ARTIFICIAL NEST EXPERIMENTS IN A FRAGMENTED NEOTROPICAL CLOUD FOREST

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Resumen. – Experimentos con nidos artificales en un bosque de niebla Neotropical fragmentado. – Realizamos experimentos con nidos artificiales en un bosque montano Neotropical en los Andes Orientales de Colombia para medir el efecto de colocar nidos en fragmentos de bosque o bosques continuos a dos alturas diferentes y durante dos estaciones climáticas. La tasa de predación de nidos no fue significativamente diferente entre fragmentos y controles. Sin embargo, encontramos que los nidos colocados directamente sobre el suelo mostraron una mayor probabilidad diaria de ser depredados que los nidos colocados un poco más alto en el sotobsoque. La tasa diaria de mortalidad (TDM) fue mas alta para los nidos en la estación de lluvias que en la estación seca. La mayor parte de los nidos depredados se atribuyeron a mamíferos (56%) y la depredación ocurrió mayormente en nidos colocados directamente sobre el suelo (78%). Nuestros estimativos de la TDM son bastante bajos (≈ 0,023) y similares a la TDM encontrados en otros sitios Neotropicales. Comparaciones de la TDM entre sitios Neotropicales y templados sugieren que no hay diferencias en las tasas de depredación experimentadas por las aves en estas áreas. Nuestros resultados sugieren que la fragmentación de estos bosques no tiene los mismos efectos negativos sobre la depredación de nidos comparado con otros bosques tropicales y templados.

Abstract. – We conducted artificial nest experiments in a Neotropical montane forest in the eastern Andes, Colombia, in order to test the effect of placing the nests in forest fragments or continuous forests, at two nest heights and for two different climatic seasons. Predation was not consistently different between nests placed in fragments and controls. However, we found that nests on the ground had a higher daily probability of being predated than nests in the understory. Also, daily nest mortality rate (DNM) was higher in the wet season than in the dry season. Most of the predated nests were attributed to mammals (56%), and predation occurred mostly on the ground (78%). Our estimates of DNM are quite low (≈ 0.023) and similar to another Neotropical montane forest and other Neotropical sites. Comparisons of DNM between Neotropical and temperate sites suggests that predation rates are similar. Our results suggest that fragmentation may not have a large negative impact in nest predation for bird populations breeding in fragments compared to other sites in tropical and temperate regions. *Accepted 13 September 2004.*

Key words: Colombia, nest predation, eastern Andes, fragmentation, tropical montane forest.

