Short Communications

The Auk 117(3):781–786, 2000

Breeding Biology of Barred Forest-Falcons (*Micrastur ruficollis*) in Northeastern Guatemala

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Little is known about the reproductive biology of most Neotropical raptors (Thiollay 1985). One particularly little-known genus is *Micrastur*, the forest-falcons, which comprise a group of six species of small to medium-sized falconids that inhabit tropical forests from central Mexico to northern Argentina (Brown and Amadon 1968, del Hoyo et al. 1994). Forest-falcons are characterized by a long tail, short wings, and a slight facial ruff (Brown and Amadon 1968, del Hoyo et al. 1994), which appear to be adaptations to tropical forest environments. Here, we report new information on the breeding biology of the Barred Forest-Falcon (*M. ruficollis*) in a relatively undisturbed lowland tropical forest in Guatemala.

Study area and methods.—We studied Barred Forest-Falcons in Tikal National Park, northeastern Guatemala (17°13'N, 89°36'W), from 1988 to 1996. Vegetation in the 576-km^2 park is semideciduous tropical forest with rolling hills ranging from 200 to 400 m elevation. Tikal has a pronounced wet and dry season. Rains usually start in May or early June and decrease by December. During our study, monthly precipitation ranged from 1 mm in March 1991 to 302 mm in September 1989. Mean annual rainfall was 1,309 mm from 1988 to 1995 (pers. obs.), and mean monthly temperatures ranged from 15°C in January to 35°C in May from 1989 to 1995.

We searched the forest daily from March through July to document activity of potential breeding pairs. Forest-falcons are most active in the morning and evening, and we concentrated our searches to these hours, usually beginning between first light and 0900. We followed pairs by sight and sound until a nest was confirmed by behavior of the birds. When possible, we climbed nest trees to observe eggs or young in cavities, sometimes with the aid of a flashlight. Nest observations totaled more than 1,800 h, most of which occurred during the breeding seasons of 1989 through 1992, with incidental observations from 1993 to 1995 and for four weeks in 1996.

For each nest, we determined laying date, clutch size, hatching success (by periodic checks of nest cavities), and fledging success. We considered the incubation period to last from the laying of the penultimate egg (usually the second) to the hatching of the second egg. We measured length and breadth of eggs to the nearest 0.1 mm with vernier calipers and egg and nestling mass to the nearest gram with a 100-g Pesola spring scale. Young were marked with dye (food coloring) on the crown soon after hatching. We measured the length of the tarsus, culmen (from cere to bill tip), tail, and wing chord of young to the nearest 1 mm.

Results.—Barred Forest-Falcons were year-round residents at Tikal, and pairs defended nesting territories during the breeding season. Barred Forest-Falcons were one of the first diurnal birds to call in the morning. On average, the first vocalizations were given 22.9 ± SD of 6.9 min before sunrise (n = 48), and calling sometimes continued until mid-morning.

Initiation of the breeding season was signaled by courtship and the investigation of nesting cavities. Courtship occurred from February to July, during which time pairs vocalized and moved through the forest together, investigated tree cavities, and engaged in courtship feeding and copulation. Pair members typically roosted separately 50 to 100 m from the nest (n = 27). In early morning, courtship usually began when the male vocalized from a roost and the female responded. Typically, the male led the female to a potential nesting cavity by repeated loud and rapid calling. The female then moved toward the vocalizing male, calling as she moved. After the female arrived, the male flew in and out of the cavity while the female perched nearby, or he waited until the female entered the cavity.

