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FIDELITY TO TERRITORY, NEST SITE AND MATE, SURVIVORSHIP, AND REPRODUCTION OF TWO SYMPATRIC FOREST-FALCONS

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ABSTRACT.—Fidelity, survivorship, and reproduction of Barred Forest-Falcons (*Micrastur ruficollis*) and Collared Forest-Falcons (*M. semitorquatus*) were studied from 1988–96 at Tikal National Park, Guatemala. Forest-Falcons are year-round residents and nest in tree cavities. Barred Forest-Falcons and Collared Forest-Falcons had 100% fidelity to territories. Breeding pairs also had 100% mate fidelity, with pair bonds perennial and long-lasting. Only one territory switch in 98 territorial years was observed during the study and that was by a widowed male to a neighboring territory with a widowed female. The rate of annual survivorship of breeding adult Barred Forest-Falcons banded in 1989 was 95.3% ($N = 7$ males) and 92.3% ($N = 7$ females). Nineteen percent of females and males that bred produced >50% of the offspring. Forest-Falcons are longer lived and have a lower rate of a territory and mate switching than similar-sized temperate-zone raptors such as the European Sparrowhawk (*Accipiter nisus*). The reproductive success of Barred Forest-Falcons during this study suggested that the factors affecting lifetime reproductive success in temperate and tropical species do not differ.

KEY WORDS: Micrastur ruficollis; *Barred Forest-Falcon*; Micrastur semitorquatus; *Collared Forest-Falcon*; *fidelity*; *survivorship*; *reproduction.*

Fidelidad territorial, sitios de nido, parejas, sobrevivencia y reproduccion de dos especies simpatricas de *Micrastur*

RESUMEN.—La fidelidad, sobrevivencia y reproducción de *Micrastur ruficollis* y *Micrastur semitorquatus* fueron estudiadas desde 1988–96 en el Parque Nacional Tikal, Guatemala. Los halcones de bosque son residentes anuales y anidan en cavidades de árboles. *Micrastur ruficollis* y *Micrastur semitorquatus* fueron 100% fieles a sus territorios. Las parejas reproductivas tambien tuvieron el 100% de fidelidad, con lazos de pareja perennes y duraderos. Tan sólo hubo un cambio de territorio durante las observaciones del año 98. Este ocurrió a partir de un macho viudo que se mudó a un territorio vecino ocupado por una hembra viuda. La tasa anual de sobrevivencia de adultos reproductivos de *Micrastur ruficollis* anillados en 1989 fue de 92.3% ($N = 7$ hembras). Diez y nueve por ciento de las hembras y los machos en reproducción produjeron > de 50% de los pichones. Los halcones de bosque tienen vidas largas y una tasa inferior de cambio de pareja y territorio que las especies de similar tamaño de las zonas templadas como *Accipiter nisus.* El éxito reproductivo de *Micrastur ruficollis* durante este estudio sugiere que los factores que afectan la reproducción durante su vida no son diferentes entre las especies de las zonas templadas y las tropicales.

[Traducción de César Márquez]

The genus *Micrastur* is a little-known Neotropical genus which includes six small- to medium-sized species. They have accipiter-like features and are characterized by long tails, short wings, and slight facial ruffs (Friedmann 1950, Wetmore 1965, Blake 1977, Brown and Amadon 1989, del Hoyo et al. 1994). These features are adaptations for the tropical forests that they inhabit from southern Texas (Lasley et al. 1994) south to northern Argentina, Paraguay and east through Brazil to the Guianas (Brown and Amadon 1989, del Hoyo et al. 1994).

Most information on this genus comes from museum notes and collections (Sclater 1918, Wetmore 1939, Friedmann 1948, Monroe 1968), or from anecdotal notes and observations (Smith 1969, Mader 1979, Willis et al. 1983, Mays 1985). Even the two most widespread species of the genus, the Barred Forest-Falcon *(M. ruficollis)* and Collared

Forest-Falcon *(M. semitorquatus)*, are little-known. Recently, however, new insights into the life histories of these two cavity-nesting species have been provided by intensive field studies in Guatemala (Thorstrom et al. 1990, Thorstrom 1993).