INTRODUCTION

Tropical montane forests represent the most

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endangered and fragmented habitats in the world (Whitmore 1997). The Neotropical montane forests of the northern Andes have been estimated to have only 5% of their original forest cover (Henderson *et al.* 1991). Recent estimates for these forests suggest that they house twice the number of bird species and three times the number of plants species
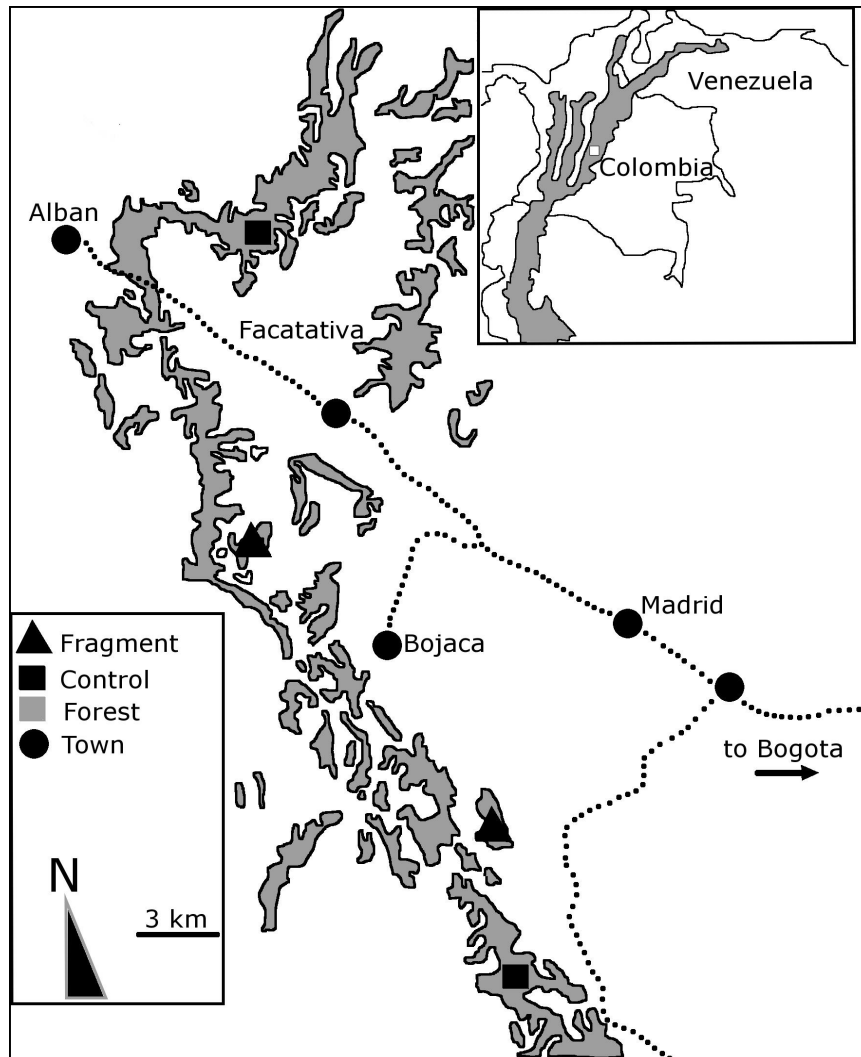
FIG. 1. Map of the study area in the western limit of the Bogotá plateau.

compared to lowland tropical forests of similar size (Henderson *et al.* 1991, Fjeldså & Rahbek 1997, Rahbek, 1997). Despite this fact, relatively few attempts have been made to understand the effects of tropical montane forest fragmentation and perturbation on the population dynamics of vertebrate and plant populations (Laurance & Bierregaard 1997). Specifically for birds, these effects can range

from higher probability of local extinction in fragments due to genetic and/or demographic stochasticity, to reductions in population growth rates due to higher predation rates, or reduced microhabitat availability for nesting.

The use of artificial nests is an economical and easy way to compare community-wide nest predation pressure between forest frag-

ments of different size or forest fragments and continuous forests. Artificial nest studies have been criticized on the grounds that they overestimate natural nest predation rates (Wilcove 1985, Haskell 1995, Willebrand & Marcström 1998, Wilson *et al.* 1998, Ortega *et al.* 1998, King *et al.* 1999, Davison & Bollinger 2000, Zanette & Jenkins 2000, Maier & Degraaf 2001, Lindell *et al.* 2004). Artificial nests lack parental defense, are not as well concealed as natural nests, or leave scents that can attract predators (Whelan *et al.* 1994). However, if the question is strictly comparative (i.e., edge vs forest interior or small fragments vs large fragments), artificial nest predation experiments are valid to assess the effects of predators assuming that the direction of the effects will be the same for natural and artificial nests, and in the treatments being compared (i.e., edge vs interior). Additionally, the use of artificial nests has some clear advantages over searching and locating natural nests. In an experimental setting, it is possible to investigate the effects of variables that are unmanageable under natural conditions (e.g., nest type and nest density) and increase sample sizes.

Despite these advantages, few studies using artificial nest experiments have been done in the Neotropics (Loiselle & Hoppes 1983, Sieving 1992, Estrada *et al.* 2002, Roper 2003, Lindell *et al.* 2004) and we only know of one published study carried out in Neotropical montane forest (Arango-Velez & Kattan 1997).

