AVIAN NEST PREDATION IN A LARGE NATURAL GAP OF THE AMAZONIAN RAINFOREST

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Abstract.—The patterns of avian nest predation along a forest-open ecotone located in a remote, undisturbed area of Colombian Amazonia were analyzed using wicker nests to determine whether or not nest predation increased along a natural gradient and whether nest predation was equivalent to that measured in temperate areas. Nest loss increased from rainforest to large, hill-top clearings in relation to the decrease of tree and shrub cover. There was no evidence, however, of a parallel increase in the abundance of egg predators. The observed nest predation indices in the Amazonian rainforests were quite similar to those obtained in large North American forests. These results are consistent with Oniki's (1979) hypothesis about the lack of differences of nest predation rates between temperate and tropical forest habitats.

DEPREDACIÓN DE NIDOS EN UN GRAN CLARO NATURAL DE LA SELVA AMAZÓNICA

Sinopsis.—Se analizó, mediante nidos artificiales, la distribución de los patrones de depredación de nidos en un gradiente natural bosque-claro de la selva amazónica de Colombia. Se intentaba comprobar si la depredación aumentaba al disminuir la cobertura forestal en un gran claro natural y si su intensidad era equivalente a la observada en zonas estructuralemente similares de áreas templadas. El índice de depredación aumentó al disminuir la cobertura de arboles y matorrales, aunque no se apreció un aumento paralelo de la abundancia de depredadores. Los índices de depredación fueron similares a los obtenidos en América del Norte con idéntica metodología, siendo por tanto consistentes con la hipótesis de Oniki (1979) sobre la falta de diferencias en la tasa de depredación de nidos entre habitats templados y tropicales.

Nest predation has been shown to be one of the main factors determining the reproductive success of birds (Ricklefs 1969). Since Ricklefs' seminal paper, patterns of avian nest predation have been increasingly studied both from theoretical (e.g., Martin 1988a, b; Slagsvold 1982) and applied approaches (Wilcove 1985). Two mutually related groups of factors, nest accessibility and nest predator community structure, have been found to determine avian nest predation rates.

Nest accessibility.—Predation pressure on open nest has been found to be stronger than on closed nests (Lack 1968, Ricklefs 1969), and predation of ground nests is usually greater than that on above-ground ones (Loiselle and Hoppes 1983, Ricklefs 1969, Slagsvold 1982, Wilcove 1985; but see Martin 1993). It also has been observed that nest predation rates usually decrease as nests become less visible (Møller 1989, Slagsvold 1982, Yahner and Cypher 1987, Yahner and Scott 1988; but see Clark and Nudds 1991). Frequently, such predation rates also increase in fragmented landscapes, where nest predators appear to be especially efficient in locating nests placed in forests edges (Andrén and Angelstam 1988, Møller 1989, Wilcove et al. 1986, Yahner and Cypher 1987, Yahner and Scott

1988, Yahner and Wright 1985; but see Angelstam 1986, Ratti and Reese 1988). Some authors have even hypothesized that the edges generated by human-made modifications of forest landscapes would act as ecological traps for breeding birds (Gates and Gysel 1978).

Nest predator community structure.—Patterns of abundance and species composition of nest predator communities are usually viewed as the ultimate determinants of patterns of avian nest predation (Angelstam 1986; Møller 1988, 1989; Sieving 1992). This hypothesis stems from results obtained in human-modified areas, where the top predators are excluded by human activities thus promoting a demographic increase of small, generalist potential nest predators. This human-induced mesopredator release (Soulé et al. 1988, Terborgh 1974) has been also fully documented for neotropical predator communities (Eisenberg et al. 1979, Emmons 1984, Glanz 1982).

Most nest predation studies have been carried out in heavily managed areas, where both kind of factors act simultaneously. Little is known, however, for natural areas in which neither habitat structure nor predator communities have been modified by human activities. It can be hypothesized that the patterns measured to date could stem from an aberrant situation in which the fast rates of change imposed by human management in recent times have strongly increased the risk of avian nest predation, without giving enough evolutionary time for bird species to become adapted to these new conditions (Gates and Gysel 1978, Santos and Tellería 1991).

Our study was carried out in a remote area with no human settlements. We analyzed, using artificial nests, the patterns of nest predation risk along a natural gradient from the Amazonian rainforest to large clearings located on the tops of rocky hills. We specifically tried to ascertain whether nest predation pressure increased along a natural forest edge in relation to the gradual decrease of tree and shrub cover, as has been observed, using identical procedures, in human-modified areas. Additionally, we compared our results with those obtained in temperate areas to ascertain whether nest predation pressure is stronger in tropical areas than in temperate ones (Gibbs 1991, Oniki 1979, Ricklefs 1969, Snow and Snow 1964).