Studies on mortality and population turnover of tropical and subtropical species could advance our understanding of the influence of ecological conditions on these parameters much more quickly than further work in northern latitudes (Newton 1984). Understanding population dynamics in tropical forests helps determine how pressures and constraints operate in these poorly-known environments and how they compare or contrast with temperate ecosystems. Using a group of color-marked individuals from the northernmost subspecies of Barred Forest-Falcon (*M. r. guerilla*) and Collared Forest-Falcon (*M. s. naso*), our objective was to characterize territory and mate fidelity, survivorship, and individual breeding performance as a comparison to similar measures in temperate raptors.

STUDY AREA AND METHODS

The study site was in Tikal National Park (576 km^2) in NE Guatemala (17°13′N, 89°36′W); it is centered around archeological ruins in a 20 km^2 area. Barred Forest-Falcons and Collared Forest-Falcons are year-round residents and secondary-cavity nesters at Tikal National Park. This park is a lowland, dry, semi-deciduous, tropical forest with an elevation from 200–350 m. Rains usually begin in May and decrease by December. Monthly mean precipitation ranged from a low of 1.0 mm in April to a high of 303 mm during September, with an annual mean rainfall of 1309 mm (1989–95, Tikal National Park unpubl. data). Mean monthly temperatures ranged from a low of 15°C in January to a high of 35°C in May, from 1989–95 (Tikal National Park).

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

We studied a population of Barred Forest-Falcons during the 1988–96 breeding seasons and Collared Forest-Falcons were studied during the 1988–93 breeding seasons. We searched the forest and visited occupied territories daily from March through July to determine the nesting activity of potential breeding pairs. Courting pairs were followed aurally and visually until a nest was confirmed.

A *nesting attempt* was defined as any nest that contained at least one egg. When possible, nest contents were checked by climbing nest trees and observing eggs or young present in the cavities. In some nests, eggs were not visible because of the structure of the nest cavity In these cases while we could not always verify presence of a clutch, we did observe conclusive evidence of incubation behavior (e.g., the female was called off the nest by the male for feeding, followed by her return to the nest). We assumed nest-site occupancy as being equivalent to the percent use of years in which pairs made nesting attempts (e.g., laid eggs or showed incubation behavior). All known alternative nest sites were checked and new nest sites were searched for in known territories.

Territory fidelity was defined as occupancy and defense of a nesting area in consecutive years (Warkentin et al 1991, Rosenfield and Bielefeldt 1996). If the same marked bird was sighted or recaptured on the same nesting area ≥2 yr after initial capture but was missing in some years, we assumed that it also occupied that nesting area in the interim years. This was based on our observations of marked birds on territories at the beginning of the breeding season during their nonbreeding years *Nest-site fidelity* was the use of the same tree-hole during the study.

Mate fidelity was the establishment of a pair bond and production of eggs by the same individuals in ≥2 consecutive years (Warkentin et al. 1991). *Frequency of nesting* was defined as number of nesting attempts divided by number of years the pair occupied the territory. *Nesting break* was defined as a breeding lapse (≥1 yr of nonbreeding) by the pair and then a breeding observation of the same pair on the same territory. *Switching mates* or "divorce" was inferred when either both members of a pair were found breeding with other partners (having produced eggs together in a previous year) or one partner was found with a different mate the following year and its original partner was subsequently trapped in a later year (Warkentin et al. 1991). *Natal dispersal* was the dispersal of young between hatch site and first breeding site *Breeding dispersal* was defined as movement of adults among nesting areas across years (Greenwood 1980).

Lifetime reproductive success (LRS) was defined as the total number of young produced by individuals during their lives (Newton 1989). *Reproductive success during the study period* (RSSP) was defined as the total number of young produced by individuals during the study period.

All trapped birds and nestlings were banded with unique combinations of two to four aluminum colored leg bands. Statistical tests were performed with Systat® (SPSS Inc., Chicago, Illinois, U.S.A.), except a few chi-square tests which were done by hand.

RESULTS

Thirty-nine adult Barred Forest-Falcons and six adult Collared Forest-Falcons were trapped (Thorstrom 1996) through the breeding season beginning in 1989. We also marked 57 nestling Barred Forest-Falcons and five nestling Collared Forest-Falcons with unique band combinations.

The nesting density for the Barred Forest-Falcon was highly saturated in the upland and transitional forests of the park. In a 6 km^2 area centered in and around the main archeological ruins of the

park, there were six Barred Forest-Falcon breeding territories (1 pair/km^2).