In this study, we investigate the effect of different artificial nest types and eggs on predation rate and compare the predation rates of these nests between large tracts of contiguous tropical montane forests and forest fragments.

METHODS

We choose two fragments (5 and 15 ha) and two large tracts (> 500 ha) of mountain cloud forest in the Colombian eastern Andes, approximately 15 km west (San Cayetano) and 20 km northwest (Zipacón and Facatativá) of the city of Bogotá. This region is an active agricultural and grazing area with remnant forest patches along the west border of the Bogotá plateau (Sabana de Bogotá) between 2600 and 2900 m a.s.l. (Fig. 1). Cloud forest fragments of different sizes and degrees of disturbance are interspersed with potato, corn, and vegetable crops, and pastures for milk-producing cattle. The two large forest sites (hereafter called controls) (Cayetano: 04º37'44"N, 74º18'49"W and Selva: 04º 52'19"N, 74º22'49"W) are located within a large tract of forest that extends from the south-west of Bogotá for approximately 50 km to the north, along the ridge of the Bogotá plateau. The two fragments (Miralejos: 04º45'82"N, 74º23'71"W and Silencio: 04º36'72"N, 79º19'21"W) are part of a mosaic of small forest fragments in a matrix of pastures. These forests vary in their slope, with large trees averaging 15 m in height. Undergrowth is dense and the sites are fairly undisturbed. Forest structure within the fragments is similar to the controls in height and general physiognomy, although the canopy is more discontinuous and there are more signs of recent human and cattle disturbance (pers. observ.). Both fragments and controls are dominated by trees of the families Asteraceae (*Ageratina* spp., *Erato* spp. and *Eupatorium* spp.), Winteraceae (mostly *Drimis* spp.), and Melastomataceae (*Miconia* spp., *Tibuchina lepidota*, *Bucquetia* spp. and *Clidemia* spp.). Plants from the families Rubiaceae (mostly *Palicourea* spp.), Ericaceae (*Macleania rupestris*) and Melastomataceae (*Miconia* spp.) are dominant in the understory, with some Orchidiaceae (*Pleurotalis* spp. and *Epidendron* spp.) and Araceae (*Anturium* spp.) growing as epiphytes or free standing. Annual temperature and precipitation are around 15° C and 600–800 mm. The

TABLE 1. Effect of nest type (12 nests in each treatment) and egg type (18 nests in each treatment) on the mean probabilities of a nest or an egg to be predated after 20 days of exposure.

		Mean probability of a nest being predated ($\pm$ SE)	Mean probability of an egg being predated ($\pm$ SE)
Nest types	Plastic	0.3 $\pm$ 0.14	0.2 $\pm$ 0.10
	Plastic-grass	0.3 $\pm$ 0.14	0.3 $\pm$ 0.11
	Grass	0.5 $\pm$ 0.15	0.4 $\pm$ 0.10
Egg types	Clay	0.6 $\pm$ 0.12	0.4 $\pm$ 0.10
	Quail	0.3 $\pm$ 0.11	0.2 $\pm$ 0.07

rainfall pattern is bimodal with two wet seasons (May–July and October–November) interspersed with dry seasons during the rest of the year.

