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Predation of artificial nests in a fragmented landscape in the tropical region of Los Tuxtlas, Mexico

Alejandro Estrada*, Andrómeda Rivera, Rosamond Coates-Estrada

Estación de Biología "Los Tuxtlas", Instituto de Biología, Universidad Nacional Autónoma de México, Apdo 176, San Andrés Tuxla, Veracruz, Mexico

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Abstract

Predation rates of artificial nests were investigated in a fragmented landscape in the lowlands of Los Tuxtlas in southern Mexico. Hen and plasticine eggs were used to assess predation pressure in four habitats: the interior of forest fragments, the forest–pasture edge, corridors of residual forest vegetation and linear strips of live fences across pastures. Three sites per habitat were used in three experimental trials. Hen and plasticine ground nests with three eggs each were alternated every 50 m along transects at each site. Predation rates on each type of nest were monitored for 9 days. Survey of potential avian and mammalian potential nest predators were conducted at each site prior to the experimental trails. Readings of amount of light illuminating the ground were taken by each nest at each site to assess exposure of nests. In general, average predation rates were significantly higher for both hen and plasticine nests in the forest–pasture edge and in the corridors than in the interior of the forest fragments. While birds and mammals were the principal predators on hen eggs in the forests, mammals were responsible for the majority (⩾70%) of eggs damaged at the other habitats. Surveys of potential nest predators showed that avian and mammalian potential nest predators were significantly more common at the forest–pasture edges and at the other habitats than in the forests. Readings of light reaching the ground suggest that concealment of nests by the vegetation may play an important role in predation risk. Our results are consistent with reports from other Neotropical rainforests indicating an increase of artificial nest predation pressures from forest interior to open habitats. Restoration of forest fragments, allowing the vegetation to grow along the forest–pasture edge and the planting of arboreal crops at the forest–pasture edges may be measures that could increase cover and nest protection. © 2002 Published by Elsevier Science Ltd.

Keywords: Forest fragmentation; Nest predation; Edge effects; Los Tuxtlas; Mexico; Neotropics; Conservation

1. Introduction

Forest fragmentation exposes the organisms that remain in the fragment to the conditions of a different surrounding ecosystem. Most of the resulting edge effects seem to be deleterious to forest fragments by causing changes in abiotic and biotic conditions (Murcia, 1995; Laurance et al., 1997). Birds and other egg laying animals may see their populations further diminished by high predation rates of nests in fragmented landscapes (Zanette and Jenkins, 2000). Predation rates of artificial nests are reported to be higher at forest edges than in forest interior habitats (Moller, 1988; Gibbs, 1991). Such patterns may result from increased edge effects (Wilcove et al., 1986; Andrén and Angelstam, 1988) or increase abundance of nest predators in small forest patches (Terborgh and Winter, 1980; Karr, 1982; Andrén 1992; Marini et al., 1995). Small forest fragments contain more edge habitat than large fragments which may result in low nesting success due to high nest predation (Small and Hunter, 1988; Temple and Cary, 1988; Hoover et al., 1995; Tellería and Díaz, 1995; Zanette and Jenkins, 2000).

Most studies of artificial nest predation have been conducted in temperate forests and very few studies have been reported for the tropics (Janzen, 1978; Loiselle and Hoppes, 1983; Gibbs, 1991; Tellería and Díaz, 1995; Latta et al., 1995; Wong et al., 1998). These studies showed that predation of nests seems to increase

* Corresponding author. Tel.: +52-294-30517; fax: +52-294-24668.

E-mail address: aestrada@primatesmx.com (A. Estrada).

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from forests to open habitats in Costa Rican, Panamanian, Amazonian and Singapore rain forests (Loiselle and Hopes, 1983; Gibbs, 1991; Tellería and Díaz, 1995; Wong et al., 1998) indicating that amount of cover may also be important in modulating predation pressure on artificial ground nests (Janzen, 1978; Latta et al., 1995). Patterns of abundance and species composition of nest predator communities have also been suggested to determine patterns of avian nest predation (Janzen, 1978; Moller, 1988, 1989; Tellería and Díaz, 1995).

Assuming that artificial nest predation rates are not indicative of natural predation rates, the use of artificial nests to study predation patterns has the advantage, over natural nests, of allowing the measure of variations in nest predation pressures along habitats types, after fixing the effect of other nest features which can also affect nest predation rates such as nest size, nest structure and eggs size (Yahner and Wright, 1985; Tellería and Díaz, 1995; Major and Kendal, 1996). The fact that not all possible variables are controlled (i.e. parent activity around nests and species-specific abilities to conceal them) does not invalidate the conclusions about the role of the variables under study (Kamil, 1988).

In the Neotropics, most predation pressure on artificial nests has been reported to be caused by birds, mammals and snakes (Loisselle and Hopes, 1983; Gibbs, 1991; Latta et al., 1995; Tellería and Díaz, 1995). Edge and open land birds such as Squirrel cuckoos (*Piaya cayana*) and Anis (*Crotophaga* spp.) have been reported as potential nest predators (Gibbs, 1991; Tellería and Diaz, 1995). Among mammals, racoons, coatis, mustelids, small *Felis* spp., tayra, opossums, *Tayassu*, *Dasyprocta, Sciurus* and *Oryzomys* have been reported to be potential nest predators in Neotropical forests (Gibbs, 1991; Tellería and Díaz, 1995) as well as lizards (such as *Ameiba*; Tellería and Diaz, 1995), boas and arboreal snakes (of the genus *Spilotes*; Skutch, 1985). Even small domestic species such as dogs, cats as well as comensal species such as rats and mice (*Mus* spp.) have been noted as potential nest predators (Latta et al., 1995).

The central aim in this paper is to assess general predation pressures on artificial nests in the interior of forest fragments, the forest–pasture edge and in linear strips of native and man-made vegetation. Such information may be useful to asses the suitability of these habitats for the persistence of nesting species. The sites investigated were located in a 90 km^2 landscape located in the north eastern section of the tropical region of Los Tuxtlas, Veracruz, Mexico. Because of the paucity of information on nest predation in the Neotropics in general and in Los Tuxtlas in particular, this paper is basically descriptive and it expands on our earlier work on the effects of forest fragmentation on birds and mammals in the same region (Estrada et al., 1994, 1997, 2000; Estrada and Coates-Estrada, 2001).

