests experiencing different fates. We thus calculated and compared the mean distance between neighbouring nests that experienced the same fate (both depredated, or both not depredated) and between those that experienced different fates (only one nest being depredated).

We used logistic regression to detect whether the risk of an individual nest becoming depredated was influenced by the following parameters: Type of edge, i.e. edge between contiguous forest and pasture and edge between forested corridor and pasture; Habitat, i.e. forest and pasture; Distance, i.e. distance from edge; Trial, i.e. during which trial the nest was placed.

Predators were divided into the following categories: 1) Large-gaped birds - the clay egg showed marks of bird predation and the quail egg was depredated, e.g. *Cyanocorax chrysops* and *Cariama cristata*; 2) Other birds - the clay egg showed marks of bird predation but the quail egg was intact, e.g. *Taraba major* and *Mimus triurus*; 3) Large-gaped mammals - judged from marks on clay eggs, e.g. *Pseudalopex gymnocercus* and *Eira barbara*; 4) Small-gaped mammals - rodents and possibly opossums; 5) Large-gaped unidentified - the clay egg was removed, had unidentifiable marks or were not depredated, and the quail egg was depredated; 6) Small-gaped unidentified - the clay egg was removed, had unidentifiable marks

or were not depredated, and the quail egg was not depredated. No predator could be identified as a reptile. One nest that was completely destroyed with the eggs showing no signs of predation and 4 nests showing signs of multiple predation were omitted from analysis. The categories of predators were pooled into birds (group 1 and 2), mammals (group 3 and 4), large-gaped predators (group 1, 3 and 5) and small-gaped predators (group 2, 4 and 6) for analysis.

SYSTAT 8.0 statistical software and JMP statistics and graphics guide from SAS Institute were used for statistical analysis.

Results

Nest-predation

The average risk of predation was similar for shrub nests (41.7 %) and ground nests (43.8 %), see Table 1. No significant difference was found on predation rates between ground nests and shrub nests in any of the different habitats (Table 2). We nevertheless chose to analyse these separately since they are likely to be vulnerable to different predators (Söderström 1998) and pooling them may obscure differences that exist for a certain nest type. Both tests of independence of nest fates showed that the risk for predation of a nest was independent of the fate of its neighbour (ground nests, $n = 120$: ($2 = 0.86$, df

Table 2. Comparisons of predation rates between artificial ground nests and shrub nests in the different habitats, using χ^2 for two-way contingency tables. FE-F: Forest edge, forested part; FE-P: Forest edge, pasture part; CE-F: Corridor edge, forested part; CE-P: Corridor edge, pasture part; F: Interior forest; P: Interior pasture.

Habitat	χ^2 (DF = 1)	p
CE-F	3.08	0.079
CE-P	3.23	0.072
FE-F	0.54	0.46
FE-P	2.00	0.16
F	0.058	0.81
P	2.89	0.089

$= 2$, $p = 0.65$; $Z = 0.41$, $p = 0.68$; shrub nests, $n = 121$: ($2 = 2.09$, $df = 2$, $p = 0.35$; $Z = 1.49$, $p = 0.14$). Each nest was thus treated as an independent sample.

Logistic regression showed that the risk of a nest becoming depredated was influenced by

Table 3. Results of logistic regression comparing risk of predation by type of edge, habitat, distance from and trial (time). The model was significant for both ground nests (log likelihood of constants only = 147.90 and fitted model = 140.91, $p = 0.007$) and shrub nests (log likelihood of constants only = 147.63 and fitted model = 124.25, $p < 0.001$).

Type of nest	Parameter	Coefficient	S.E.	p
Ground nests:				
	Constant	2.98	1.02	0.003
	Type of edge	-0.56	0.28	0.050
	Habitat	-1.32	0.58	0.022
	Distance	0.01	0.00	0.212
	Trial	-0.21	0.13	0.103
Shrub nests:				
	Constant	3.43	1.09	0.002
	Type of edge	-0.80	0.31	0.011
	Habitat	-1.79	0.62	0.004
	Distance	-0.00	0.01	0.770
	Trial	-0.01	0.14	0.945

Table 1. Number of nests used in each habitat for ground nests and shrub nests, together with number of nests depredated. Numbers in parenthesis are percentage of depredated nests. FE-F: Forest edge, forested part; FE-P: Forest edge, pasture part; CE-F: Corridor edge, forested part; CE-P: Corridor edge, pasture part; F: Interior forest; P: Interior pasture.

