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BREEDING BIOLOGY AND BEHAVIOR OF THE COLLARED FOREST-FALCON (*MICRASTUR SEMITORQUATUS*) IN GUATEMALA

Russell Thorstrom¹, José D. Ramos², & José M. Castillo²

¹The Peregrine Fund, 566 West Flying Hawk Lane, Boise, Idaho 83709 USA.

²Tikal National Park, Petén, Guatemala C.A.

Abstract. We studied Collared Forest-Falcons *Micrastur semitorquatus* in Tikal National Park, Guatemala from 1988 through 1993, documenting 9 nesting attempts. The Collared Forest-Falcon is a year-round resident, nesting in pre-existing cavities in large trees. Breeding commenced during the middle of the dry season. Egg laying occurred early March to early April, with laying peaking in early March and spanning 30 days ($n = 8$ clutches), with one exceptionally late laying date in May. The incubation period was 46–48 days at 1 nest and nestlings fledged on average at 50 days of age ($n = 5$). Only females incubated while males provided food until the mid-nestling period when the females began hunting and delivering prey to the young. Young fledged in June, early in the rainy season and were not observed again at the cavity. Of 16 eggs laid in 8 nests (mean = 2.0), 10 of 16 (63%) hatched, and 8 (80%) of those hatchlings fledged. The only reproductive losses resulted from egg depredation ($n = 2$ nests). The breeding period of the Collared Forest-Falcon lasted approximately 28 weeks from courtship to fledgling dispersal, long in comparison to similarly-sized temperate raptors. *Accepted 29 June 1999.*

Key words: *Micrastur semitorquatus*, *Collared Forest-Falcon*, *breeding biology*, *behavior*, *nests*, *Tikal National Park*, *Guatemala*.

INTRODUCTION

Little is known about the reproductive biology of most Neotropical raptors (Mader 1981, Thiollay 1985), including the forest-falcons of the genus *Micrastur*, comprising six species of small to medium-sized falconids that inhabit tropical forests from north-central Mexico to northern Argentina (Brown & Amadon 1989, del Hoyo *et al.* 1994).

The Collared Forest-Falcon (*Micrastur semitorquatus*) is the largest member of the genus and poorly known in terms of its natural history. Nearly all published information on this species comes from museum collections and incidental observations. The first egg was described in 1974 from a captive individual (Wetmore 1974) and in 1978 the first nest was reported in Venezuela where it was found in a tree cavity (Mader 1979). Recently,

the second recorded nesting was observed in Guatemala with a first description of a nestling (Thorstrom *et al.* 1990). The goal of this study was to describe in detail the breeding biology and behavior of the Collared Forest-Falcon in a relatively undisturbed lowland tropical forest of northeastern Guatemala.

STUDY AREA AND METHODS

We studied Collared Forest-Falcons in Tikal National Park, Guatemala from 1988–1992, and briefly in 1993. Collared Forest-Falcons are year-round residents and secondary-cavity nesters at Tikal National Park. This park encompasses 576 km² in NE Guatemala (17°13'N, 89°36'W). The vegetation is semideciduous tropical forest with lowland rolling hills ranging from 200 to 450 m amsl.

Schulze and Whitacre (1999) have described several forest types that occur along topographical drainage, soil type, 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, with open canopy and dense understory, occurring in low-lying sites of deep, clay-rich soils subject to seasonal flooding and drought).

Tikal National Park has a pronounced wet and dry season; rains usually commence in May or June and decrease by December. Between 1989–1995 monthly precipitation ranged from a minimum of 1.0 mm in April to a maximum of 302.5 mm during September with an annual mean rainfall of 1309 mm (pers. observ.). Mean monthly temperatures ranged from a low of 15 C in January to a high of 35 C in May.

We searched the forest and known forest-falcon territories daily from February through August to document the nesting activity of potentially breeding pairs. Forest-falcons were most active in early morning and late evening,

and we concentrated our searches for nesting activity at these hours, usually from first light to 1000 h. Active pairs were followed aurally and visually until an occupied nest was confirmed. When possible, nest contents were confirmed by climbing nest trees and observing eggs or young in nest cavities. Nests were observed from the ground (n = 3 nests) and tree platforms (n = 2 nests), using 7–10x binoculars at distances of 25–50 m.