2. Methods

2.1. Study area

The tropical rainforest of Los Tuxtlas, in the south eastern portion of the state of Veracruz, Mexico, represents the most northern limit of the lowland tropical rainforests on the American continent. While pastures dominate many of the landscapes in Los Tuxtlas, clusters of forest fragments still exist in the lowlands. In these fragmented landscapes linear strips of residual forest vegetation of variable width exist along the sides of streams and rivers. A common feature are live fences, which consist of single rows of planted posts of the trees *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Fabaceae) used to support barbed wire. The live fences crisscross the pastureland and are important to local ranchers and farmers for delimiting boundaries of the land and to enclose their cattle and/or crops. Because the posts grow rapidly, single rows of these live fences resemble narrow vegetation corridors across the pasturelands (Estrada et al., 1997).

The study sites were part of a 90 km^2 landscape in the northern vicinity of the biological research station Los Tuxtlas of UNAM (95° 00′ W, 18° 25′ N) in south eastern Veracruz, Mexico. Weather monitoring stations indicate a mean annual temperature of 27 °C (range 20–28 °C). Average annual rainfall is 4900 mm but from March to May average monthly rainfall is 112 ± 11.7 mm and from June to February this average equals $486 + 87.0$ mm. The original lowland rainforest present in the landscape was gradually converted to pasture lands between 1960 and 1970, but clusters of forest fragments remained because of steep topography or to preserve water supplies.

Ninteen species of ground dwelling birds have been reported for the forests of Los Tuxtlas and they are members of the Tinamidae (e.g., *Tinamus major*, *Crypturellus bourcardi*, *Crypturellus cinnamomeus* and *Crypturellus soui*), the Cracidae (*Crax rubra*, *Penelope purpurecens*, *Ortalis vetula*), the Rallidae (*Laterallus ruber*, *Aramides cajanea*, *Amaurolimnas concolor*, *Porzana flaviventer*) and the Columbidae (*Columbina inca*, *Columiria passerina*, *Columiria talpacoti*, *Claravis pretiosa*, *Leptotila verrauxi*, *Leptotila plumbeiceps*, *Geotrygon montana*; Schaldach and Escalante-Pliego, 1997).

2.2. Study sites

Three forest fragments, 10, 80 and 250 ha in size were selected for placement of artificial nests. These sites were isolated from other fragments by pastures and the nearest forest fragment was about 0.5 km away. The vegetation consisted of undisturbed primary forest, although the 10 ha site showed a predominance of pioneer tree species (e.g. *Cecropia obtusifolia*, *Heliocarpus* *donell-smithii*) at the edges and in some parts of the interior.

Three forest–pasture edges of another three forest fragments (20, 150 and 200 ha) were also used. These sites were separated by 2 km from one another. The pasture was grazed by cattle (grasses were about 15–20 cm in height) maintaining the abrupt change between the two ecosystems. The three corridors were represented by narrow strips (average width 50 m) of residual forest vegetation along the edges of three permanent streams. The average linear distance separating the sites from each other was ca. 1300 m. The residual forest vegetation at these sites was dominated by trees of the Lauraceae, Moraceae, Cecropiaceae, Boraginaceae and Fabaceae. These sites had a few representatives of the forest palms *Astrocaryum mexicanum* and *Bactris trichophylla*, which are common in the understorey of undisturbed forest vegetation in this region (Bongers et al., 1988) reflecting the residual nature of the vegetation found at these sites. Actively grazed pastures bordered the edges of these corridors.

The three live fence sites were located along the sides of three sinuous unpaved roads with sparse traffic consisting mainly of people on horseback or on foot and few motorized vehicles. The roads were separated from one another by 2 km and the nearest forest fragment was about 0.3 km away. The vegetation of the live fence sites was mainly *Bursera simaruba* and *Gliricidia sepium*, but other tree species (e.g. *Ficus* spp., *Cecropia obtusifolia*) established as a result of dispersal of seeds by birds and/or mammals were occasionally present.

2.3. Materials

For the nest predation experiments we used fresh hen eggs and plasticine eggs. The latter were used to determine the type of predator that attacked the eggs by the marks left on the plasticine (Wong et al., 1998). Plasticine eggs were hand made with white plasticine and rubber gloves were used to avoid contamination with human scent. Size of plasticine eggs closely approached the size variations of the hen eggs we used. We are aware of the limitations and artificiality of using hen and plasticine eggs. Hen eggs may not approach the size of eggs of small ground birds, but were used because they approach the size of eggs of several large ground nesting birds which occur in Los Tuxtlas (e.g. *T. major*, *Crypturellus boucardi*, *Crypturellus cinnamomeus*, *Crypturellus soui*, *Crax rubra* and *Penelope purpurescens*).

Because of their smell, it is possible that plasticine eggs may influence the behaviour of certain types of predators (Rangen et al., 2000). We made no assumption in this study that artificial nests resembled natural nests. We used hen and plasticine eggs because we were interested in eliciting a maximum response by potential nest predators present at the habitats investigated. Average length and width of hen eggs used was 5.4 ± 0.2 and 3.8 ± 0.2, respectively. Hand molded plasticine eggs had an average length of 5.6 ± 0.3 cm and an average width of 3.5 ± 0.1 cm.

2.4. Placement of nests

At each site and along a transect we placed on the ground five artificial nests with three hen eggs each and five artificial nests with three plasticine eggs each. No attempt was made to create any artificial nest, but designated each experimental station as nests because many ground nesting birds do not build elaborate nests. Rubber gloves and boots were worn when placing nests to reduce human scent. Nests with hen eggs and nests with plasticine eggs were alternated every 50 m along the transect. The three eggs were placed together on the ground and a few dry leaves were used to slightly cover each nest so only about 20% was visible from a distance of 10 m. In the forest fragments the nest transects were placed about 150 m from the edge. At the corridors, the transects were placed in the interior of the vegetation strip and as far away from the edge of the vegetation as possible. At the edge sites the transect followed the forest–pasture edge and nests were placed at the bottom of the standing forest vegetation. At the live fences nests were placed at the foot of the live posts or trees.