Males spent an average of 2.5 ± 1.7 min (n = 11, range 1 to 7 min) inside cavities during nest inspections. At one territory, a potential breeding pair visited four cavities in a 3-h period. Barred Forest-Falcons investigated and nested mainly in natural tree cavities (n = 66), but four nests occurred in cavities excavated by other animals. If the female entered the cavity, the male either moved off to check another nest site or left the area. Once the female appeared

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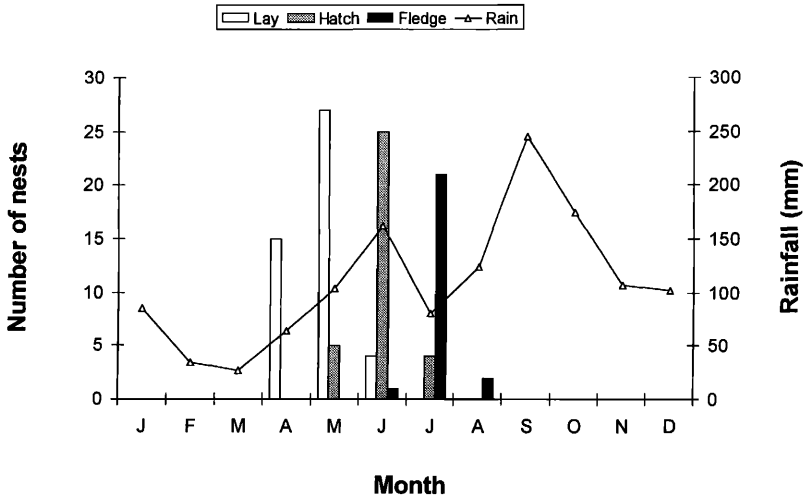

FIG. 1. Breeding cycle of Barred Forest-Falcons in Tikal National Park, 1989 to 1995, relative to average annual rainfall. Mean egg-laying date was 2 May (n = 46 clutches), mean hatching date was 6 June (n = 34 nests), and mean fledging date was 15 July (n = 28 fledglings).

interested in a site, she remained in the vicinity of the tree much of the day, visiting the cavity repeatedly during the month before egg laying. During 350 h of observation during the courtship period, the location of the female was observable for 93 h, of which 11.4 h (12.3%) were spent inside prospective nest cavities and 81.6 h (87.7%) were spent within 50 m of the nest cavity. After courtship feeding (see below), females stayed in cavities for 1 to 208 min. Barred Forest-Falcons sometimes chased other cavity-nesting birds such as parrots, woodpeckers, and toucans.

Males brought prey to females throughout the nesting cycle, including the courtship (preincubation) period. The earliest observed prey delivery by a male to a female occurred on 21 February 1989, about seven weeks before egg laying. In a typical transfer, the male returned to the potential nest site with food and made several soft "barks" to the waiting female. The female then flew to the male and gave a soft two-to-five-note begging call like that described by Slud (1964) as a rapid fowl-like cackle with a "snorting" quality. If the male had food, the female flew toward him and grabbed the food with her feet. Normally, the male copulated with the female after the food transfer but before the female began eating.

The earliest observed copulation attempt (unsuccessful) occurred on 21 February 1989, when a female shook a male off her back after a possible food-transfer 20 min earlier. The event occurred seven weeks before the earliest known egg laying. The earliest successful copulation was seen on 28 February 1989. Twenty-five of 76 copulations occurred immediately after food transfers. Copulations were not accompanied by vocalizations and lasted 3 to 7 s ($\bar{x}$ = 5 ± 1.5 s, n = 76). Copulations were observed in the morning between 0526 and 0944 ($\bar{x}$ = 0653). The highest rates of copulation were three in 1 min and eight in 5 h, both observations occurring two weeks before egg laying. Occasionally, a copulation occurred after the pair left their roost early in the morning but before they reached the prospective nest tree (5 of 76 copulations). Courtship and vocalizing also occurred before sunset during the last one-half hour to one hour before the birds went to roost. We observed no copulations or food transfers in the afternoon.

Fifty-two nests (74%) were in live trees and 18 (26%) were in dead trees. Mean nest height was 17.4 ± 4.2 m (n = 65, range 10 to 30 m), nest-tree diameter averaged 95 ± 41 cm (n = 70, range 30 to 190), and depth of nest cavities averaged 81 ± 59 cm (n = 35, range 3 to 200 cm).