In January 1998, we set-up a preliminary experiment to test the effects of both nest and egg type on the predation rates, and to select the type of nest and egg to use in forthcoming experiments. We used three nest types consisting of 1) a plastic receptacle (hereafter plastic nest), 2) the same plastic receptacle lined with leaves and moss (hereafter plastic-grass nest), and 3) a nest constructed with grass imitating open-cup nests (hereafter grass nest). We used two egg types: plasticine and quail eggs. Plasticine eggs were molded by hand with white plasticine and were about the same size as quail eggs (2.5 x 1.5 cm). We tested all possible combinations with both nest and egg type in a mixed 2–3 factor design. Nests were placed in one fragment and one control forest; in each forest, six parallel transects separated by 50 m were established from the edge into the forest and along each transect a nest with two eggs was placed at 0, 15 and 30 m from the edge, and at 1–1.5 m above the ground. The nests were visited 10 and 20 days later. In this last visit, the nests and eggs were removed. We used a pooled error mixed 2–3 factor design analysis to separate the effects of nest and egg type on the probability of predation of eggs and nests (StatSoft, Inc. 2000). The mean probability of a nest being predated did not change with nest type (Table 1, ANOVA, $F_{2,32}$ = 1.06, P = 0.35). There was no statistical significant difference in the mean probability of a nest being predated with quail or plasticine eggs (Table 1, ANOVA, $F_{1,32}$ = 2.94, P = 0.09). Similarly, the mean probability of an egg being predated was not affected by nest type (Table 1, ANOVA, $F_{2,32}$ = 0.70, P = 0.50) or egg type (Table 1, ANOVA, $F_{1,32}$ = 3.47, P = 0.07).

Since neither nest type or egg type seemed to have an effect on nest or egg predation probabilities, we decided to choose a nest which would be inexpensive to build as well as informative on the nature of the predators for our experiments on the effect of the surrounding matrix on nest predation. Of the six possible combinations of nest types and egg types, the grass-plasticine egg fulfilled these requirements. Therefore, we choose this combination for our next experiment.

We then conducted an experiment to evaluate the effects of fragmentation, nest position and climatic season on nest predation. We placed 40 grass-plasticine nests randomly (with two plasticine eggs each) in the two fragments and two controls within a 5.4-ha plot (approx. 7 nests/ha). In the fragments, the plot included some portion of the edge of the fragment, but in the controls the plot was in the interior of the forest at least 200 m away from the edge. Twenty nests were placed directly on the ground and the remaining 20 were placed in the understory between 1–1.5

TABLE 2. Number of nests predated during two seasons and at two positions in the four different sites, 20 days after nest placement. A total of 80 nests were used for each season-position combination.

Season	Position	Fragment # 1	Fragment # 2	Control # 1	Control # 2	Totals	Percent
Dry	Ground	14	12	11	11	48	60.0
	Branch	6	8	6	6	26	32.5
Wet	Ground	7	10	8	11	36	45.0
	Branch	9	14	7	12	42	52.5
	Totals	36	44	32	40	152	
	Percent	45.0	55.0	40.0	50.0		47.5

m off the ground. The experiment was replicated in two different climatic seasons: dry (March–April 1998) and wet (June–August 1998) (Total number of nests used = 320). We used cloth gloves in the manipulation of nests and eggs to minimize human odor. As in the preliminary experiment, nests were visited 10 and 20 days later. In this last visit, nests and eggs were removed if they were not lost. For both experiments, a nest was considered preyed upon if the nest and/or eggs were damaged or lost. We used 2 x 2 tests of independence to estimate the effects of surrounding matrix (fragmentation), nest position, and climatic season on the total number of nests predated. Since 9 independent tests were performed on the same set of data, we used a Bonferroni-corrected significance value at α = 0.05 (α' = 0.0055).

We calculated daily nest mortality rates (DNM) as the proportion of nests being predated per day (number of nests predated/total number of nests)/number of days. DNM was estimated twice: between 0 and 10 days, and between 10 and 20 days of exposure. In order to have error estimates of DNM for each fragment and season, we randomly selected 50 samples of 10 nests each for each combination of site and season. These re-samplings were drawn from the sample of 40 nests each to estimate DNM between 0 and 10 days. For the second estimate (between 10 and 20 days), the sub-samples were drawn from the nests that were not predated by day 10. We followed

a similar procedure to estimate DNM for nests in the ground and the understory in each season, but instead of drawing the sample from 40 nests we used a sample of 80 nests (combining fragments and controls each season). DNM was expressed as means ± 95% confidence intervals. We considered two DNM estimates to be different if their 95% confidence intervals did not overlap. We also used logistic regression to estimate the effects of fragmentation and climatic season on the total proportion of nests and eggs predated at the end of the experiment.