Fidelity to Territory, Nest Site, and Mate. Nesting activity began in March for Collared Forest-Falcons and in April for Barred Forest-Falcons. We documented 70 Barred Forest-Falcon and nine Collared Forest-Falcon nesting attempts. Males and females of both species were highly faithful to their breeding territories. The one exception, a male, switched to a neighboring territory during the 1992 breeding season when his mate disappeared early in the breeding period. That male mated with a neighboring female that had also lost its mate early in the breeding season. This male fledged five young at its original territory (1989–91) and six young on his new territory (1992–94), including two fledglings during the year of territory switching.

For Barred Forest-Falcons, the frequency of nesting (years of nesting attempts divided by the years a pair was on territory) for 16 territorial pairs (85 territorial years) was 74.1 ± 20% (±SD, range = 40–100%). We calculated nesting frequency separately for each territory; pairs nested on average 73.2 ± 21% (range = 50–100%, N = 16 pairs). This was similar to the 80 ± 20% nesting frequency for two breeding pairs of Collared Forest-Falcons (eight territorial years; range = 60–100%).

Of 70 nesting attempts by Barred Forest-Falcons, 53% (N = 37) were successful and 47% (N = 33) failed. Barred Forest-Falcon pairs that were successful tended to remain at the same nesting site while pairs that failed tended to switch to another site within the same nesting territory ($\chi^2_1 = 8.0$, $P < 0.01$). Of 40 consecutive two-year nesting attempts, 42.5% (N = 17) of the breeding pairs of Barred Forest-Falcons were successful and reused the previous year's nest site, 12.5% (N = 5) were successful but changed nest sites from the previous year the following year, 15% (N = 6) were unsuccessful but reused the previous year's nest site, and 30% (N = 12) were unsuccessful and changed nest sites from the previous year. One pair that failed in 1989 reused the same site from 1990–94 and successfully fledged young in all five years. Predation on eggs, nestling and females accounted for 91% (N = 30) of the 33 failed nests.

During this study, seven Barred Forest-Falcon males had residence periods of ≥4 yr (five were residents for all seven years) and five females had been present for ≥5 yr (four were present for seven years). Average residence period in the 7-yr study for breeding Barred Forest-Falcons banded in 1989 was 6.1 yr ± 1.5 for males (N = 7) and 5.0 yr ± 2.8 for females (N = 7). Clearly, these birds may have been on the same territories from before the time our study began, and some may have remained after it ended. The longest breeding span by a pair of Barred Forest-Falcons was at one specific nest site where they bred successfully six years out of seven.

Reproduction During the Study Period. For 27 Barred Forest-Falcon pairs, 19 of 27 females and 21 of 27 males raised 54 and 64 young to fledging age during this study, respectively (Fig. 1). Of those adults that attempted to breed, 30% (8/27) of the females and 22% (6/27) of the males produced no young. Nineteen percent (the percent of the breeders that produced more than half of the fledglings) of the females and males produced 58% (N = 44 young) and 54% (N = 49) of the fledglings, respectively. Of the 70% of females that raised young to fledging, the number fledged varied from 1–14 per female for the seven study years.

Recruitment. The overall annual productivity from 1988–95 was 1.1 (76 fledged young/70 nesting attempts) and 0.9 (8 fledged young/9 nesting attempts) for Barred and Collared Forest-Falcons, respectively. Of 57 young Barred Forest-Falcons banded from 1989–95, only one young female, banded as a nestling in 1995, was subsequently observed as a breeder; she occupied a nest site as a first-year bird in 1996 and successfully fledged two young. This natal dispersal was 4 km SE. No banded young Collared Forest-Falcons were observed entering or acquiring territories within the study area.

Barred Forest-Falcon Survivorship and Mortality. The annual rate of survivorship of breeding adults banded in 1989 was high in the seven study years; the rate for males was 95.3% (N = 7) and for females was 92.3% (N = 7). Given the high territory fidelity and, if we assume adults that disappeared from breeding territories died, then in seven years two males (4.7% mortality) and three females (7.7% mortality) disappeared. The annual turnover (change of breeding birds on territories) of males and females banded since 1989 did not differ statistically ($\chi^2_1 = 0.5$, $P > 0.10$). Although the data on adult mortality were limited, many individuals of unknown age were still alive and on the same territory for seven consecutive years.