As the laying period neared in early April, females remained within 25 m of the nest cavity, and during 33 h of nest observations they spent 14.9 h (51.1%) inside and 14.2 h (48.9%) outside the nest cavity. Earliest recorded laying dates were 13 April 1988, 16 April 1989, 15 April 1990, 15 April 1991, 22 April 1992, and 5 May 1993. Laying of first clutches spanned 31 days (13 April to 14 May, n = 44; Fig. 1). Forest-falcons laid 23 two-egg clutches and 36 three-egg clutches ($\bar{x}$ = 2.6 ± 0.5). Two pairs renested after losing their first clutch. In one case, the female laid her second clutch two to three weeks after losing her first clutch. Renesting attempts occurred in tree cavities that were 150 m and 500 m from the respective first attempts.

We determined egg-laying sequences in four

clutches. Nine of 10 eggs were laid on alternate days, and in one case a third egg was laid three days after the second. Eggs were subelliptical and dark reddish-brown with light and dark brown spots. Mean dimensions of 31 eggs were 43.8 ± 1.9 mm (range 41.0 to 47.4 mm) × 34.2 ± 1.1 mm (range 32.0 to 35.6 mm). Mean mass of 30 eggs was 28.0 ± 1.7 g (range 24.5 to 31.5 g), or 11.8% of female mass ($\bar{x}$ = 238 ± 23 g, n = 17).

Males provided all food during the incubation period. After food transfers during incubation, males spent an average of 8.3 ± 6.7 min (n = 7, range 1 to 20 min) inside the nest cavity. During incubation, females spent 91% of the time inside the nest cavity (n = 600 h). We could not determine whether incubation began after clutch completion or after laying of the penultimate egg. Based on our definition of the incubation period, incubation lasted from 33 to 35 days (n = 6).

Thirty-four clutches hatched over a 28-day span from 20 May to 17 June (Fig. 1), at the end of the dry season and the beginning of the rainy season. We determined the hatching sequence of 10 eggs at four nests. In one two-egg clutch, eggs pipped simultaneously. In one two-egg and two three-egg clutches, the first and second eggs hatched less than 24 h apart, and the third eggs hatched less than 24 h after the second.

At hatching, nestlings were covered in white natal down and had closed eyes, silvery-white talons, yellowish-white legs and ceres, and yellowish-white beaks. Young 0 to 7 days old vocalized with a high, soft "scree" while being handled. The eyes were open by the second or third day after hatching, at which time the young could hold up their heads. At this age, nestlings had brownish-black irides and bluish-black pupils. Nest attendance (proportion of time in nest cavity; n = 201 h of nest observations) by one female declined steadily from 97% during the first week posthatching to only 6.3% by the sixth week posthatching.

By the age of 14 to 21 days, young actively footed researchers, and several began to feign death when we looked inside nest cavities. By the age of three to four weeks, the entire brood sometimes participated in feigning behavior. At five weeks of age, young were fully feathered and near fledging. One to two days before they fledged, nestling females weighed an average of 203 ± 17 g (n = 10), compared with an average of 219 ± 9.1 g (n = 4) for adult females. The average measurements of females at fledging were culmen, 14.2 mm; tail, 97 mm; and wing chord, 144.7 mm. Body mass of males at fledging averaged 180.0 ± 8.0 g (n = 7), compared with 168.0 ± 6.1 g (n = 7) for adult males. The average measurements of males at fledging were culmen, 12.9 mm; tail, 87.8 mm; and wing chord, 132.4 mm. For both sexes, the bill, tail, and wings were not fully grown at fledging. The average measurements for adult females and males, respectively, were culmen, 16.0 mm and 14.5 mm; tail, 173.2 mm and 163.0 mm; and wing chord, 177.7 mm and 166.1 mm.