The experiment was repeated three times in each site between April and August coinciding with the breeding season (March–September) of many resident bird species at Los Tuxtlas (AE, personal observations). The interval between the first and second experiment was 30 days long and between the second and third experiment it was 40 days long. In total the fate of 135 hen eggs and 135 plasticine eggs were monitored per habitat type (3 eggs per nest $\times$ 5 nests = 15 $\times$ 3 sites = 45 eggs per habitat $\times$ 3 experimental trials = 135 eggs).

2.5. Classification of damages

Both hen and plasticine nests were checked by one of us daily for a period of 9 days. At each nest we noted the number of eggs damaged. Damage types were classified for hen eggs as perforated, cracked and smashed. Those eggs that had been moved outside the nest area and those that had disappeared were also recorded. In the case of plasticine eggs, examination of the marks left on the eggs allowed us to classify damages as pecked, scratched, scratched and gnawed, gnawed, bitten, pecked and gnawed and stepped on. We also recorded the number of plasticine eggs found outside the nest and those that had disappeared. Damaged hen and plasticine eggs were removed on each observation day to diminish detection clues by odour or sight and further test the efficiency of potential predators in locating nests.

In the case of hen eggs, perforation of the shell was taken as evidence of damage by birds. Eggs smashed or disappeared from the nest were considered to have been attacked by mammals. For those found outside of the nest or those with cracks we considered the predator as undetermined. Signs of beak marks in plasticine eggs were considered to be caused by birds. Eggs with scratches and evidence of gnawing as well as those with gnawing marks alone, eggs with evidence of bites and eggs with evidence of having been stepped on, were considered to have been attacked by mammals. Eggs showing both pecking and gnawing marks were considered to have been damaged by both birds and mammals. Eggs found outside of the nest and those with undetermined damages because we could not discern whether the mark left on the egg was caused by a bird or a mammal were classified as having been damaged by undetermined agents.

A careful examination of damages caused by mammals on plasticine eggs allowed us to separate those eggs with small gnawing marks alone and with small gnawing marks and small scratch marks as having been caused by small rodents (mice, squirrels) from those caused by larger sized mammals. For comparison, we used tooth imprints made with skulls of rodents and other mammalian taxa housed in the collection of mammals at the Los Tuxtlas Research Station. Because of variation in individual tooth imprint sizes we could not positively identify the species, but were able to separate the imprints made by small rodents from those caused by larger mammals.

2.6. Sampling of potential predators

Surveys of potential nest predators at each site were conducted before the experimental trials. To determine relative abundance (sighting frequency) of diurnal and nocturnal mammals at each site, surveys were conducted between 06:00 and 10:00 by walking slowly ($<$ 1 km h^{-1}) and quietly along a transect and recorded the time and location of each individual or group encountered. Nocturnal surveys were conducted, on moonless and non rainy nights, on the same transects between 19:00 and 23:00. Transects were walked in one day and one night at each site of each habitat. Average transect length was 2.0 ± 0.3 km. A total of 24 h of surveys was completed at each of the four habitats investigated.

Small rodents were sampled in one night at each site by placing 20 baited Sherman live traps along a sinuous transect running parallel to the artificial nest transect with each trap separated from the next by 25 m. Traps were retrieved the next morning and captured rodents were released after identification. Captures were expressed as number of captures per trap night. A total of 60 trap nights were completed in each habitat studied.

To survey potential avian nest predators at each site, we used the fixed-radius census points in a linear transect sampling procedure (Hutto et al., 1986). All perching or ground moving birds detected by sight within a 25 m radius of the point-count center were recorded. Each count lasted 5 min and at least 30 min elapsed between counts at each point. Count points at each site were established at 100-m intervals for a total of 20 points. We conducted all bird counts at each site in two mornings between 06:30 and 10:00 hrs and avoided sampling in heavily overcast and rainy days. Birds counted were identified to species. Our records excluded those species detected flying across the landscape and well above canopy level. Crepuscular and nocturnal (e.g. Strigidae and Caprimulgidae) species were not recorded. Taxonomic nomenclature for birds followed the American Ornithologist's Union (1983).

2.7. Measures of visual exposure of eggs during the day

To obtain a measure of average visual exposure of nests at each habitat, we used a light meter to measure, at knee height, the amount of light illuminating the ground at each point where each nest was placed at each site. Readings at each site were taken between 12:00 and 14:00 and on sunny and clear days and are expressed as lux per square meter.

2.8. Data analysis

We found no differences (Friedman's test in both cases $P > 0.05$) for both hen and plasticine eggs in the total number of eggs attacked among experimental trails. Similar results were obtained when comparing the resulting data for each vegetation type. Thus, results from the three experiments were combined to examine trends in the data. Data were expressed as the percent of nests attacked or as mean number of eggs damaged. The forest sites were compared with the other habitats using the t test and the Mann–Whitney test and differences among habitats were examined using the Kruskal–Wallis test (Fitch, 1992). Means and standard deviations are provided throughout the text.

3. Results

3.1. Habitat differences

The average number of nests with hen eggs surviving per habitat at the end of 9 days was 13.2 ± 1.1 for forests, 10.7 ± 2.3 for forest–pasture edges, 10.9 ± 2.4 for corridors and 12.6 ± 1.8 for live fences (Fig. 1). Significant differences in these averages were evident between forests and edges ($t = 2.94$, d.f. 9, $P = 0.01$) and between forests and corridors ($t = 2.54$, d.f. 9, $P = 0.02$), but not between forests and live fences ($t = 1.59$, d.f. 9, $P = 0.14$). In the case of plasticine eggs, the average number of nests surviving at the end of the experiment was 12.1±1.9 for the forest sites, 8.6±3.9 for the edge sites, 9.6±2.6 for the corridor sites and 9.4±3.2 for the live fence sites (fig. 1). Significant differences in these values were found between forests and edges ($t=2.46$, d.f. 9, $P=0.03$) and between forests and corridors ($t=2.38$, d.f. 9, $P=0.03$). Marginally significant differences were found between forests and live fences ($t=2.17$, d.f. 9, $P=0.05$).