Habitat	Ground nests		Shrub nests	
	n	n _{depredated}	n	n _{depredated}
FE-F	60	25 (41.7)	60	29 (48.3)
FE-P	48	15 (31.2)	48	9 (18.8)
CE-F	60	36 (60.0)	60	45 (75.0)
CE-P	48	18 (37.8)	48	10 (20.8)
F	36	21 (58.3)	36	22 (61.1)
P	36	11 (30.6)	36	5 (13.9)
Total	288	126 (43.8)	288	120 (41.7)

Table 4. Results of logistic regression comparing risk of predation by type of edge, habitat, distance from and trial (time), with the edge-habitat interaction included. The model was significant for both ground nests (log likelihood of constants only = 147.90 and fitted model = 140.57, $p = 0.012$) and shrub nests (log likelihood of constants only = 147.63 and fitted model = 122.98, $p < 0.001$).

Type of nest	Parameter	Coefficient	S.E.	p
Ground nests:				
	Constant	4.00	1.61	0.013
	Type of edge	-1.24	0.87	0.155
	Habitat	-2.03	1.04	0.051
	Distance	0.01	0.00	0.210
	Trial	-0.21	0.13	0.102
	Type of edge x habitat	0.48	0.58	0.407
Shrub nests:				
	Constant	5.53	1.74	0.001
	Type of edge	-2.20	0.94	0.019
	Habitat	-3.31	1.16	0.004
	Distance	-0.00	0.00	0.768
	Trial	-0.01	0.14	0.945
	Type of edge x habitat	1.04	0.65	0.110

type of edge and habitat for both ground and shrub nests (Table 3). Nest predation was higher for both ground and shrub nests in forests than in pastures. Predation rates were also higher for both ground and shrub nests at edges along forested corridors compared to edges neighbouring contiguous forests. Distance and trial did not influence the risk of predation. Following these results, we were interested in seeing whether an interaction existed between type of edge and habitat. The interaction proved not significant for both ground nests and shrub nests (Table 4). The latter model did not improve the explanatory power of the model for either ground nests (difference in log likelihood ($2 = 0.69$, $df = 1$, $p > 0.05$) or shrub nests (difference in log likelihood ($2 = 2.55$, $df = 1$, $p > 0.05$). We

Table 5. Comparisons of predation rates between interior forests and forested parts of the edges and between interior pastures and pasture parts of the edges for artificial ground nests and shrub nests, using χ^2 for two-way contingency tables. FE-F: Forest edge, forested part; FE-P: Forest edge, pasture part; CE-F: Corridor edge, forested part; CE-P: Corridor edge, pasture part; F: Interior forest; P: Interior pasture.

Comparison	χ^2 (DF = 1)	p
Ground nests:		
FE-F – F	2.50	0.11
FE-P – P	0.005	0.95
CE-F– F	0.026	0.87
CE-P– P	0.44	0.51
Shrub nests:		
FE-F– F	1.48	0.22
FE-P– P	0.35	0.55
CE-F– F	2.06	0.15
CE-P– P	0.68	0.41

therefore retain the first model (Table 3).

There were no significant differences between the risk of predation at the controls in the interior forests and interior pastures compared to the forested and pasture parts of the edges respectively (Table 5). No edge effect was thus detected for either ground nests or shrub nests neither within 100 m from the edges nor within 400 m from the edges.

Identification of Predator Categories

The clay egg captured on average 83.3 % of the total predation in this study, the plastic egg 75.2 % and the quail egg 62.6 %. The division of predators into categories means that category 2 and 6 (being distinguished from category 1 and 5 respectively by the fate of the quail egg) could have been exposed to some predation events by large-gaped predators that decided not to prey upon the quail egg. We believe this to be only a minor bias since the quail egg was the only egg that offered a reward for the predator, and would therefore rarely be left.

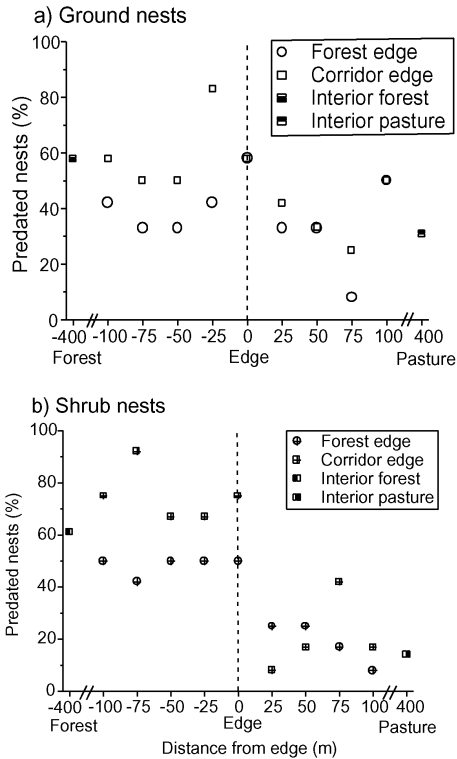


Fig. 3. Scatter-plots showing percentage depredated nests for a) ground nests and b) shrub nests at measured distances from the habitat edge.

