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# NEST-SITE CHARACTERISTICS AND BREEDING DENSITY OF TWO SYMPATRIC FOREST-FALCONS IN GUATEMALA

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**Resumen. – Características del sitio de los nidos y densidad de parejas de dos halcones de bosque simpátricos en Guatemala. –** El Halcón de Cuello rojo (*Micrastur ruficollis*) y el Halcón de Collar (*M. semitorquatus*) anidan en cavidades y tienen distribución geográfica similar pero son diferentes en tamaño corporal. Para el Halcón de Cuello rojo y el Halcón de Collar, la altura media de los nidos sobre el suelo fue de 17 y 20 m respectivamente, en árboles de diámetro medio 95 y 167 cm a la altura del pecho y profundidad media de la cavidad del nido de 81 y 47 cm respectivamente. El árbol más usado para la nidificación de los halcones de bosque fue *Cedrela mexicana*: 33% de los nidos para *M. ruficollis* y 44% para *M. semitorquatus* fueron en esa especie. Nidos en árboles vivos fueron más exitosos que en árboles muertos o troncos. La distancia promedio entre nidos vecinos fue de 1.04 y 3.28 km para el Halcón de Cuello rojo y el Halcón de Collar, respectivamente. La densidad de parejas basada en la distancia promedio entre nidos, fue una pareja territorial/0.98–1.08 km$^2$ para el Halcón de Cuello rojo y una pareja territorial/9.6–10.5 km$^2$ para el Halcón de Collar.

**Abstract. –** The Barred Forest-Falcon (*Micrastur ruficollis*) and Collared Forest-Falcon (*M. semitorquatus*) are cavity nesters with similar geographic distributions but differences in body size. For Barred and Collared forest-falcons, nest height averaged 17 and 20 m above ground, nest tree dbh averaged 95 and 167 cm, and nest depth averaged 81 and 47 cm, respectively. Most forest-falcon nesting attempts were in *Cedrela mexicana*: 33% for Barred and 44% for Collared forest-falcons. Nesting attempts in live trees were more successful than those in dead trees or snags. Inter-nest distances averaged 1.04 and 3.28 km for Barred and Collared forest-falcons, respectively. The breeding density calculated from inter-nest distance yielded estimates of 1 territorial pair/0.98–1.08 km$^2$ for Barred Forest-Falcons and 1 territorial pair/9.6–10.5 km$^2$ for Collared Forest-Falcons. *Accepted 4 April 2001.*

**Key words:** Barred Forest-Falcon, *Micrastur ruficollis,* Collared Forest-Falcon, *M. semitorquatus,* nest characteristics, breeding density, Guatemala.

## INTRODUCTION

Among Neotropical birds, raptors are one of the least studied groups (Robinson and Wilcove 1989) and consequently relatively little is known about their basic natural history, biological requirements, food habits, distribution, population structure and dynamics (Thiollay 1985).

Two species of forest-falcons, the Barred Forest-Falcon *(Micrastur ruficollis)* and Collared Forest-Falcon *(M. semitorquatus)*, are the most widespread of the forest-falcons, and little is known about their life histories (Mader 1979, Thorstrom 1990). Recently however some new insights into the life histories of two of these secretive forest-falcons have been provided by an intensive field study targeting these species (Thorstrom *et al.*1993). In this paper I report nest characteristics, breeding success related to tree species used for nesting and nesting density of marked individuals from the northern-most subspecies of Barred Forest-Falcon (*M. r. guerilla*) and Collared Forest-Falcon (*M. s. naso*) in a tropical environment.

## STUDY AREA AND METHODS

The study site was in the ruins and central area (17°13'N, 89°36') of Tikal National Park (576 $km^2$) in northeastern Guatemala. This park is a lowland, dry, semi-deciduous, tropical forest with an elevation from 200 to 350 m. A description of the weather in Tikal is given in Thorstrom *et al.* (2000).

Within the park, Schulze & Whitacre (1999) have described several forest types that occur along topographical drainage, soil type, and moisture gradients. Two extremes of this forest type continuum are upland forests (tall, semi-evergreen forests on well-drained shallow soils) and bajo forests (low in stature, open canopy with dense understory, occurring in low-lying sites of deep clay-rich soils, subject to seasonal flooding and drought).