Fledging occurred at 35 to 44 days of age ($\bar{x}$ = 38 ± 3 days, n = 13), and fledging dates of different broods spanned 40 days (25 June to 3 August; Fig. 1) with a mean of 15 July ± 10 days. Sexes varied by one to three days in time to fledging, with females tending to develop slower than males. Of 35 fledglings identified to sex, 19 (54%) were males and 16 (46%) were females. The overall sex ratio at fledging did not vary among years (χ^2 = 5.25, df = 3, $P > 0.1$). When fledging, the young fluttered from the nest to a nearby branch or tree in the understory vegetation approximately 10 m above the ground. No young returned to nest cavities after fledging.

Two to three days after fledging, one young was killed by a boa (*Boa constrictor*) and one by a gray fox (*Urocyon cinereoargenteus*). We discovered the remains of two others within 25 m of their nest trees four days after fledging. Two young that disappeared from another nest one week after fledging may have been preyed upon. Young usually remained within 100 m of the nest tree one to two weeks after fledging.

We found eight young associated with swarms of army ants (*Eciton* spp.) three to four weeks after fledging. The young usually hunted from perches 1 to 2 m above the ants. On several occasions, escaping cockroaches, crickets, and beetles were caught by young forest-falcons, and several times young chased small birds at ant swarms. By three weeks after fledging (63 to 72 days old), young chased any small animals on the ground and were seen catching small lizards. Four weeks after fledging, four trapped birds had fully grown tail feathers.

Young dispersed from their natal areas (n = 5 radio-tagged birds) four to seven weeks after fledging. At one site in 1989, two young were fed by the adult male for six weeks after fledging. The young remained in an area approximately 250 m south of the nest tree and vocalized at morning roosts in a manner similar to adults, but softer. After week six, the transmitter on one young failed and the two fledglings could not be located. In 1991, a young female dispersed seven weeks after fledging and remained 1,900 m northeast of the nest in an area of low, dense "bajo" forest for at least three months.

Dispersal patterns of young were difficult to determine, but we know from radio telemetry that several young moved 2 to 3 km from their natal areas within a few months after independence. One young that we banded in 1990 and another in juvenal plumage in 1989 were observed in areas between occupied territories 10 months after the previous year's fledging period. Young retain their juvenal plumage for at least one year after hatching. One female banded as a nestling in 1995 successfully nested in juvenal plumage in 1996, 3.5 km from her natal nest.

From 1988 to 1995, 154 eggs were laid in the 59 nests for which we obtained clutch sizes. Laying of first clutches peaked in early May ($\bar{x}$ = 2 May ± 2 days), and mean laying dates did not vary among years (F = 0.29, df = 2 and 18, $P > 0.5$). Egg-laying dates were not correlated with rainfall from 1989 to 1993 (F = 0.9, df = 4 and 24, $P > 0.5$). Hatching success (% of observed eggs that hatched) did not differ from 1989 to 1993 (χ^2 = 1.7, df = 4, $P > 0.7$), nor did average hatching date (6 June ± 2.5 days) for first-laid clutches (F = 1.7, df = 2 and 11, $P > 0.2$) or the proportion of all hatchlings that fledged (χ^2 = 0.3, df = 3, $P > 0.9$). More than half (62%) of all eggs hatched, and 77% of hatched nestlings fledged, for an average of 1.1 young fledged per breeding attempt and 0.8 young per territorial pair (Table 1). Overall, 37 of 68 (54%) fully documented Barred Forest-Falcon nests produced at least one fledgling (Table 1). Neither of the two second nesting attempts was successful. Reproductive success did not differ among years (1989 to 1995; χ^2 = 3.1, df = 6, $P > 0.75$). One pair raised 14 fledglings over five years. Egg predation by mammals, birds, and snakes was the most important cause of nesting failure (n = 18 nests). Other losses resulted from predation of nestlings (n = 9), predation of adult females during incubation or brood rearing (n = 3), and unknown causes (n = 3).