Observations (n = 264 periods, ranging from 49 – 830 min) of nesting Collared Forest-Falcons and fledglings totaled 13.1 h (1988), 218.5 h (1989), 390.2 h (1990), 569.3 h (1991), 303.7 h (1992), and 57.2 h (1993). For each nest found, we determined laying date, clutch size, hatching success (by periodic checks of nest cavities one to two weeks, and behavior), and fledging success and dates. The incubation period was the time (days) from laying to hatching of the penultimate egg. Adults and fledglings were trapped using methods described by Thorstrom (1996). We measured length and breadth of eggs to the nearest 0.1 mm with vernier calipers, and egg and adult mass to the nearest 1 g with a 300 g and nearest 10 g with 1000 g Pesola spring scales. The dimorphism index of mass was calculated using the formula in Snyder and Wiley (1976).

Reproductive variables were defined as: Nesting attempts, nests that contained at least one egg; eggs laid, number of observable eggs laid in climbable nests; mean clutch size, number of observable eggs laid per nesting attempt; egg success, percent of observable eggs that hatched; fledging success, percent of young surviving to fledging; productivity, number of young fledged per nesting attempt; overall productivity, number of young fledged per territorial pair; and reproductive success, percent of total nesting attempts that fledged at least one young. Reproductive variables follow Newton (1979) and Steenhoff & Kockert (1982). All young in accessible nests (n = 6

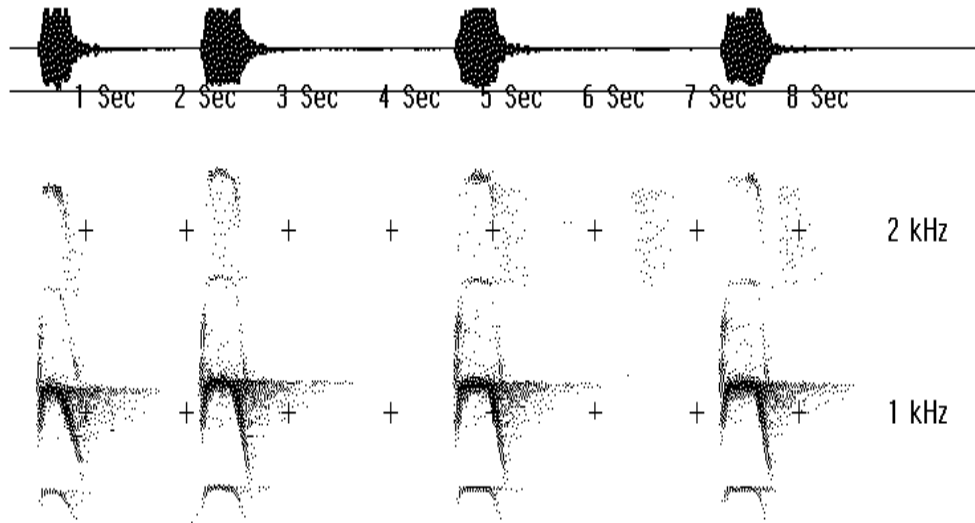


FIG. 1. Spectrogram of the song of the Collared Forest-Falcon at Tikal National Park, Guatemala.

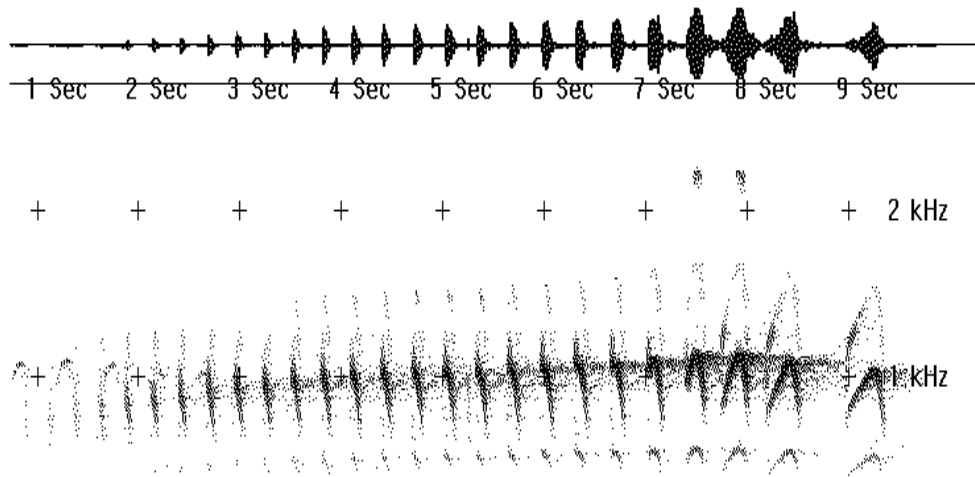


FIG. 2. Spectrogram of the fast call of a female Collared Forest-Falcon at Tikal National Park, Guatemala.

young) were banded prior to fledging.