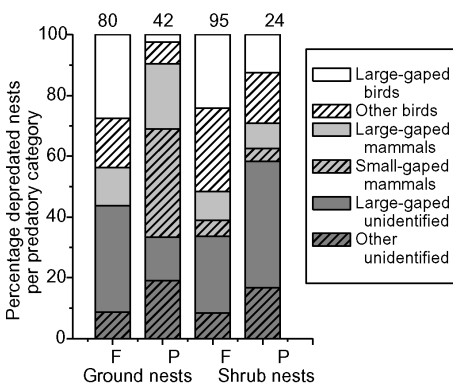


Fig. 4. Proportions of depredated nests per predator category for shrub and ground nests in pastures and forested areas and proportions of depredated nests per predator category for shrub nests in forested parts of forest edges and corridor edges. Numbers above bars denote number of depredated nests. F = Forests, P = Pastures, FE = Forest edge, CE = Corridor edge.

Table 6. Comparisons between predator categories on artificial ground nests and shrub nests in different habitats using Fisher's exact test. G-P: Ground nests in pastures; G-F: Ground nests in forested habitats; S-P: Shrub nests in pastures; S-F: Shrub nests in forested habitats.

Habitats	Mammals – Birds p	Small-gaped – Large-gaped Predators p
G-P – G-F	< 0.0001 ^a	0.0001 ^a
G-P – S-P	0.0022 ^a	0.074
S-P – S-F	0.69	0.82
S-F – G-F	1.00	0.036

^a Significant after Bonferroni correction ($P_{\text{Bonferroni}} = 0.0062$, $n = 8$).

Different habitats and nest-sites were vulnerable to different categories of predators (Fig. 4). Ground nests in pastures were more often depredated by mammals and less by birds than both shrub nests in pasture and ground nests in forested areas (Table 6). Ground nests in pastures were also relatively more depredated by small-gaped predators than ground nests in forested areas. Predators could unfortunately not be identified to species, and cameras would be needed to identify specific predators. No further analysis was made on the identity of predators due to small sample sizes.

Discussion

Edge and Habitat Effects

We found a difference in predation rates between habitats for both ground and shrub nests. Nests in forested parts of the edges ran a higher risk of being depredated than nests in pasture parts of the edges.

Although no difference in relative predator composition could be detected for shrub nests, there was a significant difference in number of nests depredated. We suggest two possible reasons for this difference. First, there was a higher number of birds in forested areas, where cover is abundant, than in pastures (Areskoug, unpu-

bl.), and this seems to be the case also for potential avian nest predators (personal observation). Many bird species may avoid open areas with reduced cover in pastures, even when a food resource, such as an artificial nest, is available only a short distance from the forested areas. The cover and height of vegetation types in pastures did not influence the level of predation (Eriksson, unpubl.), even though large shrubs may provide good perching sites for avian predators. Second, some potential mammal predators may be excluded from predation on shrub nests in pastures, since branches may be too weak for larger predators to climb on. The shrubs in pastures are also more dense and spiny in their lower regions than the trees that were used as substrates in forested areas and thus make it more difficult for potential predators to reach the nests. This is supported by the relatively high frequency of mammal depredation on ground nests in pastures. This leads to a relatively low predation by both birds and mammals on shrub nests in pastures.

There was a difference in relative predator composition for ground nests in forests compared to pastures. Mammals were relatively more important as predators in pastures, whereas birds were major predators in forested areas. Mammals may be more prone to use pastures for travelling and foraging than birds. This is supported by Areskoug (unpubl.) who found significantly more bird species in forested areas than in pastures, with distinct bird communities in the two habitats, whereas most mammal species were at least occasionally found also in the pasture.