Several assistants and I studied a population of Barred Forest-Falcons in the 1988 through 1995 breeding seasons and for four weeks in April and May in 1996, and a population of Collared Forest-Falcons from 1988 to 1993 breeding seasons. We searched the forest and visited occupied territories daily from February through July to determine the nesting activity of potential breeding pairs. Courting pairs were followed aurally and visually until a nest was confirmed. An occupied nest was defined as a tree where pair vocalizations, courtship and courtship feeding, copulating, incubating, brooding, and repeated prey-carrying occurred. When possible, nest contents were confirmed by climbing nest trees. Nest height was measured in plumb-line distance from lip of the entrance and nest depth from the entrance interior to the floor of the cavity. Nest tree diameter was measured at breast height (dbh). Inter-nest distance was determined by Global Positioning System (GPS) and nest locations plotted on a topographical map. Breeding density was determined from the mean neighbor distance between nests following Selås (1998). The area for one nesting territory was $\pi r^2 * 1.158$ (1.158 is a constant that includes the area of non-overlap between neighboring territories). Territory size per pair was also calculated by squaring the mean internest distance.

Detailed nesting habitat analyses are based on five Barred and five Collared forest-falcon nests. Only five Collared Forest-Falcon nests were known at the time of nesting habitat analysis in 1992; five Barred Forest-Falcon nests were randomly chosen from among 21 known nest trees. Five circular plots were sampled at each nest; one was centered on the nest tree and four others were located 50 m in each cardinal direction. Hence, for each forest-falcon species, 25 plots, totaling 1.01 ha, were sampled. All trees > 7.5 cm in dbh were identified to species, and dbh measured.

Descriptive statistics are mean followed by standard deviation (SD). Statistical tests were performed with Systat®, excepting a few chi-square tests. The sum probability of a type I error for all group comparisons alpha was set at 5%.

In Tikal National Park female Barred Forest-Falcons (mean = 238 g, SD = 23 g; n = 17; range 207–307 g) weighed about 42% more than males (mean = 168 g, SD = 5.5; n = 13, range 156–175 g) and female Collared Forest-Falcons (mean = 870 g, SD = 63 g; n = 6, range 792–940 g) weighed about 48% more than males (mean = 587 g, SD = 17.6 g; n = 4, range 563–605 g).

## RESULTS

*Barred and Collared forest-falcon nests.* No Barred or Collared forest-falcons were observed building nests. All nests were in tree cavities and had a decayed wood substrate. Barred

Table 1. Nest height, nest depth, nest tree diameter (dbh = diameter at breast height), and inter-nest distance of Barred and Collared forest-falcon nests, Tikal National Park, Guatemala 1988-1993.

| Nest characteristics | Barred Forest-Falcon | | Collared Forest-Falcon | |
|---|---|---|---|---|
| | Mean ± SD | Range | Mean ± SD | Range |
| Nest height (m) | 17.4 ± 4.2 | 10.0-30.0 | 19.9 ± 3.1 | 15.7-24.0 |
| Nest depth (cm) | 80.9 ± 58.8 | 3.0-200.0 | 47.4 ± 34.4 | 23.0 ±100.0 |
| Nest tree dbh (cm) | 94.8 ± 40.5 | 30.0-190.0 | 167.0 ± 91.1 | 90.0-314.0 |
| Inter-nest distance (m) | 1039 ± 273 | 376-1550 | 3281 ± 387 | 3008-3554 |
| Number of nest trees | 39 | | 6 | |

and Collared forest-falcons are secondary cavity-nesting species (classification of Waters *et al.* 1990). Most nesting attempts by Barred Forest-Falcons (66/70) and all Collared Forest-Falcon nesting attempts were in non-excavated cavities. Nearly all non-excavated cavities appeared to have developed through decay, where a limb had broken off or the tree's heartwood rotted opening the interior.

All Barred Forest-Falcon nest trees except one were in upland forest (n = 38). Collared Forest-falcon nest trees were in hill-base and transitional forests, between upland and *bajo* forests. Collared Forest-Falcon nests were higher, larger and had greater inter-nest spacing on average than Barred Forest-Falcon nests (see Table 1).

*Nest tree species.* Seventy Barred Forest-Falcon nesting attempts were in 39 trees of 15 species. Most of the 70 nesting attempts, 33% (n = 23) were in *Cedrela mexicana* (Meliaceae), 10% (n = 7) in *Brosimum alicastrum* (Moraceae), 9% (n = 6) in *Acacia dolichostachya* (Fabaceae), and 9% (n = 6) in *Trophis racemosa* (Moraceae). Nine Collared Forest-Falcon nesting attempts involved 5 tree species: 44.4% (n = 4) in *Cedrela mexicana*, 22.2% (n = 2) in *Swietenia macrophylla* (Meliaceae), 11.1% (n = 1) in *Lonchocarpus castilloi* (Fabaceae), 11.1% (n = 1) in *Spondias mombin* (Anacardiaceae), and 11.1% (n = 1) in *Manilkara zapota* (Sapotaceae).