Vocalizations were recorded with the intent of using voice print analysis to identify individuals. Vocalizations were recorded from 1989–1991 near nest sites and by walking underneath a calling bird. Tape recordings of

forest-falcon vocalizations were made with a Marantz PMD 221 cassette recorder using a Sennheiser ME 80 directional microphone. Spectrograms were produced using Spectrogram 3.2.1. (R. S. Horne). All values given are mean \pm standard deviation (SD).

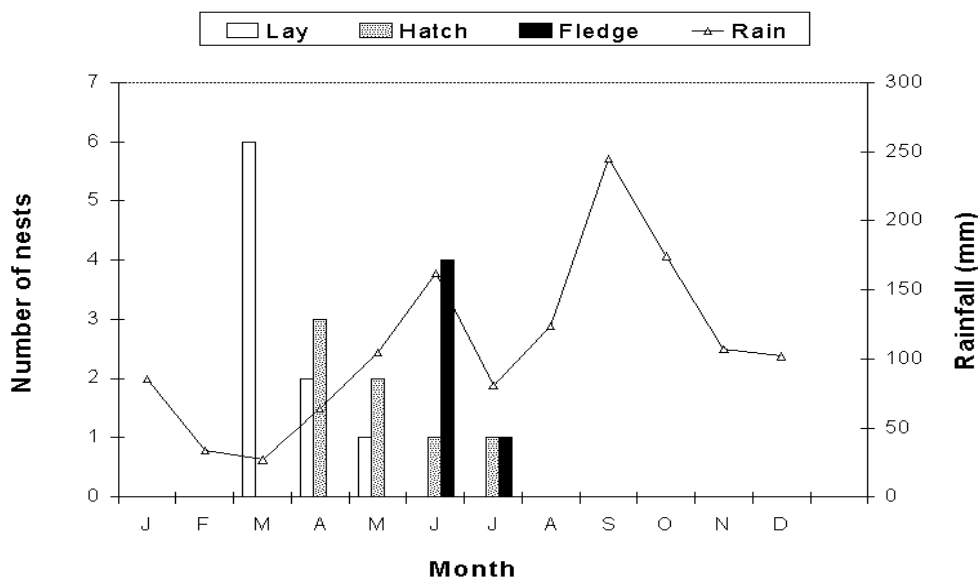


FIG. 3. Breeding cycle of Collared Forest-Falcons from 1989 to 1993 in Tikal National Park, Guatemala, relative to average annual rainfall from 1989 to 1993 (average = 1309 mm). The mean egg laying date was 7 March ($n = 8$ clutches), the mean hatch date was 28 April ($n = 7$), and the mean fledgling date was 13 June ($n = 5$ fledglings).

RESULTS

Collared Forest-Falcons are moderately size dimorphic, females (mean = 870 g, SD = 63 g; $n = 6$, range 792–940 g) weighing about 48% more than males (mean = 587 g, SD = 17.6 g; $n = 4$, range 563–605 g) for a dimorphism index (Snyder & Wiley 1976) value of 13.1.

Courtship activities occurred from February through May. Males and females vocalized a three- to four-note call before sunrise, sometimes continuing until mid-morning (Fig. 1). Collared Forest-Falcons first calls occurred 36.2 ± 10.2 min before sunrise ($n = 39$ observations). Female Collared Forest-Falcons used a call that included a series of notes that increased in tempo compared to the normal three- or four-note call (Fig. 2).

Males brought prey to females throughout the nesting cycle, beginning during the court-

ship (pre-incubation) period. When the male returned to the potential nest site with food for the waiting female, the female would fly to the male to receive the food item, using soft "ahr" calls. If the male had food, the female would fly to him and take it by grabbing it from his foot with her feet. We observed 2 copulations, lasting from 5–8 seconds and not accompanied by vocalizations.