To identify the type of predator, we examined the marks left on the plasticine eggs. We established three different categories: mammals (incisor and other tooth marks and nail stamps and scratches), birds (triangle-shaped perforations and nail stamps) and unidentified (stamps and marks not assigned to a particular predator type). Chi-square tests of independence were used to test for differences between number of nests predated by birds and mammals during different seasons, ground positions and surrounding. Bonferroni-corrected significance values were used for α = 0.05 (α' = 0.0055).

RESULTS

There were no significant differences between the number of nests predated in controls and forest fragments (χ^2_1 = 0.421, P = 0.516), dry and wet seasons (χ^2_1 = 0.105, P = 0.745) or

TABLE 3. Daily rate of nest mortality (DNM ± 95% confidence intervals) as estimated from 50 re-samplings of 10 nests each for each combination of position and season. These re-samplings were drawn from a sample of 80 nests on the ground and 80 nests above the ground for each treatment to estimate DNM between 0 and 10 days. For the second estimate (between 10 and 20 days) of DNM, the sub-samples were drawn from the nests that were not predated by day 10. The asterisks denote the result of comparing the mean DNM between ground and above the ground for the same time period.

Position	Dry season		Wet season	
	0–10 days	10–20 days	0–10 days	10–20 days
Ground	0.040 ± 0.0179	0.036 ± 0.0018	0.032 ± 0.0016	0.020 ± 0.0011
Above the ground	0.021 ± 0.0014*	0.012 ± 0.0011*	0.034 ± 0.0015	0.036 ± 0.0028*

*Non overlapping means.

nest on the ground and nests off the ground ($\chi^2_1 = 1.684$, $P = 0.194$). Season and surrounding matrix were independent on the number of nests being predated ($\chi^2_1 = 0.032$, $P = 0.857$) as well as nest position and surrounding matrix ($\chi^2_1 = 0.053$, $P = 0.816$, Table 2). Although nest position and season were independent on the number of nests predated ($\chi^2_1 = 4.647$, $P = 0.031$); nests located on the ground showed a slight tendency of being more predated during the dry season, while nests above the ground showed a tendency of being more predated during the wet season (Table 2).

We tested for differences between sites and seasons on DNM using two estimates of this rate: up to 10 days and between 10 and 20 days. For the first estimate, DNM overlapped highly in the dry season except for the first forest fragment which was marginally different from the other three forests. During the wet season, there was no consistent difference in DNM between fragments and controls but forests that were close geographically were more similar to each other (fragment 1 and control 1, fragment 2 and control 2). DNM between 10 and 20 days of the experiment were overall lower in the dry season and fragments seemed to have a higher DNM (but control 2 had a comparable DNM). During the wet season, all forests except fragment 2

had DNM comparable to the dry season. Therefore, no consistent directional differences in daily rates of nest mortality were found between fragments and continuous forests (i.e., being higher in fragments than continuous forests or *vice versa* consistently). DNM rates for both seasons were higher during the first 10 days of the experiment (mean = 0.032, SE = 0.0017, n = 8) than during the second 10 day period (mean = 0.025, SE = 0.0038, n = 8).

However, we did find significant differences in the daily rate of nest mortality between nests located on the ground and nests located above it (Table 3). Nests had a higher DNM when they were placed on the ground during the dry season (ground mean = 0.038, understory mean = 0.017). During the wet season this difference was only apparent between DNM calculated between 10 and 20 days.

Predator identification. In most of the nests that were predated (114/152), we could clearly distinguish between mammalian and bird predators. Eggs that were manipulated by mammals showed clear signs of incisive gnawing and nail scratching. Eggs manipulated by birds showed triangle-shaped punctures and superficial deformations in the plasticine as if the egg was picked up with a

TABLE 4. Number of nests predated by mammals and birds at two different positions (nests placed on the ground and nests placed between 1-1.5 m above the ground on a branch) during two different seasons. Nests in which the predator was not unequivocally identified were classified as not identified.