3.2. Type of nest predator

A comparison across habitats showed that, in both hen and plasticine nests, no differences were detected in the average number of eggs attacked by birds (Table 1, Mann–Whitney test, $P>0.05$ in all cases). However, the average number of eggs attacked per nest by mammals, for both hen and plasticine nests, was significantly lower in the forests than at the other habitats than (Table 1; Mann–Whitney test: $P<0.05$ in all cases). Undetermined agents were responsible for only 8 and 11% of hen and plasticine eggs attacked, respectively (Table 1).

3.3. Damage to plasticine eggs by mammals

Small scratch and gnawing marks as well as small gnawing marks alone indicated that small rodents accounted, on average, for 69% of damages to plasticine eggs by mammals. Other undetermined mammals accounted for the rest. At the forest sites small rodents accounted for 90% of damaged eggs by mammals. At the edges they accounted for 64%, at the corridors for 75% and at the live fence sites for 59%. One percent of the damaged eggs had evidence of attacks by both birds and rodents.

3.4. Surveys of potential nest predators

Visual surveys detected the presence of 17 mammalian potential nest predators at the forest sites. Three of these were species are scanssorial (climbing; *Bassariscus sumichrasti*, *Potos flavus* and *Caluromys derbianus*). Six of the 17 species were detected in the forest habitats only; 11 species were recorded at the edges and 11 species in the corridors. In the live fences we detected nine species (Table 2).

Seven of the species detected in our surveys were common among habitats. These were three marsupials (*Didelphis marsupialis*, *Philander opossum*, *Didephis virginianus*), one scanssorial rodent (*Sciurus aureogaster*) and three carnivores (*Felis yagouraoundi*, *Mustela frenata* and *Procyon lotor*; Table 3). Detection rates for this group of species, except *Felis yagouraoundi*, were 0.09±0.06 ind h^{-1} for the forests, 0.23±0.11 ind^{-1} for the edge, 0.17±0.01 ind^{-1} for the corridor and 0.16±0.01 ind^{-1} for the live fences. Differences between forests and each of the other habitats in these rates were statistically significant (Mann–Whitney test: $P<0.05$ in all cases).

Trapping with Sherman live traps resulted in the of seven small rodent species. Three of them (*Oryzomys melanotis*, *Tylomys nudicaudus* and *Peromyscus leucopus*) were captured only in the forests. Another four (*Peronysicus mexicanus*, *Heteromys desmarestianus*, *Sigmodon hispidus* and *Oryzomys palustris*) were

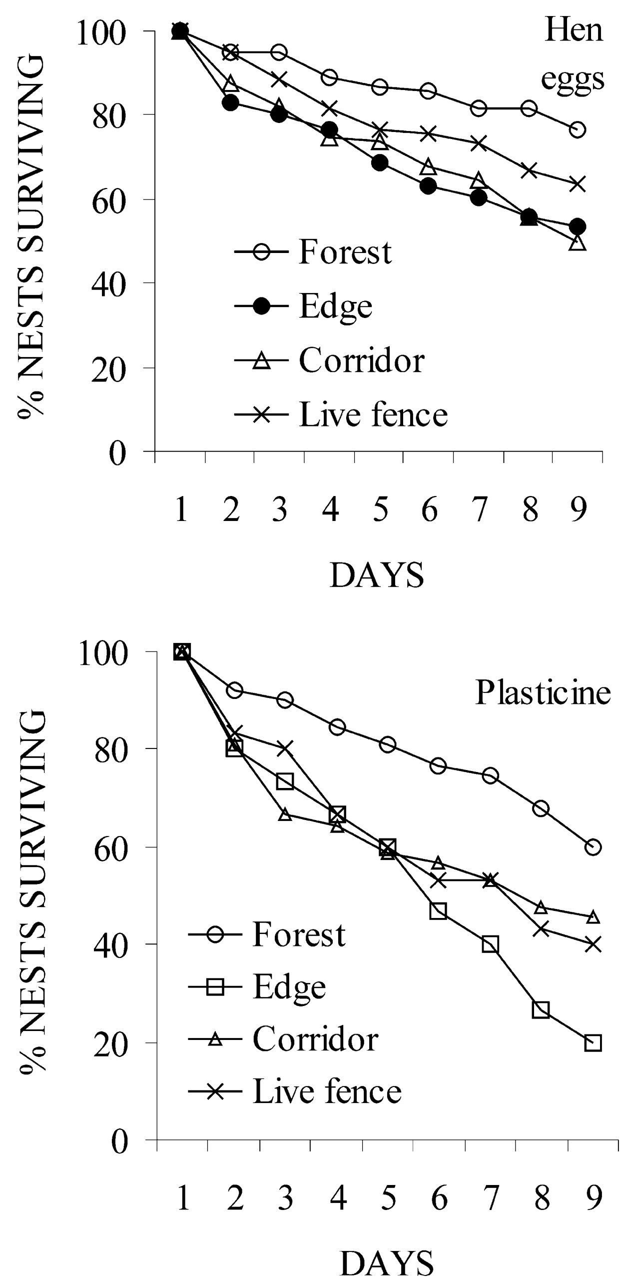

Fig. 1. Upper and lower graphs show the average percent of nests with hen eggs and nests with plasticine eggs surving at the habitats investigated, respectively. Note the higher survival rate of nests in the forest sites compared with the other habitats for the period under consideration.