Of the 10 forest-falcon nest sites included in the habit analyses, all were in trees 52 cm dbh or larger, while trees of this size comprised only 72 of 1,376 trees in our 50 sample plots (and belonged to 16 of the 108 species found in the plots). To assess whether the two forest-falcon species showed selectivity with respect to tree species, Monte-Carlo simulations were conducted, assuming that only those 72 trees > 51 cm in diameter were potentially acceptable to the forest-falcons. Both forest-falcon species showed positive selectivity for *Cedrela mexicana* ($P < 0.001$), and for no other tree species.

*Reproductive success in species specific nest trees.* Only mature and older-aged trees provided nesting cavities for Barred and Collared forest-falcons. Nests in *Cedrela* produced 31% of the 75 young Barred Forest-Falcons fledged in this study. For Barred Forest-Falcons during this 7 year study, 11 breeding pairs occupied only one nest tree, four used two different nest trees (alternative nests), four utilized three nest trees each, and two occupied four different nest trees. The Barred Forest-Falcon pairs that occupied only one nest tree (i.e., one nesting cavity used per territory) raised 55% of the 75 fledglings, whereas breeding pairs that used four different nest trees/cavities per territory raised only 9% of the young. There was no relationship between nest tree dbh and number of young fledged.

Of 70 Barred Forest-Falcon nesting attempts, nesting success was significantly different between live and dead trees (snags) ($\chi^2_1$ = 6.1, $P < 0.05$). Most nests in live trees were successful (33/51) and most nests in dead trees failed (14/19). The 11 pairs that switched nest sites the following year after failure were not significantly different than pairs that were successful and did not switch nest sites (n = 15) ($\chi^2_1$ = 7.6, $P > 0.1$). Breeding pairs with several nests (alternative nest sites) in their territory raised fewer young than breeding territories with only one continuously used nest ($\chi^2_3$ = 30.00, $P < 0.001$).

Among Collared Forest-Falcons, only one pair had two documented nest sites (one alternative nest). In 1990, it nested in a *Spondias mombin*, fledging two young, and in 1991 and 1992 it used a *Swietenia macrophylla* and fledged three young.

*Inter-nest distances and breeding density.* Barred Forest-Falcon inter-nest distance for nests of different pairs averaged 1.04 km based on the minimum spanning tree method (range = 0.38–1.55 km, SD = 0.27, n = 39) resulting in territories occupying 0.98 km$^2$ per pair for maximum packing and 1.08 km$^2$ per pair for the squaring method. For Collared Forest-Falcons, the mean inter-nest distance among six neighboring occupied nests was 3.28 km (range = 3.0–3.5 km, SD = 0.39) yielding an estimate of territories averaging 9.6 km$^2$ per pair for maximum packing and 10.5 km$^2$ for the squaring method. Hence in 100 km$^2$ of similar habitat in our study area, we estimate an average density of 100 territorial pairs of Barred Forest-Falcons and 10 territorial pairs of Collared forest-falcons.

## DISCUSSION

In Tikal National Park, Barred Forest-Falcons are dependent on the primary forest for food resources and nesting habitat and Collared Forest-Falcons occupy a broader range of habits and are considered a forest-edge species, breeding from transitional to bajo forests, and foraging throughout the different habitat types.

Several nest sites were used consecutively from year-to-year by forest-falcons. For Barred Forest-Falcons, cavities do not seem to be limiting on some territories because several pairs had up to four alternative nests, but for Collared Forest-Falcons and other Barred Forest-Falcons, it appears that nest sites are limiting. Several Barred Forest-Falcon pairs only used one nest site throughout this study.

The higher nesting success of Barred Forest-Falcons in live trees versus dead trees shows that predation might contribute to nest failures in dead trees and snags. Possibly, predators remember and visit cavities of snags and dead trees more frequently when searching for food resources.

Despite the fact that nests of Barred and Collared forest-falcons were often situated in different forest types, the two forest raptors overlapped strongly in the species and size of nest trees used. Both raptors showed high affinity for large trees over 50 cm in diameter. While statistical tests showed a significant preference for nesting in *Cedrela*, this species is unusually valuable as a nest tree for many species due to the large cavities frequently formed where rotten limbs have fallen, and to their emergent stature.