Position	Dry season			Wet season		
	Mammals	Birds	Not identified	Mammals	Birds	Not identified
Ground	41	0	8	24	1	9
Branch	7	10	7	12	18	12
Total	48	10	15	36	19	21

semi-opened bill.

The total number of nests predated by mammals (84/114) was significantly larger than the number of nests predated by birds (29/114, $\chi^2_1 = 27.50$, $P = 1.56 \times 10^{-7}$, Table 4). Additionally, there were more nests preda-ted by mammals on the ground than off-the-ground ($\chi^2_1 = 45.50$, $P = 1.51 \times 10^{-11}$). Most of mammal-predated nests were at the ground level during the dry season (41/48), with an increase of off-the-ground nest predations in the wet season (12/36). In contrast, bird-pre-dated nests were exclusively observed off the ground (28/29) and, although there were more bird predated nests during the wet sea-son, there were no significant differences in the location of nests being predated between seasons ($\chi^2_1 = 0.11$, $P = 0.739$). Overall, the number of nests predated by mammals and birds did not differed significantly between seasons ($\chi^2_1 = 3.57$, $P = 0.058$, Table 4).

DISCUSSION

The results of our preliminary experiment to select an egg and nest type appropriate for the main experiment showed that all possible combination of nest and egg type had a simi-lar chance of predation. However, we are somewhat cautious about the conclusiveness of these results due to a small sample size (n = 6 nests for each egg-nest types). In fact, several studies have found that egg type and nest type strongly affect the likelihood of pre-dation. In particular, plasticine eggs are more

predated than other egg types (Bayne *et al.* 1997, Goodner *et al.* 1998, Bayne & Hobson 1999, Cotterill & Hannob 1999, Rangen, *et al.* 2000, Maier & Degraaf 2001). Quail eggs are less predated than smaller eggs, because small predators are unable to crack the thick shells of these eggs (Roper 1992, Maier & Degraaf 2000, Saveglj *et al.* 2003). Although some attributed these effects to scent attraction (Whelan *et al.* 1994), other studies have shown that scent does not affect predation on artifi-cial nests (Skagen *et al.* 1999, Bayne & Hob-son 1999). Our intention with this experiment was to quickly find an egg and nest type that would increase the probability of detecting the activity of predators, not to conclusively test the effects of these different nest and egg types on predation probabilities. Since we could not favor any particular nest-egg type, we chose the most economical and informa-tive (grass nest and plasticine eggs). Plasticine eggs have the advantage over other egg types in providing indirect information on the nature of the predator by marks left on them (Bayne *et al.* 1997, Goodner *et al.* 1998) although they may overestimate natural preda-tion rates (Maier & Degraaf 2001).

The results of our main experiment on the effect of cloud forest fragmentation on preda-tion of artificial nests suggest no difference in the probability of a nest being predated or in the rate of predation between fragments and continuous forest tracts. This result is consis-tent with many other studies (Taylor & Ford 1998, Wong *et al.* 1998, Cotterill & Hannob