Morning courtship activities lasted from before dawn until early morning (2–3 h after sunrise). In the late evening, courtship occurred prior to sunset during only the last one-half to one hour before the birds went to roost.

Nests. We documented 9 nesting attempts in 5 territories by Collared Forest-Falcons from 1988–1993. Nearly all the same nest sites were occupied in consecutive years. Only one out of 4 territorial pairs changed nest sites

from 1990 to a site 500 m NW in 1991. Nest sites ($n = 6$) were in natural tree cavities in the main trunk ($n = 3$) and in cavities formed by the rotting of a branch ($n = 3$). Three nest sites had two or more entrances and three had only one entrance. Average dimensions of the main nest entrance were 55.9 x 38.9 cm (SD = 37.2 x 12.6 cm, $n = 6$, range 16 x 22 to 60 x 62 cm) and mean cavity depth was 37.4 cm (SD = 19.1, $n = 6$, range = 23–65 cm).

Five species of trees were used for nesting. *Cedrela mexicana (odorata)* was used 4 times (44%), *Swietenia macrophylla* twice (22%), and *Spondias mombin* (11%), *Manilkara zapota* (11%) and *Lonchocarpus castilloi* (11%) once each. The mean nest height was 19.9 m (SD = 3.1, $n = 6$, range 15.7–24.0 m) and the mean nest tree diameter was 167 cm (SD = 91 cm, range 90–314 cm).

Egg laying, incubation and hatching. The earliest recorded laying dates were 20 March 1989, 1 March 1990 and 8 March 1991. Most eggs were laid during the dry season and laying peaked in March (mean laying date = 7 March, SD = 8.2 days, $n = 8$ clutches) and spanned 30 days from 1 March to 1 April, ($n = 8$ clutches) except for one exceptional late laying in May 1992 at the start of the wet season (Fig. 3). One nest had a one-egg clutch, six nests had two eggs, and one nest had a three-egg clutch, for a mean of 2.0 (SD = 0.5). For 9 eggs, the mean dimensions and mass were 56.4 mm (SD = 2.1, range 53.3–59.5 mm) x 43.6 mm (SD = 1.5, range 41.6–46.3 mm) and 53.4 g (SD = 2.6, range = 49.5–58.0 mm), respectively. Egg mass represented 6% of mean female mass of 870 g; thus, the modal two-egg clutch represented 12% of mean female mass.

In May 1992, a late nesting attempt by Collared Forest-Falcons occurred after a Black Vulture's (*Coragyps atratus*) egg was removed by researchers from the nest site in

March. Of the two eggs laid, one hatched on 4 July, 46 days from the laying of the second egg and 48 days from the laying of the first egg. Hence, the incubation period was 46–48 days.

Only females incubated, while males provided all food until mid-nestling period when the females began hunting and delivering prey to the young. Eggs hatched during the late dry season, from 16 April to approximately 16 May (Fig. 3). The average hatching date was 28 April (SD = 5.0 days, $n = 7$ hatchlings), excluding the late nesting attempt in 1992.

Nestling period. The six young Collared Forest-Falcons that were examined hatched with white natal down, eyes closed, silvery white nails, yellowish white legs and ceres, and short, yellowish white, deep and laterally compressed beaks. By the second and third days after hatching (Day 0 equals hatching) eyes were open and young held their heads up. They had brown-black irises and blue-black pupils.

By one to two weeks after hatching (7–14 days), the cere, feet, and toes were yellowish white and nails were light gray. The egg tooth was still faintly present. During the second to third week (14–21 days), the young actively defended themselves. The facial skin around the eyes was turning yellow-green, the upper and lower mandibles at the proximal base were changing light gray, and the primaries were emerging. Females began leaving the nest to hunt for the nestlings during this period. First foraging attempts by females occurred when the young ranged from 17–21 days ($n = 3$ nests).

During their third to fourth week of age (21–28 days), tail feathers were emerging, the mandibles were turning grayish black near the cere, and legs and feet were nearly adult in size. Natal down between the eyes and beak had disappeared, the iris was a dark chocolate

brown in contrast to the lighter brown eyes of the adults, and the facial skin was turning greenish olive. Breast and auricular feathers began emerging, and wing coverts were growing rapidly. Females began roosting outside of the nest cavity from 22–26 days of age of nestlings ($n = 2$ nests). During the fourth to fifth week (28–35 days), nails were turning black, body feathers were developing, natal down was disappearing, and mandibles were changing to a brownish-yellow color towards the distal end. Facial skin was a dark greenish olive, the cere was yellowish green, and the legs and tarsi were yellowish white. By five to six weeks of age (35–42 days) down feathers had mostly disappeared, and the juvenile contour feathers nearly covered the body. Tail feathers were one-third developed and chest feathers began showing bars of dark coloration.