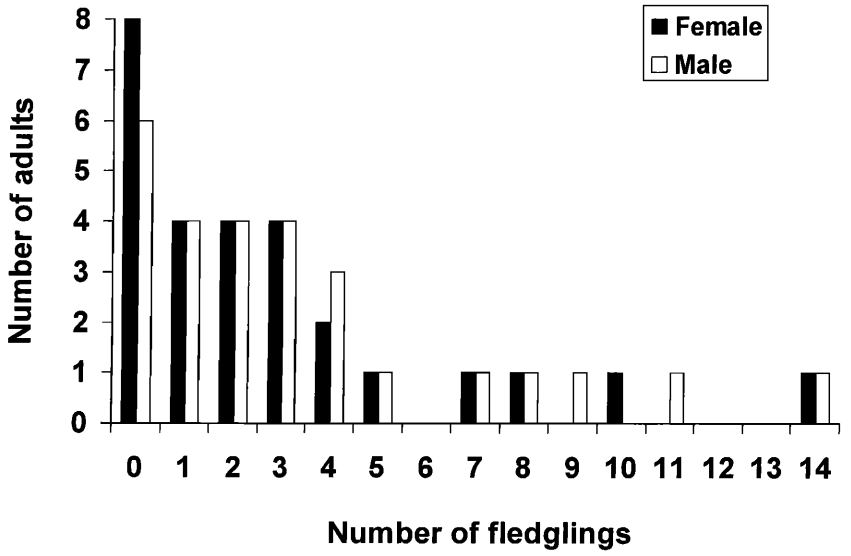

Figure 1. Number of fledglings produced by 27 pairs of Barred Forest-Falcons at Tikal National Park, Guatemala, 1989–95.

DISCUSSION

Barred and Collared Forest-Falcons are year-round residents in Tikal National Park. Territories of Barred Forest-Falcons were more aggressively defended from conspecifics than were those of Collared Forest-Falcons. Intruders into defined territories were unbanded, nonpaired forest-falcons searching for territorial vacancies, but no intruders were observed acquiring a territorial position from residents.

Our results showed that the breeding strategy of these two cavity nesting forest-falcons follows patterns thought to be characteristic of tropical birds (Skutch 1985): long-lived individuals, long reproductive cycles with pairs not necessarily breeding every year, sedentary, long residency periods, and high survivorship.

Fidelity. Pair bonds of forest-falcons appear to be strong and perennial, as we observed in Barred Forest-Falcons. We believe that pair bonds are strong and even longer lasting in Collared Forest-Falcons because of their larger size and presumed greater longevity.

Barred Forest-Falcon pairs had higher territory and mate fidelity (100%) than European Sparrowhawks (*Accipiter nisus*) (Newton and Marquiss 1976) and Eurasian Kestrels (*Falco tinnunculus*; Village 1990) (Table 1). Nest-site vacancy in known territories during the study years was 27%, and nearly all cases were due to pairs taking a break from breeding between nestings even though the mated pairs were present on their breeding territories.

European Sparrowhawk occupancy of nesting territories occurred when females remained in good habitats rich in food but frequently changed nesting territories after failed nesting attempts (Newton 1986). For Eurasian Kestrels, year-round resident males tended to remate with the same female whereas migratory males did not (Village 1990). The 100% mate fidelity of forest-falcons is contrary to observed pair fidelity of resident European Sparrowhawks (Newton 1979) and migratory Eurasian Kestrels (Village 1990), which experienced high levels of mate switches and re-pairings. For forest-falcons the only mate changes that occurred were replacements of females known to have been killed and several males that disappeared. In contrast to sparrowhawks and kestrels, forest-falcons remained on the same territory and reused the same nest after failing in that site the previous year or changed nest sites within the same territory.

On several occasions forest-falcon pairs returned to a nest site they had used two or three years earlier. In general, pairs that reused the same nest site raised more young than pairs that switched nest sites. We speculated that pairs at nest sites that were successful and used continuously were occu-

Table 1. Fidelity, residence periods, survivorship, and reproduction in Neotropical forest-falcons in Guatemala (this study) and temperate raptor species.