Table 1
Number of hen and plasticine eggs attcked in each nest by birds and mammals in each habitat investigated[a]

Nest	Hen				Plasticine			
	Forests	Edges	Corridors	Live fences	Forests	Edges	Corridors	Live fences
Attacked by birds								
1	5	1	6	5	0	0	0	0
2	2	1	4	1	0	1	0	0
3	2	3	3	3	0	2	0	1
4	4	0	0	0	0	0	0	0
5	4	5	4	0	0	0	7	0
Total	17	10	17	9	0	3	7	1
Mean	3.4	2.0	3.4	1.8				
S.D.	1.3	2.0	2.2	2.2				
Attacked by mammals								
1	4	11	5	8	8	15	11	10
2	3	11	5	6	7	15	14	20
3	1	9	10	7	8	14	12	11
4	2	15	9	7	9	14	10	15
5	7	4	16	9	8	19	9	15
Total	17	50	45	37	40	77	56	71
Mean	3.4	10	9.0	7.4	8.0	15.4	11.2	14.2
S.D.	2.3	4.0	4.5	1.1	0.7	2.1	1.9	4.0
Undetermined agents								
	0	0	1	0	0	0	1	1
	2	0	0	0	1	3	2	1
	2	3	0	0	0	5	2	1
	2	0	0	1	1	4	0	1
	3	1	1	1	2	3	3	1
Total	9	4	2	2	4	15	8	5
Mean	1.8	0.8	0.4	0.4	0.8	3.0	1.6	1.0
S.D.	1.1	11.7	10.5	8.6	0.8	1.9	1.1	0.0

[a] The total for each nest is from three sites per habitat and three experimental repetitions per site carried out between March and September 2000.

captured in the four habitats investigated (Table 2). Average capture rates (captures per trap night) for this group of four species were 0.02 ± 0.002 in the forests, 0.17 ± 0.03 in the edges, 0.15 ± 0.06 in the corridors and 0.17 ± 0.08 in the live fences (Table 3). Differences between forests and each of the other habitats in these rates were statistically significant (Mann-Whitney test: $P<0.05$) in all cases.

In the case of potential avian nest predators, species such as *Cyanocorax morio*, *Quiscalus mexicanus*, *Dives dives*, *Psarocolus montezuma* and *Pitangus sulphuratus* dominated the bird assemblages at the non forest sites (Table 3). Average detection rates (mean number of birds per 20 count points) for this group of bird species were $0.26+0.17$ in the forests, $3.5+2.1$ in the edges, $2.4+0.13$ in the corridors and $2.4+0.22$ in the live fences. Differences between forests and each of the other habitats in these rates were statistically significant (Mann–Whitney test: $P<0.05$) in all cases. The edge habitat not only had a predominance of the above four bird species, but it also included seven raptors (e.g. *Buteo magnirostris*, *Buteogallus anthracinus*) among those species contributing to $\geqslant 50\%$ of the records (Table 3).

Readings of the amount of light reaching the ground at each site indicated that significantly more light reached the ground at the non forest habitats than at the forest interior habitat, suggesting a greater exposure of nests to visually oriented predators during the day (Fig. 2). The average amount of light (mean number of lux per square meter) illuminating the ground, was 9.37 ± 3.6 in the forest fragments, 353.75 ± 133.0 in the forest–pasture edges, 201.05 ± 108.72 in the corridors and 512.5 ± 85.5 in the live fences. The differences between the forest and the other habitats were significant (Mann–Whitney test: $P<0.001$ in all cases). Amount of light penetrating to the ground in each habitat was found to be closely related to number of hen and plasticine eggs attacked (Fig. 2).

4. Discussion

Results of the experimental trials clearly showed that a significantly higher number of nests were attacked by predators in the forest–pasture edges and in the corridors than in the forest habitats. In spite of the fact that in the forest sites we detected a larger assemblage of

Table 2
Sighting rates [average (± S.E.) number of individuals h^{-1}] or, for *Nasua narica*, groups h^{-1}; 24 h of survey per habitat] of mammals in the habitats studied[a]

Species	Forests		Edges		Corridors		Live-fences	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Visual surveys								
Didelphis marsupialis (common opossum)	0.13	0.08	0.50	0.10	0.33	0.13	0.25	0.10
Philander opossum (common gray four-eyed opossum)	0.21	0.11	0.46	0.12	0.25	0.11	0.21	0.11
Sciurus aureogaster (red-bellied squirrel)	0.04		0.13	0.05	0.17	0.03	0.17	0.02
Didelphis virginianus (Virginia opossum)	0.08	0.02	0.17	0.03	0.13	0.01	0.17	0.02
Mustela frenata (long-tailed weasel)	0.04		0.08		0.13	0.01	0.08	
Procyon lotor (northern racoon)	0.04		0.08		0.04		0.08	
Nasua narica (white-nosed coati)	0.58	0.20	0.50	0.20				
Bassariscus sumichrasti (cacomistle)	0.13	0.05	0.13	0.01	0.08		0.08	
Potos flavus (kinkajou)	0.08		0.13	0.01	0.08		0.08	
Felis yagouaroundi (jaguarundi)	0.04		0.04		0.04		0.04	
Galictis vittata (grison)	0.04		0.04		0.04			
Eira barbara (tayra)	0.13	0.04			0.08			
Sciurus deppei (Deppe's squirrel)	0.13	0.03						
Dasyprocta mexicana (agouti)	0.13	0.03						
Pecari tajacu (collared pecari)	0.04							
Caluromys derbianus (Central American woolly opossum)	0.04							
Felis pardalis (ocelot)	0.04							
Survey with Sherman live traps								
Peromyscus mexicanus (Mexican deer mouse)	0.03	0.01	0.20	0.09	0.17	0.09	0.10	0.02
Heteromys desmarestianus (spiny pocket mice)	0.03	0.01	0.15	0.08	0.13	0.05	0.05	0.01
Sigmodon hispidus (cotton rat)	0.02	0.01	0.20	0.07	0.22		0.30	
Oryzomys palustris (rice rat)	0.02	0.01	0.13	0.05	0.08		0.23	
Oryzomys melanotis (rice rat)	0.02	0.01						
Tylomys nudicaudus (naked-tailed climbing rat)	0.02	0.01	0.02					
Peromyscus leucopus (white-footed deer mice)	0.02	0.01						

[a] Also shown are the trapping rates for rodents (individuals per trap night; 60 trap nights per habitat). Edges refers to the forest–pasture edge.