At six to seven weeks of age (42–49 days) the tail feathers were half-, and wings two-thirds-grown and few natal down feathers remained. Mandibles were colored dark brown-black. Young males ($n = 5$) had buffier chests than did young females ($n = 3$). Collared Forest-Falcons fledged from 46 to 56 days of age (mean = 50.0, SD = 4.2 days, $n = 5$). The average date of fledging was 13 June (SD = 9.3 days). Five males and three females fledged. Young fledged during the beginning of the rainy season (Fig. 3). Four nestlings were fitted with tarsal-mounted transmitters before fledging. When fledging, young fluttered from the nest to a nearby branch or tree ($n = 3$ young). No young returned to the nest cavities after fledging ($n = 5$ fledglings). Observations during the fledgling period in 1990 and 1991 totaled 401.9 h ($n = 5$ fledglings).

Young were fed on the ground or on fallen trees by both adults. Young remained within 100 m of the nest during the first week after fledging ($n = 21$ observations totaling 99.1 h ranging from 4–11.2 h per observation

during the first week of fledging). Young remained separated (10–50 m) and flew weakly or ran on the ground from one perch to another except during feedings. All fledglings roosted in the upper canopy for the night ($n = 4$ fledglings).

By two weeks after fledging (63–70 days), young remained together and chased each other on the ground, in the vines, and trees. When adults arrived with food, young flew to the adult and the first arriving received food. Young without food would watch, vocalize, and wait for siblings to finish, and then the next young would eat if any food remained.

By three weeks after fledging (70–77 days), young started moving farther from their nest sites and were capable of longer flights, at times flying more than 200 m to reach the adult with food. During this period young were found once at an army ant swarm, where they watched and pursued insects and lizards for 2 h during an 8 h observation period, similar to descriptions by Willis *et al.* (1983), Mays (1985), Thorstrom (1993) and Robinson (1994). The adult female at one nest site in 1991 stopped delivering food to the young during the second week after fledging. The adult male was the sole provider thereafter. By the fourth week after fledging (77–84 days), young were extremely active in playing and chasing and appeared interested in watching other animals ($n = 4$ fledglings). During this period two fledglings were observed eating beetles they caught. On 7 July 1990, the male (80 days of age) and female (82 days of age) fledglings were observed chasing squirrels and chachalacas for the first time.

At one nest during the middle of the post-fledging period an extra adult male forest-falcon (determined from unbanded status and size) began delivering prey items to two fledglings. This new male performed all observed prey deliveries ($n = 36$ prey items), and during four observation periods he delivered two

TABLE 1. Reproductive parameters and success of Collared Forest-Falcons (1988–1993) at Tikal National Park, Guatemala.

Year	Territorial pairs	Number of nesting attemps	Number of nests with confirmed clutches	Number of eggs in confirmed clutches	Mean clutch size	Number of eggs hatched (%)	Number of young fledged (%)	Fledglings/ breeding attemps (n)	Fledglings/ territorial pair (n)	Fledglings/ successful pair (n)	Breeding success/ territorial pair (%) ^a	Overall reproductive success (%) (n) ^b
1988	1	1	?	?	?	1	?	?	?	?	?	?
1989	1	1	1	2	2.0	0	0	0	0	0	0	0
1990	2	1	1	2	2.0	2	2	2.0	1.0	2.0	50	100 (1/1)
1991	4	3	3	7	2.3	4	3	1.0	0.75	1.3	50	66 (1/2)
1992	2	2	2	4	2.0	2	2	1.0	1.0	1.0	25	50 (1/2)
1993	3	1	1	1	1.0	1	1	1.0	0.3	1.0	20	100 (1/1)
Total	13	9	8	16	2.0	10 (63)	8 (80)	0.9 (8/9)	0.7 (8/11)	1.6 (8/5)	39 (5/13)	63 (5/8)

^aBreeding success is proportion of nests that fledged at least one young per cumulative territorial pair.