Discussion.—Diurnal forest birds tend to concentrate long-range communication in the early morning (Henwood and Fabrick 1979). Predawn and early morning vocalizations of Barred Forest-Falcons probably serve to advertise territory occupancy and defend against potential intruders, as well as to attract mates and maintain pair bonds. Barred Forest-Falcons produced low-frequency notes, which may enhance long-range communication in forests (Morton 1975, Wiley and Richards 1982). We saw no aerial courtship displays, nor did Whitacre and Turley (1990) observe them while conducting raptor surveys from emergent trees. The lack of aerial displays suggests that vocalizations are the main signaling device for Barred Forest-Falcons.

Skutch (1950) noted that many Neotropical species begin to nest earlier or later depending on the rains, whereas others nest at about the same time each year regardless of fluctuations in the onset of the rainy season. Egg-laying dates of Barred Forest-Falcons were relatively synchronous among pairs and did not differ among years. The breeding season of Barred Forest-Falcons at Tikal began in February and early March, the start of the dry season, and extended through the beginning of the wet season, lasting nearly 20 weeks from courtship to the dispersal of young. Each stage of the breeding cycle was longer than that of several similar-sized raptors that breed at temperate latitudes, including Eurasian Sparrowhawks (*Accipiter nisus*), Eurasian Kestrels (*Falco tinnunculus*), and Merlins (*F. columbarius*). Compared

TABLE 1. Reproductive success of Barred Forest-Falcons in Tikal National Park, Guatemala, 1988 to 1995.

Year	No. of territorial pairs	No. of nesting attempts	Mean clutch size	No. of eggs hatched	No. of young fledged	No. of fledglings per nesting attempt	No. of fledglings per territorial pair	No. of fledglings per successful pair	Breeding success per territorial pair[a]	Breeding success per documented attempt[b]
1988[c]	4	4	2.5	2	—	—	—	—	—	—
1989	8	8	2.9	11	8	1.0	1.0	2.7	38	38
1990	9	8	2.8	12	11	1.4	1.2	2.8	44	50
1991	12	12	2.7	12	12	1.0	1.0	2.0	50	50
1992	14	6	2.8	10	9	1.5	0.6	1.8	36	50
1993	14	11	2.6	16	10	0.9	0.7	1.7	43	55
1994	18	12	2.5	20	11	0.9	0.6	1.8	33	50
1995	19	9	2.3	14	14	1.6	0.7	2.0	37	78
Total	98	70	2.6	97	75	1.1	0.8	2.0	38	54

[a] Proportion of nests that fledged at least one young per cumulative territorial pair (n = 98).
[b] Proportion of nests that fledged at least one young per fully documented nesting attempt (n = 68).
[c] In 1988, the outcome of two nests that contained nestlings was not documented and the other two failed (see Thorstrom 1990).

with Barred Forest-Falcons, temperate raptors of similar size also lay smaller eggs; have a smaller egg mass relative to female body mass; lay larger clutches; and have shorter incubation, nestling, and postfledging periods (Table 2).

Several forest-falcon young exhibited death feigning in the presence of intruders at the nest, similar to waterfowl responses to predation by captive red foxes (*Vulpes vulpes*; Sargeant and Eberhardt 1975). Death feigning may reduce the vulnerability of forest-falcon nestlings to predators that visually search cavities for food.

Young dispersed at five to seven weeks after fledging (10 to 12 weeks of age) during late August and September, which is the wettest time of year at Tikal. Young Barred Forest-Falcons reached independence quickly, unlike some other Neotropical raptors. White Hawks (*Leucopternis albicollis*; Draheim 1995), Gray-Backed Hawks (*L. occidentalis*; Vargas 1995), and Great Black-Hawks (*Buteogallus urubitinga*; Seavey and Gerhardt 1998) have extended postfledgling dependency periods, a characteristic of many large raptors that breed in the tropics.