Table 3
Bird species accounting for >50% of records in surveys at each habitat[a]

	Forests		Edges		Corridors		Live-fences	
Species	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Dives dives (melodius blackbird)	0.40	0.10	7.29	2.20	2.62	1.60	2.00	0.10
Quiscalus mexicanus (boat-tailed grackle)	0.15	0.08	3.45	1.10	2.50	1.30	2.50	0.10
Cyranocavax morio (brown jay)	0.35	0.12	3.02	1.60	2.50	1.20	2.25	0.20
Pitangus sulphuratus (great kiskadee)	0.40	0.09	2.10	0.80	2.60	1.40	2.20	0.10
Psarocolius montezuma (montezuma oropendola)	0.09	0.01	2.10	1.10	1.90	1.10	3.30	0.30
Buteogallus anthracinus (common black hawk)			0.50	0.10	0.45	0.10	0.50	0.30
Herpetotheres cachinnans (laghing falcon)			0.50	0.30	0.20	0.10	0.45	0.30
Buteo magnirostris (roadside hawk)			0.09	0.01	0.50	0.10	0.30	0.10
Falco rufigularis (bat falcon)	0.25	0.14						
Buteo nitidus (gray hawk)			0.25	0.09	0.15	0.07	0.10	0.05
Leptodon cayanensis (gray-headed kite)			0.18	0.08			0.15	0.06
Micrastur semitorquatus (collared forest falcon)	0.10	0.05						
Rostrhamus sociabilis (snail kite)			0.09	0.01				

[a] Number refers to the mean number (± S.E.) of birds detected per 20 count points (two morning counts at each site). Note the higher detection rates of species such as *Dives dives*, *Quiscalus mexicanus*, *Cyranocovax morio*, *Pitangus sulphuratus* and *Psarocolius montezuma* at the forest–pasture edges, corridors and live fences than in the forests.

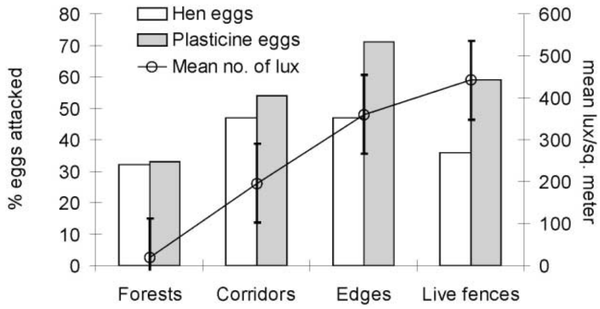

Fig. 2. Average readings (30 readings per habitat; bars indicate standar error) of light (wave length in nm) penetrating to the ground at each habitat investigated. Also shown is the mean number of hen and plasticine eggs attacked by nest predators at each habitat. Habitats are arranged according to the amount of cover, corridors consisted of residual forest vegetation along the sides of streams and are this strips of forest. Note the higher exposure and predation pressure on plasticine eggs at the other habitats. Predation pressure was higher only in the corridors and forest–pasture edge than in the forest habitats.

potential nest predators (24 species of mammals and seven species of birds) than in the forest–pasture edge and the corridors (13–16 species of mammals and 9–11 species of birds), both types of eggs survived longer in the forest interior than in these two other habitats. Increased stature and structural complexity of the vegetation at the forest fragments versus the corridors and forest–pasture edges, might provide a substantially greater volume of habitat for predators to search for nests and in which birds can hide nests (Latta et al., 1995). Our data on light readings suggests that it is possible that concealment of nests by the vegetation in the forest habitats may have resulted in less predation events recorded in these sites. In contrast to the forest interior, artificial nests were probably more exposed to predators at the forest–pasture edge and in the narrow vegetation corridors. The lack of significant differences in predation rates of artificial nests between the forest interior and the live fences could be the result of potential predators using these lineal habitats as walkways or flyways, rather than as habitats solely for foraging (Estrada et al., 1994, 1997).

Rates of nest predation were greatest at the forest–pasture edge suggesting an increased exposure of nests to potential predators that visit these habitats. Many potential eggs predators in the tropics are scanssorial and may favour the tangled and dense vegetation of the forest edge (e.g., squirrels, opossums, kinkajous, ring-tailed cats, tayras, etc.). Increased illumination during the day and possibly at night by star and moon light may facilitate detection of nests by both diurnal and nocturnal predators at the non forest sites. The forest–pasture edge may be visited by mobile forest interior mammal species (e.g. *Dasyprocta mexicana, Pecari tajacu*, *Nasua narica*, *Eira barbara*, *Felis spp*.) and by edge and open habitat mammals (e.g. *Didelphis*, spp., *Mustela frenata*, *Sciurus aureogaster*, *Procyon lotor*), some of which may use linear strips of vegetation to move through the landscape (Estrada et al., 2000). Birds rely on visual clues for locating their prey so the more open forest–pasture edges, corridors and live fences may be more suitable habitats for this.

In the temperate zone, increase nest predation along habitat edges has been reported by Gates and Gysel (1978), Chasko and Gates (1982), Bringham and Temple (1983), Andrén et al. (1985), Wilcove et al. (1986), Andrén and Angelstam (1988), Burger (1988), and Moller (1989). The prevailing explanation for increased predation near forest edges has been the high concentration of predators based in the surrounding matrix entering the forest to forage (e.g. Angelstam, 1986; Andrén and Anglestam, 1988; Small and Hunter, 1988). However, no clear edge effects on artificial nest predation were reported in Scandinavian forests (Nour et al., 1993). In contrast to our results, no elevated artificial nest predation was reported at the forest–pasture edge in Costa Rican forests (Gibbs, 1991) and a lack of association between predation rates of artificial nests and distance to forest edge was noted in Singapore forests (Wong et al., 1998). However, nest predation pressure was observed to increase significantly from forests to open habitats in Costa Rican (Gibbs, 1991), Belizean (Burkey, 1993), Amazonian (Tellería and Díaz, 1995) and Puerto Rican forests (Latta et al., 1998).

Pastures represent an environmental extreme compared with forest-interior habitats and provide minimal cover for animals that dwell primarily in forest. A similar situation may be true for the narrow corridors which are basically all edge and for the live fences. However, the extreme diurnal environmental conditions of the forest–pasture edge and of the other linear habitat may not exist for nocturnal mammals. Our visual and live trap surveys at the habitats investigated indicated that 62% of the medium and small sized mammals detected were nocturnal. Our data also showed that the majority of the damage recorded on plasticine eggs at the non forest habitats were caused by small nocturnal rodents. Larger scratch and tooth marks suggests that other diurnal and nocturnal mammals may have been responsible for the rest of the damages caused to plasticine eggs.