There were differences in predation rates on both ground and shrub nests between the two types of edges, as corridor edges demonstrated significantly higher predation. Both types of edges might act as pathways for predators, but the forested corridors may channel these in higher concentration compared to the forest edge. These corridors are narrow, possibly consisting only of edge-habitat for the species of concern. Even though no edge effect was detected, the exposure of double edges at the corridors, in addition to a possible congregation of

moving predators, appear to render birds nesting in corridors more vulnerable to predation. Major et al. (1999) also concluded that linear strips of remnant woodland habitat (50 - 90 m wide) at a study-site dominated by agriculture in New South Wales, Australia, seemed disadvantageous as habitat for breeding birds due to increased risk of nest predation. We could not determine whether the higher risk of predation in forested corridors was due to higher concentrations of predators or due to more effective foraging patterns. There is a need for future studies to estimate predator compositions and concentrations and also to study movements and behaviour of predators in the different habitats and type of edges. Further studies are needed with a focus on predation risk on natural nests.

No increase in nest predation were found closer to edges between pastures and forested areas (Fig. 3a and 3b, Tab 3). Such edge effects have been documented (Gibbs 1991, Paton 1994, King et al. 1998), but so has the lack of such an effect (Nour et al. 1993, Marini et al. 1995, Bayne and Hobson 1997). Many studies have used quail or chicken eggs (See Paton 1994). There are recent studies suggesting that edge effects might disappear when small-gaped predators are important nest predators, since these may be more important in the interior of habitats (Haskell 1995, Nour et al. 1993). Small predators are often not able to depredate quail eggs and we suggest that small eggs should be included whenever the aim is to detect predation events by all predator categories. Our sample sizes did not allow for different predator categories to be analysed separately. We found six other studies that used eggs of modelling clay or plasticine and included distances from edges in their designs. Five of these (Nour et al. 1993, Bayne and Hobson 1997, Hannon and Cotterill 1998, Keyser et al. 1998, Matthews et al. 1999) failed to detect an edge effect, whereas Møller (1989) found that exposed ground nests in forests near forest-agricultural edges experienced higher predation rates.

The lack of an edge-effect in our study could also be an effect of the dry Chaco's short histo-

ry of forest fragmentation. We performed this study in a forest-dominated landscape recently (1970s) exposed to forest clearings. It is thus possible that there has as yet been little adaptation of the predator fauna to an increased amount of open landscape. Andrén (1995) in a review found nine studies that suggested that increased predation close to forest-farmland edges was an effect of farmland predators (e.g. corvids) penetrating into the forest. These studies were performed in Scandinavia and North America, regions with a long history of human-induced fragmentation as compared to our study-site. Many areas that are valuable for conservation purposes today do however experience a similar situation as the dry Chaco, with a recent and very rapid rate of deforestation, where there will be little time for species to adapt to the altered environment.

Some predators may develop a search pattern during a nest predation experiment, which may lead to changed levels of predation at the latter stages of the experiment. We found no difference in nest predation as the experiment proceeded, i.e. number of trials. We therefore conclude that the development of a search pattern did not influence the results of this study.

Most research on corridors have focused on their function as movement channels between remnant habitat patches, and few have discussed the fate of species and/or individuals using these corridors. The result of this study is in support of Major et al. (1999) and Vander Haegen and DeGraaf (1996) who conclude that corridors (50 - 90 m) and narrow riparian buffer strips (< 150 m), respectively, should not automatically be seen as beneficial for wildlife. If nesting bird species become exposed to higher predation risks in forested corridors than in other forested areas, as suggested for shrub nesters in this study, the value of a corridor as movements channels must be balanced against such costs (Simberloff and Cox 1987).

Artificial nest predation studies tend to focus on forested habitats and have predominantly been performed in the Northern Hemisphere (see Paton 1994, Söderström 1999). Söderström

(1999) suggested in his review that mammals may play a comparatively larger role in nest predation in tropical forests as compared to temperate zones. We found birds to be a major predator category in forested areas at our study site on both ground and shrub nests. Our study-site, with its comparatively simple vegetation structure, may be more justly compared to temperate conditions with a high proportion of predation events by visually searching predators.

The dry Chaco is listed as a global 200 ecoregion by the World Wildlife Fund. It is a unique and very diverse faunal landscape (Redford et al. 1990) and to a high extent very poorly studied. In Paraguay, there is fortunately still time to address the issues of fragmentation, edge effects and corridors, since much natural habitat is still intact. But the rate of fragmentation is high and occurs on a large scale. For the purpose of management advice regarding ecosystem connectivity and landscape planning, research should start today.

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