^bOverall reproductive success is proportion of nests that fledged at least one young per fully-documented nesting attempt.

TABLE 2. History of breeding attempts by Collared Forest-Falcons at Tikal National Park, Guatemala (1988–1993)

Nesting year	Cedro (1988)		Aguadita (1990)		La Curva (1991)		El Caoba (1991)		Caoba (1993)	
	NA ^a	Fled ^b	NA	Fled	NA	Fled	NA	Fled	NA	Fled
1988	1	?								
1989	1	0								
1990	0	0	1	2						
1991	0	0	1	1	1	2	1	0		
1992	1	0	1	2						
1993									1	1
Total	3	?	3	5	1	2	1	0	1	1

^aNA is the number of nesting attempts.

^bFled is the number of young fledged.

?, i.e., the outcome in 1988 was not observed.

Keel-billed Toucans (*Ramphastos sulfuratus*) a day to the fledglings. Both parental birds stopped delivering food to the young when this unbanded male took over the provisioning role. In the fifth week after fledging (84–91 days of age), the extra male had led both young to an area 2.5 km south of their nest site and they ranged to 3.5 km from the nest by week seven. During week eight after fledging (105–112 days of age) the fledgling male was found dead, apparently killed by another raptor. The fledgling female was still attended by this extra adult male until week 11 after fledging (126–133 days of age) when we lost radio contact with her. We assumed she had reached independence and dispersed. In 1991, another young radio-tagged female dispersed from her natal territory at week six after fledging (92–99 days of age).

Reproductive success. From 1988 to 1993, 16 eggs were laid in eight nests of Collared Forest-Falcons for an average clutch size of 2.0 (Table 1). Ten (63%) of 16 eggs hatched and 8 (80%) of the hatched nestlings fledged for an

average of 0.9 young fledged per breeding attempt. Overall reproductive success for 8 fully-documented nests was 63.0% ($n = 5$ nests). The nest located in 1988 was excluded (Thorstrom *et al.* 1990) since the fledging date was not recorded. The main cause of nest failure was predation on eggs ($n = 2$ nests), probably by mammalian or avian predators. One nest also lost one of two nestlings in 1991 due to unknown causes. One four-week-old nestling died in the nest when the adults stopped delivering prey to the young; they appeared to have abandoned the young. There was no observation of renesting by Collared Forest-Falcons when first nesting attempts failed during the egg or nestling stage. Not all territorial pairs bred in consecutive years (Table 2.).

DISCUSSION

Forest-falcons are forest-dependent species, and their calling behavior is the principal means of locating and communicating with mates, neighbors, and other conspecifics. Col-

lared Forest-Falcons vocalized each morning except during periods of rain. The ritual pre-dawn and early morning vocalizations probably serve to attract potential mates and to advertise territorial occupancy. Diurnal species tend to concentrate their long-range communications in the first hours of day and to a lesser extent in the evening (Hanwood & Fabrick 1979). Forest-falcons called in late evening, prior to roosting, suggesting that this period is also suited for them to broadcast their vocalizations and assess the distribution of conspecifics. Occasionally, on brightly moonlit nights Collared Forest-Falcons called between 2300 and 0400 h. Vocalizations of Collared Forest-Falcons were composed of low frequency notes. Morton (1975) and Wiley & Richards (1982) suggest that low frequency notes for long-range communications are advantageous because such frequencies suffer less attenuation by forest vegetation than do higher frequencies.

Females gave the normal call and a faster tempo vocalization near the nest site. We suggest that this faster call is a form of auditory display for females to broadcast their breeding status to conspecifics. We and Whitacre & Turley (1990) saw no aerial displays performed by Collared Forest-Falcons, but their morphological counterparts (*Accipiter* spp.) in temperate regions do indulge in display flights over the canopy.

The dimorphism index value of 13.1 shows that Collared Forest-Falcons are dimorphic on a scale of 0 (no dimorphism) to 20 (high dimorphism). Raptors feeding on the most maneuverable prey (birds) are highly dimorphic, i.e., Sharp-shinned Hawk *Accipiter striatus* (Snyder and Wiley 1976) and European Sparrowhawk *A. nisus* (Newton 1979). Collared Forest-Falcons in this study had a weight dimorphism index similar to that of the Cooper's Hawk *A. cooperii* (12.9), which predominately feeds on birds and mammals (Snyder and Wiley 1976).