METHODS

Field work was carried out in the Sierra de Chiribiquete (Caquetá-Guaviare departments, Colombian Amazonia; 0°56′N, 72°42′W) during a Spanish-Colombian expedition performed in November–December 1992. The study area is a remote region with no human settlements since the beginning of this century, when it was occupied by a nomadic Indian tribe now extinct. Today the area is a National Park of 1,250,000 ha covering the whole hill range and the surrounding rainforests. The nearest human settlement, Miraflores (Guaviare department), is located 70 km northeast along a large tract of intact rainforest.

The Sierra de Chiribiquete is a mountain range composed by sandstone

hills whose plain tops are between 600 and 800 m elevation, whereas the basal rainforest is at 300 m. Both the tops and the slopes of the hills are strongly washed by the tropical rains, thus producing a progressive reduction of soil depth and vegetation development from the basal forest to the hill tops. Apart from the surrounding Amazonian rainforest, three broad vegetation types can be recognized along this altitudinal gradient (see Estrada and Fuertes 1993 for a full description of the vegetation of the study area). (1) Forest, dominated by big trees of *Ormosia macrophylla, Dimorphandra pennigera, Cyrilla racemiflora* and *Clusia columnaris,* which are located at the base of the hill slopes as well as in deep gorges between hills. (2) Dense woodlands of small trees of *Bonnetia martiana* and *Senefelderopsis chiribiquetiensis* which grow on poorly developed soils along the treeline. (3) Clearings, covered by shrubby patches composed by *Bonnetia martiana, Tepuianthus savannensis* and *Clusia chiribiquetensis* covering the plain tops of the hills. They are arranged as a mosaic of shrub and grass patches, and rocky outcrops (Estrada and Fuertes 1993).

The structure of the vegetation was characterized by estimating cover of bare rocks, grasses and litter at ground level, the number of trunks of less than and more than 30 cm DBH, and average tree height on circular plots of 25-m radius centered around nest locations.

The main purpose of the expedition was to catalog the animal and plant communities inhabiting the Chiribiquete National Park. A team of 20 people including ornithologists, mammalogists and herpetologists collected data over 15 d on the abundance of vertebrates by means of direct observation (lizards, birds), mist nets (forest birds), live traps (small mammals) and track searching (big mammals). The results obtained were too scarce to be presented as abundance indices, despite the large sampling effort. We detected lizards from the genus *Ameiva* and *Tupinambis* in the open vegetation of the hill tops; two species of birds which are potential nest predators, Squirrel Cuckoo (*Piaya cayana*) and Rufous-winged Ground-Cuckoo (*Neomorphus rufipennis*; one individual bird of each species in the open tops and in the basal forests, respectively); and tracks or single sightings of mammals such as peccaries (*Tayassu* spp.), tayras (*Eira barbara*), monkeys (*Lagothrix flavicauda*) and cats (*Panthera onca* and small *Felis* spp.) in the basal forest, as well as other big mammals such are tapirs (*Tapirus terrestris*). In addition we also caught rodents from the genus *Oryzomys* and *Echimys* (which are potential nest predators; see Roper 1992) and small granivorous rodents from the genus *Oligoryzomys* in basal forests.

We placed 140 artificial nests with two quail (*Coturnix coturnix*) eggs each in the three vegetation types previously defined. Nests were muddied to make them as inconspicuous as possible. They were placed at 20-m intervals along paths opened in the vegetation (30 + 30 nest locations along two paths in forests, 40 along one path in *Bonnetia* woodlands, and 40 along one path in the clearings). We placed two nests at each location, one of them on the ground, and the other attached to a shrub or tree

TABLE 1. Vegetation structure changes along the open-forest ecotone of the hills of the Sierra de Chiribiquete. Mean ± SD of variables obtained from 25-m radius circular sampling locations are shown. n = number of sampling locations. See text for further details.

Habitat	Forest ($n = 20$)	*Bonnetia* ($n = 20$)	Hill tops ($n = 30$)
% herb cover	2.4 ± 4.6	21.9 ± 26.5	36.0 ± 14.0
% litter cover	91.2 ± 12.2	66.8 ± 31.2	13.0 ± 11.4
% rock cover	2.2 ± 5.9	11.3 ± 18.4	51.6 ± 15.8
# trunks <30 cm DBH	485.0 ± 499.5	3068.0 ± 3795.0	43.6 ± 46.9
# trunks >30 cm DBH	3.7 ± 5.4	0	0
Shrub height (m)	2.2 ± 0.9	1.9 ± 1.2	1.4 ± 0.4
Tree height (m)	17.8 ± 3.6	6.7 ± 1.7	3.5 ± 0.7

branch 1–2 m above ground. Nests were exposed to predators for seven consecutive days, then checked and removed.