SPECIES (SOURCE)	TERRITORY FIDELITY	MATE FIDELITY	RESIDENT PERIOD (yr)	ANNUAL SURVIVOR-SHIP	% OF BREEDERS WHICH PRODUCED 50% OF OFFSPRING	% OF BREEDERS WHICH PRODUCED NO OFFSPRING
Tropical Cavity Nesters						
Barred Forest-Falcon (this study)	100%	100%	>6.1	92–95%	19% males 19% females	22% males 30% females
Collared Forest-Falcon (this study)	100%	100%	>4	95%	na[a]	na[a]
Temperate Cavity Nesters						
Eurasian Kestrel (Village 1990)	71–76%	38–52%	1.6	66%	nd[b]	nd[b]
Eastern Screech-Owl (Gehlbach 1989, Gehlbach 1994)	68%	76%	2.9–3.2	69%	21% females	14% females
Temperate stick nesters						
European Sparrowhawk (Newton 1989)	50–57%	24%	1.4–1.5	67–71%	20% females	16% females
Merlin (James et al. 1989, Warkentin et al. 1991)	42%	20%	nd[b]	69-71%	na[a]	na[a]

[a] Not applicable (small sample).
[b] No data.

pying optimal nesting cavities. Another possibility was that no or few alternative potential nest sites (cavities) existed within the forest-falcons' territories.

We did not know how much pair compatibility and experience affected breeding success, but some pairs that failed continued breeding in consecutive years while others did not. Original resident pairs that did not breed were observed together and engaged in nest inspection during the early breeding season but did not lay eggs. Lack of successful breeding, either through nonlaying or failure, did not cause pairs to divorce and move to new territories. Pair experience appears to be an important component of successful nesting in hole-nesting kestrels (Village 1990) and many other species of raptors (Newton 1979, 1986).

Some pairs had breeding breaks of two or three years (nonbreeding periods) and then they resumed breeding again, paired with the same mate as in previous nesting attempts. There was no synchrony within the study population in the breeding breaks and no correlation between the outcome of prior nests and the tendency to take a breeding break. We do not know why there was a lack of annual breeding by several territorial pairs but suggest that this probably relates to some breeding mechanism peculiar to tropical environments where birds have long life spans and low productivity.

Residence Periods. In 1989, of the seven breeding Barred Forest-Falcon pairs banded, five males and four females were still alive and resident in their original territories in 1996. Unfortunately, we were not able to follow this study population longer, but we suspect that several of these forest-falcons could still be alive and maintaining territories beyond 10 yr. In contrast, the longest resident period for a pair of European Sparrowhawks staying together was 4 yr (Newton 1986). All forest-falcons except for one male spent their study period lives on territories where they were originally found.

Pairs that failed during one season stayed on the same territory and usually nested again but typically at a different nest site. Our results showed that territory turnover was extremely low for these forest-dwelling raptors. In only one of the 70 Barred Forest-Falcon nesting attempts did birds change territories or mates after a failed breeding attempt. Newton and Marquiss (1991) showed in a removal experiment on both sexes of sparrowhawks that nearly 50% of territorial vacancies were filled by resident birds that may not have otherwise attempted to breed that year. This explained the recruitment of new unbanded individuals into territorial vacancies but not the territorial switch of one male to a neighboring widowed female. In another removal experiment on a passerine, Marra and Holmes (1996) suggested that males respond to female availability and not to habitat vacancies. This may explain the switch by this male to a neighboring territory where a breeding female was available.

European Sparrowhawks had average periods of residence on territories of only 1.4 and 1.5 yr for males and females, respectively (Newton 1986). For Eurasian Kestrels the average period of residence was 1.6 yr for both sexes (Village 1990; Table 1). Tropical forest-falcons had a much longer residence period on territory than these two temperate species, suggesting that constraints such as predation, competition for territories, and food resources operate differently in these two environments.

Reproduction During the Study Period and Recruitment into the Breeding Population. Barred Forest-Falcons varied greatly in the number of young they produced to fledging. During this study, forest-falcons with long and continuous breeding produced more fledglings because more breeding attempts increased the number of successful efforts and fledglings. Of those that attempted to breed, 22% of males and 30% of females produced no young during this 7-yr study (Table 1, Fig. 1). Although the sample size of RSSP by forest-falcons was small, it was probably representative for this species at Tikal and also similar to observations of LRS in temperate raptors. In the cavity-nesting Eastern Screech-Owl (*Otus asio*), 14% of the breeders produced no young (Gehlbach 1989), and for European Sparrowhawks, with data on 142 females, Newton (1986) found that 16% of those that attempted to breed produced no young during their lives. In Sweden, 20% of 92 male Merlins (*Falco columbarius*) produced no young during their lifetime (Wiklund 1996).