Collared Forest-Falcons, the larger species, required a larger nest site to accommodate their larger body size. Collared Forest-Falcons occupied the larger nest cavities, found only in mature and older trees of large diameter, nearly doubling the average diameter of Barred Forest-Falcon nest trees (see Table 1). Although a wide range of tree species were utilized for nesting, *Cedrela* was the species occupied more frequently than any other tree by both forest-falcon species. *Cedrela* provided nearly half of Collared Forest-Falcon nest sites and one-third of Barred Forest-Falcon nest sites. Some Barred and Collared forest-falcon pairs have continued to use established nest sites annually. The Cedró nest site located in 1988 (Thorstrom *et al.* 1990) has been used annually, but with no success. Unfortunately, *Cedrela* is also an attraction for commercial logging. The apparent preference for large *Cedrela,* and perhaps for very large trees in general, presents a potential conservation challenge.

Historically, the logging industry in Petén and adjacent regions has focused mainly on selective logging of *Cedrela* and *Swietenia.* Most of the region has been logged at least once, and large, marketable specimens of *Cedrela* and *Swietenia*, often sparsely distributed at best, are now much rarer. The fact that logging of these valued lumber species continues apace, despite low standing crops and slow regeneration that threaten the viability of the logging industry, could limit the availability of nest sites, not only for forest-falcons, but for many kinds of wildlife.

*Breeding density.* Breeding Barred and Collared forest-falcons in Tikal National Park occupied an average of 1.0 and 10.0 km$^2$ per territorial pair for both methods, respectively. Neighboring territories were evenly spaced throughout the study area even though forest-falcons were somewhat specific in their nesting requirements, i.e., upland forests for Barred Forest-Falcons and transitional forests for Collared Forest-Falcons. In a 100 km$^2$ area, we estimate that the breeding density would include approximately 100 territories for Barred Forest-Falcons and 10 territories for Collared Forest-Falcons.

In South America, density estimates were determined for several species of territorial forest-falcons. In a 100 km$^2$ area in French Guinea with four species of *Micrastur*s, Thiollay (1989a) estimated that the potential breeding densities were in the order of 4 territorial pairs for the Barred Forest-Falcon, and 5 territorial pairs for Collared Forest-Falcons, i.e., 25 and 2 times less than the density estimate at Tikal. In Amazonian Peru at Manu National Park with three resident species of *Micrasturs*, Terborgh *et al.* (1990) and Robinson and Terborgh (1997) estimated the number of territorial pairs per 100 ha at 1.5–2.0 for Barred Forest-Falcons and at 0.25 for Collared Forest-Falcons. This was 0.5–1 and 2 times greater than the density estimated at Tikal.

We suspect that a difference in the tropical forest habitats, (dry in Tikal National Park, slightly wetter in Manu National Park with rainfall averaging slightly more than 2000 mm per annum, and wet in French Guiana), may have contributed to this large difference between species territory size. Another possibility was that the surveying methods used in South America (spot mapping and strip transect census) may have missed the main breeding period or the early dawn vocalizations when most forest-falcons were actively calling. For a reliable density estimate of breeding raptors in a primary rain forest, the best strategy should be the design of a particular census method for each species (Thiollay 1989b). Following radio-tagged birds should be strongly encouraged and may be the only way to confirm the actual territory size of most species (Thiollay 1989b).

My estimates, using radio-tagged individuals for territory size and internest distance, may reflect a more accurate estimation of the species' breeding density because Thiollay (1989a) did not use actual neighboring breeding territories to estimate forest-falcon densities. A more likely explanation for the difference between Barred and Collared forest-falcon densities in Tikal, Manu, Peru and French Guiana (low) is the diversity of forest-falcon species: four species in French Guiana, three in Peru, and only two in Tikal. It is possible that generic packing results in greater interspecific resource competition and lower densities of widespread forest-falcons in French Guiana.

In French Guiana, the Lined Forest-Falcon *(M. gilvicollis)*, rather than the Barred Forest-Falcon, had the highest raptor density during strip transect censuses for calls (Thiollay 1989b). Using call censuses, Klein & Bierregaard (1988) also estimated a high density of Lined Forest-Falcons at two to four pairs per 100 ha, but with radio telemetry they estimated home ranges for Lined Forest-Falcons in Brazil at 0.4 to 0.5 $km^2$. I assume that these home ranges yield an approximate density of two territorial pairs per square kilometer. Thiollay's (1989a) estimate in French Guiana for this species was two territorial pairs per 6 $km^2$ which is 6 times less than the radio telemetry estimate in Brazil, even though both study areas aren't widely separated by distance, species and climatic patterns. This suggests that Thiollay's (1989a, 1989b) census methods of Lined Forest-Falcons did not accurately estimate the number of territorial pairs per unit area or that some other constraint(s) may be limiting the density of this forest-falcon species in French Guiana.

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