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.

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, Möller 1989, Wilcove et al. 1986, Yahner and Cypher 1987, Yahner and Scott
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; Möller 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 (Tapirus 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.

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

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
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
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 attributed 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 themselves 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 disappeared without disturbance were most frequent in Bonnetia 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 pattern: 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 concentrated 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 inPanamá 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 localities, 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 observed in the Chiribiquete forests as compared to Barro Colorado forests, where 100% of ground nests and 19% of above-ground nests were depredated 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 differences 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.
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LITERATURE CITED