1999, Leite & Marini 1999, Matthews *et al.*
1999, Zanette & Jenkins 2000). However, a
large number of artificial nest experiments
have found an inverse relationship between
fragment size and predation probability
(Small & Hunter 1988, Yahner & Scott 1988,
Gibbs 1991, Langen *et al.* 1991, Sieving 1992,
Yahner & Delong 1992, Nour *et al.* 1993,
Keyser *et al.* 1998, Wilson *et al.* 1998), includ-
ing the only published study in Neotropical
cloud forests (Arango-Velez & Kattan 1997).
The ability to detect the effects of fragmenta-
tion on nest predation is very dependent on
the spatial and temporal scale of the study
(Stephens *et al.* 2004), on the nature of the
predator community, and on the specific
effects of fragmentation on its composition
(see review by Chalfoun *et al.* 2002). If preda-
tors prefer disturbed habitats or edges, one
would expect an increase in predation with
fragmentation and a clear edge effect (Gibbs
1991, Cooper & Francis 1998, Söderström
1999, Boulet & Darveau 2000). On the other
hand, if predators come from within the frag-
mented habitats, there should be little or no
edge effect and no relationship between the
degrees of fragmentation and predation
(Small & Hunter 1988, Nour *et al.* 1993,
Bayne & Hobson 1997, Arango-Velez & Kat-
tan 1997, Gardner 1998, Taylor & Ford 1998,
Wong *et al.* 1998, Degraaf *et al.* 1999, Mat-
thews *et al.* 1999, Maier & Degraaf 2000, Nie-
haus *et al.* 2003) unless population density of
the predators is affected by fragmentation. In
at least one case, it has been shown that major
predators change according to the size of the
fragment (Nour *et al.* 1993).

In our cloud forest sites, small mammals
were the predominant predators (75% vs 25%
attributed to birds), and this may explain the
lack of an observed fragmentation effect
since many small mammals are still able to
persist in small forest fragments (Arango-
Velez & Kattan 1997). In other tropical sites,
mammals also have been reported as the main
nest predators (>70%, Estrada *et al.* 2002). In
temperate zones where the predators (e.g.,
raccoons, crows) seem to live in the sur-
rounding matrix and be favored by forest
fragmentation, predation is usually higher in
forest fragments and edges (i.e., Wilcove
1985, Andrén & Angelstam 1988, Andrén
1992, Huhta *et al.* 1996, Niehaus *et al.* 2003).

The results of our experiment showed a
surprisingly lower predation rate (0.023 and
0.025 predated nests per nest per day in the
dry and wet seasons respectively) than
expected (if all nests were predated DNM =
0.05). In terms of number of nests predated
per day, these figures correspond to 3.6 and
4.0 nests/day, respectively. These figures are
similar to predation rates observed in artificial
nests in other Neotropical sites. Arango-Velez
& Kattan (1996) report between 2.4–3.7 pre-
dated nests/day in a Neotropical cloud forest
in the western Colombian Andes with similar
sample size to this study (n = 30 nests vs n =
40 nests in this study). Using a similar number
of nests (n = 45), Estrada *et al.* (2002), in a
lowland rain forest in Los Tuxtlas, Mexico,
reported nest losses of 3.5–3.8 nests/day with
artificial nests using hen eggs, and 3.6–4.0
nests/day when using plasticine. If artificial
nest predation grossly overestimates natural
nest predation (Ortega *et al.* 1998, Wilson *et al.*
1998, King *et al.* 1999, Zanette & Jenkins
2000), then natural predation rates in this sys-
tem are even lower. This is a rather surprising
result given that nest predation is supposed to
be higher in the tropics than in the temperate
zones (Oniki 1979, Skutch 1985).

A recent review comparing artificial nest
predation rates between tropical and temper-
ate sites did not find any significant differ-
ences and, when only shrub nests were
compared, both natural and artificial tropical
nests had a lower predation risk than their
temperate counterparts (Söderström 1999).
All these results seem to contradict the preda-
tion hypothesis to explain smaller clutch sizes

in tropical birds, one of the most prevailing dogmas in ornithology (Martin *et al.*, 2000).

We encourage more studies to use artificial nests to estimate the potential effects of predators in tropical bird communities, and to compare the effects of habitat disturbance/fragmentation on nest predation. While artificial nest predation rates usually overestimate natural predation rates, this does not preclude their usefulness for comparative purposes under the assumption that the direction of the effect (but not necessarily its magnitude) is similar between natural and artificial nests (Major & Kendall, 1996). A good estimate of the effect of predators is of paramount importance for designing better conservation and management strategies for bird populations in Neotropical montane forests.

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