The use of artificial nests instead of natural nests for studying nest predation rates has the advantage of allowing us to check variations in nest predation pressure along physiognomic and geographic gradients according to nest locations, after fixing the effect of other nest characteristics which can also affect nest predation rates, such as nest size, nest structure and egg size (e.g., Martin 1987, Roper 1992, Sieving 1992). 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 (see Kamil 1988 for a discussion of the effect of secondary variables on the validity of the conclusions obtained in field experiments). This method does not intend to analyze nest predation rates for particular species (unless the method is previously calibrated; Martin 1987) but to analyze and compare patterns of predation risk. In fact, this lack of representativeness is a common problem when we use natural nests of a given species to extrapolate the conclusions obtained to other species.

RESULTS

Vegetation structure changed from the forests to the hill tops. Herb and rock cover decreased, and litter cover increased along this gradient. Tree and shrub height, as well as the number of large trunks also decreased, whereas the number of small trunks was greatest in the dense *Bonnetia* woodlands found between the forests and the hill tops (Table 1).

Overall, of the 140 experimental nest placed in the forests and clearings, 15 were lost due to termites (Nasutitermitinae) building nests around them, hence impeding their detection by predators. Out of the remaining 125, 33 (26.4%) were preyed upon (Table 2). The statistical significance of these results, as well as their coincidence with the patterns found by Gibbs (1991) in Costa Rica using the same methodology, were

TABLE 2.   Proportions of wicker nests preyed upon in La Selva Reserve (Costa Rica; Gibbs 1991) and in the Sierra de Chiribiquete (Colombia; this study). The number of nests for each habitat/location/study area are shown in parentheses. Habitats in both study sites have been tentatively ordered along a vegetation structure gradient from the forest interior to open pastures.

	Habitat type		
Gibbs (1991): This study:	Forest Forest	Forest/second growth *Bonnetia*	Forest/pasture Hill tops
Nest location			
Ground			
Gibbs (1991)	24 (90)	60 (57)	10 (30)
This study	38 (29)	44 (16)	57 (14)
Above-ground			
Gibbs (1991)	10 (90)	23 (57)	10 (30)
This study	0 (29)	6 (18)	32 (19)
Total			
Gibbs (1991)	17 (180)	42 (114)	10 (60)
This study	19 (58)	24 (34)	42 (33)

tested by means of the fit of log-linear models to the four-way contingency table generated by the factors study site*nest location*habitat*eggs removed/non-removed (Sokal and Rohlf 1981). There were no effects of the study sites in the proportion of nests whose eggs were removed nor significant site*location*habitat interaction (Table 3), thus indicating that our results were closely similar to those found by Gibbs (1991). Within sites, both Gibbs's (1991) and our results showed a significant effect of both nest location and habitat type on the proportion of nest whose eggs were removed, although results also showed significant site*habitat and, to a lesser extent, site*location interactions (Table 3). Nest predation pressure was stronger on ground nests than on above-ground ones, and increased significantly from forests to open habitats in both study sites (Table 2). Total nest predation in Chiribiquete hill tops was larger than

TABLE 3.   Results of the fit of log-linear models to the four-way contingency table generated by the factors study site × nest location × habitat × eggs removed/non-removed (Sokal and Rohlf 1981).

Effect	G^2	df	P
Study site	1.10	1	0.295
Nest location	35.24	1	≪0.001
Habitat	20.15	2	≪0.001
Site × location	4.75	1	0.029
Site × habitat	17.59	2	<0.001
Location × habitat	5.63	2	0.060
Site × location × habitat	1.34	2	0.511

in open pastures of Costa Rica, mostly as a consequence of larger rates
of nest predation on ground nests (Table 2).

Quail eggs disappeared without any remains (a feature usually attrib-
uted to the predation by birds or reptiles; Best and Stauffer 1980, Green
et al. 1987) in 16 out of the 33 depredated nests (48.5%). For 10 nests
(30.3%) we found remains of bitten eggs; the remaining seven nests
(21.2%) had been moved from their original placement, three of these
nests also containing egg shell remains or even appeared bitten them-
selves by the nest predator. These latter features are typical of mammal
predators, although we did not find grasped shells or droppings, which
would have indicated predation from rodents (Green et al. 1987; Santos
and Tellería 1991, 1992).