Nest trees were among the largest trees in the forest of Tikal National Park. The apparent preference for mature and old-aged trees is they provide ideal natural cavities for forest-falcons because of their physical characteristics. Six of 9 nesting attempts were in prized commercial lumber species and this presents a potential conservation challenge not only for forest-falcons, but for many kinds of wildlife.

Nests described in this study were similar to the first and only nest described for this species by Mader (1979). In gallery forests of the Venezuelan llanos, Mader (1979) suggested that this species nests during the wet season (April–November). Mader (1979) flushed a nestling from its nest on 20 August 1979, and we estimate its age to be approximately 45–50 days based on our experience. We suggest that in Venezuela the incubation period commenced during the middle of May, the start of the rainy season, and hatching occurred around the first of July. In Guatemala, we documented the seasonal nesting period of this species commencing at the start of the dry season with fledging occurring at the start of the rainy season which contrasts with Mader (1979) which could be an exception since his observation was based on one nesting record.

The only exception in Tikal was the late nesting attempt in May 1992 and we believe this was due to the nest site being occupied by Black Vultures before the forest-falcons initiated courtship behavior. Apparently, the forest-falcon pair did not have an alternate nest site available and waited for their historic nest to be vacant.

The incubation (45–48 days), nestling (46–56 days), and post-fledgling (56–77 days) periods were synchronized seasonally with fledging occurring in late June usually after the first peak of the rainy season. The long incubation, nestling, and post-fledgling periods extended the breeding cycle of the Col-

lared Forest-Falcon to nearly 28 weeks, which is protracted in comparison to similarly-sized temperate-zone raptors such as the Northern Goshawk (*A. gentilis*) (20–21 weeks) (Reynolds & Wight 1978, Palmer 1988a) and the Prairie Falcon (*Falco mexicanus*) (19–20 weeks) (Enderson 1964, Palmer 1988b). Newton (1979) suggested that tropical environments offer more stable food supplies which lead to populations to be near saturation level so development is slow and breeding recruitment is more difficult. We also suggest that temperate species have a more rapid breeding strategy than tropical species because of their shortened breeding season caused by environmental conditions.

Young developed their flight skills as their plumage reached full development. Interactions with other animals and amongst themselves presumably were important for developing hunting skills. Young dispersed during late August and September, the wettest time of year at Tikal.

Of particular interest was the prey delivery behavior of an extra-pair adult starting at week 4 of the post-fledging period. Helpers have been documented in Harris Hawks (*Parabuteo unicinctus*) (Mader 1975, Bednarz 1987), Galapagos Hawks (*Buteo galapagoensis*), Bald Eagles (*Haliaeetus leucocephalus*), and Red-tailed Hawks (*B. jamaicensis*) (Mader 1975). Bednarz (1987) reported for the Harris Hawk that there are more nonpaired birds than nest sites available, and a helping bird will acquire experience and possibly an opportunity to breed. Future research should investigate whether such “helping” behavior occurs frequently in these forest-falcons and if so, whether helpers are related to the parental pair.

Larger species within a taxonomic group of raptors tend to produce smaller clutches than small species (Brown 1976, Newton 1979, Johnsgaard 1990). The Collared Forest-Falcon had a smaller average

clutch size (2.0) than its congener, the Barred Forest-Falcon (2.8) at the same study site (pers. observ.). The low reproductive output and protracted breeding season documented for this neotropical raptor follow the general trend of other tropical raptors (Brown 1971, Mader 1982, Delannoy & Cruz 1988, Seavey *et al.* 1998). The reproductive success of the Collared Forest-Falcon was 63% for nests that produced at least one fledgling, similar to its congener the Barred Forest-Falcon (54%) but the reproductive output of fledglings was very low, only 0.9 fledglings per breeding attempt. In the Collared Forest-Falcon, egg predation was the greatest cause of nest failure similar to results to date for other tropical raptors such as the Barred Forest-Falcon (pers. observ.), Puerto Rican Sharp-shinned Hawk (Delannoy & Cruz 1988), Laughing Falcon (Parker 1997) and Plumbeous Kite (Seavey *et al.* 1998). Even though the data are limited, Collared Forest-Falcons pairs showed breeding in consecutive years. Birds that had failed in one year tended not to breed the following year. Birds that were successful such as the Aguadita pair tended to breed continuously from one year to the next.

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