In studies on LRS, Newton (1989) concluded proportions of nonreproductive birds tended to be large in those long-lived species which bred only in certain years and also in short-lived passerines with high predation of nest contents. Barred Forest-Falcons have both high predation of nest contents and a long life span with breeding only in certain years (Thorstrom et al. 2000). Nonbreeding

years among established breeders are frequent in species subject to annual fluctuations in conditions and in long-lived species subject to more stable conditions (Newton 1989). These and other factors may be operating in the tropical environment of Barred Forest-Falcons.

In comparison to LRS studies of European Sparrowhawks, where 20% of females produced 50% of all fledged young (Newton 1986) and Eastern Screech-Owls where 21% of females produced 50% of offspring, 19% of breeding forest-falcons produced 54–58% of all young reared to fledging age in this 7-yr study period. This similarity of the LRS values in the studies in Newton (1989) and the RSSP value for Barred Forest-Falcons suggest that the environmental factors affecting LRS in temperate and tropical species do not differ. Newton (1989) suggested that chance events, and not environmental conditions and phenotype, were responsible for most of the variation in LRS between individuals.

Survivorship and Mortality. Snow and Lill (1974) reported that Neotropical passerines are long-lived compared to their temperate zone counterparts, but in a comparative study between temperate and tropical birds, Karr et al. (1990) found no support for this long-standing view. However, we found a very high survival rate for Barred Forest-Falcons during the study period (92–95% annually) which gave support to the idea that tropical forest raptors, at least, are long-lived. In North America, Sharp-shinned Hawks (*Accipiter striatus*), a comparable-sized raptor to Barred Forest-Falcons, rarely live beyond 5 yr with only 19% surviving more than 3 yr (Palmer 1988). Among other temperate-zone raptors, Village (1990) estimated a survival rate of 66% per annum for adult Eurasian Kestrels, and Newton (1986) estimated 67–71% for European Sparrowhawks (Table 1). Because forest-falcons are long-lived, we expect that once a territorial position is acquired, most individuals remain sedentary on that site until their death. If a bird moves, it may miss out in trying to obtain a territory and future breeding opportunities. In such a scenario, selection for sedentary behavior, 100% territory and mate fidelity, high frequency of nesting, a long period of residence, and high survivorship result in maximizing lifetime reproductive success.

In Eurasian Kestrels, Village (1990) reported that females seemed to have a lower survival rate than males based on a lower persistence in the breeding population, whereas the opposite was true for European Sparrowhawks (Newton 1986). We also had a shorter mean resident period for female Barred Forest-Falcons (5.0 yr) than for males (6.1 yr), and this difference was caused by predation during the nesting season. In contrast, in Merlins predation on nests during incubation was the principal factor limiting lifetime reproductive success of males (Wiklund 1996).

In our study, two adult female deaths resulted from predation during the incubation and nestling stages. Male mortality was never documented, but several males disappeared from the territories they had previously occupied for several years. We suspect that these males may have died (perhaps of old age) or were preyed upon, creating territorial vacancies rather than having dispersed to other territories outside the study area. Recruitment of new breeders occurred only on nesting territories that lost a breeder. With the one exception of a single male switching to a neighboring territory, no banded birds were observed to change territories due to nest failure.

Breeding populations of Barred and, most likely, Collared Forest-Falcons appear to be stable in Tikal National Park. Breeding territories may be difficult to acquire, and once there is a vacancy a forest-falcon will take over the territory and remain there until it dies. Competition for breeding territories probably inhibits birds from switching or searching for new areas. The seven years of this study were inadequate to follow the life spans of a cohort of forest-falcons. Several individuals were still alive and on territories after seven years, and we do not know how long study pairs had been on territory nor their ages when they first acquired their territories. Ten years or more might suffice for a long-term study of the Barred Forest-Falcon but be insufficient for the larger Collared Forest-Falcon. We suggest that future studies of Barred Forest-Falcons and Collared Forest-Falcons should examine populations throughout their geographic distribution and make comparisons with this study. These studies should concentrate on demographic parameters.

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