The rate of nest-site occupancy (71%) was high and similar to that of the tropical Puerto Rican Sharp-shinned Hawk ([*Accipiter striatus venator*], 74%; Delannoy and Cruz 1988). Barred Forest-Falcons had low productivity, a breeding strategy similar to that of other tropical raptors, which may result in low recruitment into the breeding population. Among 70 nesting attempts, two individual females were recorded with immature (brown) eye color, but both were in adult plumage, suggesting that young birds do not normally breed until acquiring adult plumage.

More than half (54%) of the nesting attempts produced at least one fledgling, which was similar to that of cavity-nesting Collared Forest-Falcons (*Micrastur semitorquatus*; Thorstrom et al. 2000) and Laughing Falcons (*Herpetotheres cachinnans*; Parker 1997) at Tikal. The most vulnerable stages of reproduction, incubation and brood rearing, accounted for 91% of nesting failures. Most failures appeared to be due to predation. We believe that predation may affect lifetime productivity of forest-falcons owing to their small size and probable vulnerability to the broad range of predators found in tropical forests.

In summary, compared with temperate raptors of similar size, Barred Forest-Falcons have a small clutch size, relatively large eggs, a long incubation period, long nestling and postfledging dependency periods, low productivity, and a high rate of nesting failure. This cavity-nesting species was greatly affected by nest predation, which seems to be the important variable that resulted in low productivity, as observed in some other Neotropical raptors such as the Puerto Rican Sharp-shinned Hawk (Delannoy and Cruz 1988) and the Laughing Falcon (Parker 1997).

TABLE 2. Breeding parameters of Barred Forest-Falcons compared with similar-sized temperate raptors.

Species	Female mass (g)	Egg mass (g)	Relative egg mass[a]	Clutch size	Incubation period (days)	Nestling period (days)	Post-fledgling period (weeks)	Source
Sharp-shinned Hawk (*Accipiter striatus*)[b]	171	19	10.8	2–3	32	28–32	4–6	Delannoy and Cruz 1988
Eurasian Sparrowhawk (*Accipiter nisus*)	300	23	7.7	4–6	32–35	26–30	3–4	Newton 1986
Barred Forest-Falcon (*Micrastur ruficollis*)	238	28	11.8	2–3	33–35	35–44	5–7	This study
Eurasian Kestrel (*Falco tinnunculus*)	220	21	9.5	4–6	28	28–32	3–4	Tinbergen 1940
Merlin (*Falco columbarius*)	215	22	10.2	3–5	28–32	26–32	2–3	Newton et al. 1978
Eurasian Hobby (*Falco subbuteo*)	230	24	10.4	2–3	28	28–32	4	Newton 1979

[a] Egg mass as % of female body mass.
[b] Puerto Rican subspecies from tropics.

Acknowledgments.—This study was part of the Maya Project conducted by The Peregrine Fund in cooperation with the Instituto Nacional de Antropologia y Historia, Centro de Estudios Conservationistas Guatemala, and Consejo Nacional de Areas Protegidas Guatemala. We thank Sr. Rogel Chí Ochaeta and the rest of the staff of Tikal National Park. A special thanks to William Burnham, J. Peter Jenny, and David Whitacre of The Peregrine Fund for assistance and support. We thank James Wiley, David Whitacre, Lloyd Kiff, Tom Cade, Rob Bierregaard, Paul Salaman, and Rick Gerhardt for helpful suggestions on earlier drafts of the manuscript and the Raptor Biology Program at Boise State University for providing assistance to RT. We thank Alejandro Manzanero Quixchán, Carlos Solano Mateo, José María Castillo, Amilcar Morales Gutierrez, Feliciano Gutierrez Ramírez, Raul Ramírez, Victor Manuel Moro Méndez, Francisco Girón Manzanero, Hector de Jesús Girón Manzanero, Oscar René Artola, Oscar Annibal Aguirre, Oliverio René Ba, and Eladio Martínez Ramírez for assisting with field work.

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Received 29 March 1999, accepted 23 August 1999.
Associate Editor: K. L. Bildstein