Eggs that dissapeared without disturbance were most frequent in *Bon-
netia* woodlands (seven out of eight depredated nests), followed by the
hill tops (seven out of 14), and by basal forests (two out of 11). Nests that
were moved or that contained egg shell remains showed an inverse pat-
tern: one out of eight in *Bonnetia* woodland, seven out of 14 in the hill
tops, and nine out of 11 in the forests. Frequency of eggs that disappeared
was higher in above-ground nests (six out of seven) than on ground nests
(10 out of 26). Hence, nest predation by mammals appeared to be con-
centrated in the forests, whereas in the open shrubby areas and dense
Bonnetia woodlands, most nest were probably preyed upon by birds and
lizards. These latter would probably have been the main predators of
ground nests.

DISCUSSION

The mammalian nest-predator community inhabiting the study area
appeared to be impoverished as compared to those described for other
tropical places, such as Barro Colorado in Panamá and La Selva in Costa
Rica (Gibbs 1991, Loiselle and Hoppes 1983). Mammal nest predators,
such as *Sciurus, Dasyprocta* and *Nasua,* are common in these two locali-
ties, whereas they were not detected in the Sierra de Chiribiquete. This
difference could be attributed to the more natural mammal community
inhabiting our study site, in which mesopredator release (Soulé et al.
1988) did not appear to have taken place. The low abundance of these
mammalian predators would explain the low nest predation indices ob-
served in the Chiribiquete forests as compared to Barro Colorado forests,
where 100% of ground nests and 19% of above-ground nests were dep-
redated in only 2 d (Loiselle and Hoppes 1983). These differences in nest
predator communities, however, do not explain the close coincidence of
our results with those obtained by Gibbs (1991) in La Selva forests (Table
2). Thus, it appears that the relationship between the abundance and
species composition of nest predator communities and nest predation
pressure is weak when these features are compared across sites. The dif-
ferences in nest predation indices according to nest location and habitat
type between Chiribiquete and La Selva were mostly due to the larger
removal rates on ground nests located in the open hill tops found in

Chiribiquete (Table 2). This result can be attributed to the incidence of lizards in Chiribiquete, a kind of nest predator not mentioned by Gibbs, and which appear to have been the main predator of ground nests in the open tops of Chiribiquete. Gibbs (1991) attributed to the forest mammal community most of the nest predation pressure he measured. These animals do not seem to be prone to forage in open areas (Gibbs 1991), whereas Chiribiquete lizards appear to be specifically adapted to exploit these unforested tracts. Lizards would have replaced forest mammals as ground nest predators in the ecotonic and open areas of the forest-open gradient of Chiribiquete. The combined effect of both kinds of ground predators could thus explain the smoother increase of ground-nest-predation indices as vegetation cover decreased found in Chiribiquete as compared to the much stepper one found by Gibbs (Table 2).

The above-ground nest predation pressure also increased as vegetation structure became less complex. Birds appear to have been the main above-ground nest predators in Chiribiquete, despite their low abundances and diversities (*Crotophaga* spp. was not present, and nest robbers such as *Piaya* spp. were very scarce; see Gibbs 1991). Birds rely on visual clues for locating their prey, so that the decrease in the complexity of the vegetation towards the open tops would have facilitated nest detection. It thus appears that an increase in nest predation risk is not always associated with changes in the nest predator community structure such as those associated with human activities (i.e., the increase in crow densities in fragmented forests of Europe and North America). Nest predation pressure could also increase in natural conditions when nest accessibility increases, an effect which is also associated with human activities in the studies reported to date. Nest predation does not imply extreme adaptations, so that it is likely that some individuals of a species or a group of species in any given community could act as potential nest predators, which could destroy a large portion of avian nests once a given threshold of nest accessibility has been reached.

Our results also support Gibbs's (1991) conclusion about the lack of differences between the predation rates on forests bird nests in tropical areas as compared to temperate ones. Higher predation rates have been invoked to explain the smaller clutch sizes found in tropical forests birds (Ricklefs 1969, Snow and Snow 1964). Alternatively, Oniki (1979) hypothesized that there are no differences in such predation rates. Both our results and those reported by Gibbs (1991) are quite similar to those obtained using the same methodology in large North American forests (both type of artificial nests and exposure time): 37% in Missouri (7 d of exposure time; Burger 1988) and 13% in Maine (8 d of exposure; Small and Hunter 1988) for ground nests, and an average of 25% for ground and above-ground nests in Maryland and Tennessee forests (7 d of exposure; Wilcove 1985). Thus, the information available is consistent with Oniki's (1979) hypothesis about the lack of differences of nest predation rates in temperate and tropical forests habitats.

ACKNOWLEDGMENTS

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