In our study we found most cases of egg predation attributable to mammals at the habitats investigated. Similar finding have been reported for wet forests in Costa Rica (Gibbs, 1991) and Singapore (Wong et al., 1998). Extirpation of large predators from small forest fragments and a subsequent increase in numbers of small, omnivorous mammals (Terborgh and Winter, 1980) may explain the elevated rates of artificial nest predation by mammals in our study. Our results support the general idea that predation on ground nesting birds in fragmented landscapes in Los Tuxtlas may be unusually high due to elevated density of medium and small size mammal nest predators (see Karr, 1982, for similar conclusions in BCI, in Panama). While it is possible that the odour of plasticine eggs may have attracted an unusual number of mammals to the nests, our data also showed that a high number of attacks on hen nests by mammals took place, supporting the idea that mammals are the major predators of ground nests. It is also possible that removal of eggs by mammals may have lowered the availability of both hen and plasticine eggs to birds.

Many ecological effects of strips of vegetation have been noted, including their use as corridors by predatory corvids (Angelstam, 1986). At Los Tuxtlas, we have recorded great numbers of individuals of edge and open habitat bird species (e.g., *Cyanocorax morio*, *Quiscalus mexicanus*, *Dives dives*, *Pitangus sulphuratus*, *Psarocolus montezuma*) using linear strips of vegetation along the sides of streams and live fences along side dirt roads (Estrada et al., 1997, 2000). These strips of vegetation may facilitate movement of other potential nest predators across the landscape. We have seen marsupials (*Didelphis marsupialis*, *Didelphis virginianus* and *Philander opossum*), mustelids (*Mustela frenata*, *Gallictis vitata*) and even dogs and cats using these strips of vegetation when moving across the pasture (Estrada et al., 1994).

In spite of the predominance of potential avian nest predators at the forest–pasture edge, corridors and live fences, we found no differences in predation rates by birds on hen or plasticine eggs between the forest sites and these habitats. Accessibility of nests (e.g. ground versus above-ground nests) may determine rates of nest predation by birds (Yahner and Wright, 1985; Wilcove et al., 1986; Yahner and Cypher, 1987; Andrén and Angelstam, 1988; Yahner and Scott, 1988). It is possible that the observed low predation rates by birds on hen and plasticine eggs may have been the result of nests having been placed on the ground and partly concealed by us with dry leaves. Predation of artificial nests by birds has been reported to be higher in above ground nests than on ground nests in Amazonian and in Puerto Rican rain forests (Latta et al., 1995; Tellería and Díaz, 1995). At Los Tuxtlas, we have seen birds such as *Cyanocorax morio* and *Quiscalus mexicanus*) at the forest edge prey on arboreal nests of humming birds and small doves.

Reptiles such as *Ameiba* lizards and some Colubridae species (*Boa*, *Spilotes*) have also been reported to be important nest predators in Costa Rican and Amazonian rainforests (Gibbs, 1991; Tellería and Díaz, 1995). It is possible that some of the eggs recorded as disappeared by us may have been taken by Colubridae species. However, the high number of disappeared hen eggs recorded by us (50% out of a total sample of 219 eggs) and the low number of encounters of Colubridae snakes during our surveys ($n=3$ for all habitats) suggests that it is possible that the majority of the eggs were removed by mammals. Marsupials such as *Didelphis* spp., *Philander opossum* and rodents such as *Peromyscus mexicanus and Sciurus aureogaster,* common in our faunistic surveys, tend to predominate among the remaining mammal populations in forest fragments <400 ha in size in these landscapes (Estrada et al., 1994). Over the years we have seen humans collecting eggs from ground nests of *Crax rubra*, *Tinamus major* and *Ortalis vetula* among other bird species in forest fragments, in the forest–pasture edges and in corridors of vegetation, adding to the predation pressures upon remaining bird populations. Cats and dogs accompanying ranchers and farmers may also prey on nests. Eggs may also be damaged by cattle that penetrate the forest or feeds at the forest edge. At one of our forest–pasture edge sites, a plasticine egg had the tooth imprints of a cow.

The generality of our study is limited because of the few sites sampled, the use of hen and plasticine nests and the fact that only ground nests were used in the experimental trials. Our study is based on artificial predation that may not be indicative of natural predation rates (Haskel, 1995, Ortega et al., 1998). The results we have presented probably assess general predation pressure by generalist predators and may be useful for testing nest vulnerability (Sieving, 1992) and may only provide an estimate of relative predation rates (Loisselle and Hopes, 1983). In way of contrast, higher predation rates in natural nests than in artificial nests are reported in Puerto Rican rain forests, indicating that the level of predation recorded on artificial nests may underestimate actual predation levels (Latta et al., 1995). In short, predation rates on artificial nests can not be translated to actual predation rates of natural nests, and should be used only as a means of answering questions of general predation rates in different habitats (Latta el al., 1995).

Keeping the above in mind, our study suggests that, in fragmented landscapes at Los Tuxtlas, nest predation pressures on ground nests seem to be higher in more exposed habitats such as the forest–pasture edge and in narrow strips of vegetation than in the forest interior. In contrast to the forest interior where an almost equal proportion of eggs were attacked by birds and mammals, the majority of predation pressure at the more open habitats seems to be caused by diurnal and nocturnal mammals, and small rodents seem to be particularly important. The greater exposure of nests and the presence and activity of potential nest predators in the forest–pasture edges, in narrow strips of residual forest vegetation and in live fences suggests that these are high risk habitats for nesting species. The high level of fragmentation of the landscape in which the habitats investigated are found suggests high edge habitat availability for nest predators and high rates of nest predation in these landscapes may indicate reduced local viability and hence reduced numbers (Zanette and Jenkins, 2000).

From a conservation viewpoint, our results suggest that a good local conservation strategy is to identify, maintain and restore existing forest fragments that may be population sources of birds and of other nesting animals. Efforts may be needed as well in designing land management scenarios to reduce local forest edges. Allowing the vegetation to recover along the forest–pasture edge may result in more cover and lower detectability of nests. The planting of arboreal cash crops (e.g. citrus, allspice or mixed crops) at the forest pasture edge, may also increase cover and may provide additional nesting substrate and vegetation area for nesting species.

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References

American Ornithologists Union, 1983. Check-list of North American Birds. American Ornithologist Union. Allen Press, Lawrence, Kansas.

Andrén, H., 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 69, 544–547.

Andrén, H., Angelstam, P., 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69, 544–547.

Andrén, H., Angelstam, P., Lindtrón, E., Widén, P., 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45, 273–277.

Angelstam, P., 1986. Predation on ground nesting birds' nest in relation to predator densities and habitat edge. Oikos 47, 365–373.

Bringham, M.C., Temple, S.A., 1983. Have cowbirds caused forest songbirds to decline? Bioscience 33, 31–35.

Bongers, F., Popma, J., Meave del Castillo, J., Carabias, J., 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. Vegetatio 74, 55–80.

Burger, L.D., 1988. Relations between forest and prairie fragmentation and depredation of artificial nests in Missouri. MS thesis. University of Missouri, Columbia, Missouri.

Burkey, T.V., 1993. Edge effects in seed and egg predation at two neotropical rain forest sites. Biological Conservation 66, 139–143.

Chasko, G.G., Gates, J.E., 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. Widlife Monographs 82, 1–41.

Estrada, A., Coates-Estrada, R., 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography 24, 94–102.

Estrada, A., Coates-Estrada, R., Meritt Jr., D., 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography 17, 229–241.

Estrada, A., Coates-Estrada, R., Meritt Jr., D.A., 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodiversity and Conservation 6, 19–43.

Estrada, A., Cammarano, P., Coates-Estrada, R., 2000. Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. Biodiversity and Conservation 9, 1399–1416.

Fitch, R., 1992. WinSTAT, The Statistics Program for Windows. Kalmia, Cambridge, MA.

Gates, J.E., Gysel, L.W., 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59, 871–883.

Gibbs, J.P., 1991. Avian nest predation in tropical wet forest: an experimental study. Oikos 60, 155–161.

Haskel, D.C., 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology 9, 1316–1318.

Hutto, R.L., Pletschet, S.M., Hendricks, P., 1986. A fixed radius point count method for nonbreeding and breeding season use. Auk 103, 593–602.

Hoover, J.P., Brittingham, M.C., Goodrich, L.J., 1995. Effects of forest patch size on nesting success of wood thrushes. Auk 112, 146–155.

Janzen, D.H., 1978. Predation on eggs on the ground in two Costa Rican forests. American Midland Naturalist 100, 467–470.

Kamil, A.C., 1988. Experimental design in ornithology. In: Johnson, R.F. (Ed.), Current Ornithology, vol. 5. Plenum Press, New York, pp. 313–446.

Karr, J.R., 1982. Avian extinction on Barro Colorado Island, Panama: a reassessment. American Naturalist 119, 220–239.

Latta, S.C., Wunderle, J.M., Terranova, E., Pagán, M., 1995. An experimental study of nest predation in a subtropical wet forest following hurricane disturbance. Wilson Bulletin 107, 590–602.

Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-De-Merona, J., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. Science 278, 1117–1118.

Loiselle, B.A., Hoppes, W.G., 1983. Nest predation in insular and mainland rainforest in Panama. Condor 85, 93–95.

Major, R.E., Kendal, C.E., 1996. The contribution of artificial nests experiments to understanding avian reproductive success: a review of methods and conclusions. Ibis 138, 298–307.

Marini, M.A., Robinson, S.K., Heske, E.J., 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. Biological Conservation 74, 203–213.

Moller, A.P., 1988. Nest predation and nest ste choice in passerine birds in habitat patches of different sizes: a study of magpies and blackbirds. Oikos 56, 215–221.

Moller, A.P., 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos 56, 240–246.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. TREE 10, 58–62.

Nour, N., Matthysen, E., Dhondt, A.A., 1993. Artificial nest predation and habitat fragmentation: different trends in birds and mammal predators. Ecography 16, 111–116.

Ortega, C.P., Ortega, J.C., Rapp, C.A., Backenslo, S.A., 1998. Validating the use of artificial nests in predation experiments. Journal Wildlife Management 62, 925–932.

Rangen, S.A., Clark, R.G., Hobson, K.A., 2000. Visual and olfactory attributes of artificial nests. Auk 117, 136–146.

Schaldach, W.J., Escalante-Pliego, P., 1997. Lista de aves. In: Gonzalez-Soriano, E., Dirzo, R., Vogt, R. (Eds.), Historia Natural de Los Tuxtlas. Universidad Nacional Autónoma de México, Mexico City , pp. 571–588.

Sieving, K.E., 1992. Nest predation and differential insular extinction among selected forest birds of Central Panama. Ecology 73, 2310–2328.

Skutch, A.F., 1985. Clutch size, nesting success, and predation on nests of tropical birds, reviewed. In: Buckley, P.A., Foster, M.S., Morton, E.S., Ridgely, R.S., Buckley, F.G. (Eds.), Neotropical Ornithology. Ornithological Monographs 36, Washington, DC , pp. 575–603.

Small, M.F., Hunter, M.L., 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia (Berl.) 76, 62–64.

Tellería, J.L., Díaz, M., 1995. Avian nest predation in large natural gaps of the amazonian rain forest. Journal Field Ornithology 66, 343–351.

Temple, S.A., Cary, J.R., 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2, 340–347.

Terborgh, J., Winter, B., 1980. Some causes of extinction. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachussetts, pp. 119–133.

Wilcove, D., McLelland, C.H., Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation Biology. The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachussetts, pp. 237–256.

Wong, T.C.M., Sodhi, S.S., Turner, I.M., 1998. Artificial nest and seed predation experiments in tropical lowland rainforest remnants in Singapore. Biological Conservation 85, 97–104.

Yahner, R.H., Wright, A.L., 1985. Depredation on artificial ground nests: effects of edge and age plot. Journal Wildlife Management 49, 508–513.

Yahner, R.H., Cypher, B.L., 1987. Effects of nest location on depredation of artificial arboreal nests. Journal Wildlife Management 51, 178–181.

Yahner, R.H., Scott, D.P., 1988. Effects of forest fragmentation on depredation of arttificial nests. Journal Wildlife Management 52, 158–161.

Zanette, L., Jenkins, B., 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. Auk 117, 445–454.