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THE FOOD HABITS OF SYMPATRIC FOREST-FALCONS DURING THE BREEDING SEASON IN NORTHEASTERN GUATEMALA

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ABSTRACT.—The food habits of Barred (*Micrastur ruficollis*) and Collared Forest-Falcons (*M. semitorquatus*) were studied in Tikal National Park, Guatemala. On a numerical basis for 405 identified prey for Barred Forest-Falcons, lizards (*Anolis* spp., *Ameiva* or *Cnemidophorus* spp., *Laemanctus* spp., and *Corytophanes* spp.) were the most numerous prey type comprising 61.5% of the diet. For Collared Forest-Falcons, on a numerical basis of 170 identified prey, mammals represented the greatest proportion at 45.9%. On a biomass basis, lizards (37.3%) and birds (36.8%) were equally important in the diet of Barred Forest-Falcons but, for Collared Forest-Falcons, mammals (47%) and birds (45.4%) were the most important prey. Food-niche overlap was 0.49 between the two forest-falcons and prey that overlapped were mice, rats, bats, birds (*Momotus* spp., *Dendrocincla* spp.), and lizards (*Corytophanes* spp.). The wider food breadth of the Collared Forest-Falcon was probably attributable to the greater diversity of bird species in its diet. The Collared Forest-Falcon is approximately 3 times the size of Barred Forest-Falcons but the mean weight of its prey (MWP) was 10 times greater ($\bar{x}$ = 239 g) than that of Barred Forest-Falcons ($\bar{x}$ = 24 g).

KEY WORDS: *Barred Forest-Falcon*; Micrastur ruficollis; *Collared Forest-Falcon*; Micrastur semitorquatus; *food habits*; *niche overlap*; *niche breadth.*

Hábitos alimenticios de dos halcones de bosque simpatricos durante la estación reproductiva en el noreste de Guatemala

RESUMEN.—Los hábitos alimenticios de *Micrastur ruficollis* y *Micrastur semitorquatus* fueron estudiados en Parque Nacional Tikal, Guatemala. En una base numérica de 405 presas identificadas para *Micrastur ruficollis,* las lagartijas (*Anolis* spp., *Ameiva* o *Cnemidophorus* spp., *Laemanctus* spp., y *Corytophanes* spp.) fueron el tipo de presa más numeroso o sea el 61.5% de la dieta. Para *Micrastur semitorquatus,* en una base numérica de 170 presas identificadas, los mamíferos representaron la proporción mayor con el 45.9%. En relación a la biomasa, las lagartijas (37.3%) y aves (36.8%) fueron igualmente importantes en la dieta de *Micrastur ruficollis,* pero para *Micrastur semitorquatus,* los mamíferos (47%) y aves (45.4%), fueron las presas más importantes. El traslape del nicho alimenticio fue de 0.49 entre los dos halcones de bosque y las presas que se traslaparon fueron ratones, ratas, murciélagos, aves (*Momotus* spp., *Dendrocincla* spp.), y lagartijas (*Corytophanes* spp.). El espectro más amplio de la dieta de *Micrastur semitorquatus* fue probablemente atribuible a la mayor diversidad de especies de aves en su dieta. *Micrastur semitorquatus* es 3 veces el tamaño de *Micrastur ruficollis* pero su peso medio fue 10 veces mayor ($\bar{x}$ = 239g) que el de *Micrastur ruficollis* ($\bar{x}$ = 24 g).

[Traducción de César Márquez]

Neotropical birds of prey are poorly known, especially the forest-dependent species which are inconspicuous in their habits. The secretive forest raptors of the genus *Micrastur* are among the least-studied raptors and most accounts of their diets come from stomach contents of museum specimens or incidental observations (Dickey and van Rossem 1938, Friedmann 1948, Smith 1969, Izawa 1978, Mader 1981, Willis et al. 1983, Mays 1985, Trail 1987, Rappole et al. 1989, Thorstrom et al. 1990). The most detailed account of the food habits of this genus is given by Robinson (1994), but it too is limited to incidental observations.

The Barred Forest-Falcon (*Micrastur ruficollis*) is perhaps the most common raptor in Neotropical forests. It has the widest distribution of any forest-falcon, occurring from southeastern Mexico to northern Argentina, Paraguay, and east through Brazil and the Guianas (Brown and Amadon 1989, del Hoyo et al. 1994). It ranges from humid lowland and foothill forests to higher subtropical and montane forests reaching its limit near 2500 m. In-

formation on the diet of the Barred Forest-Falcon suggests that it feeds mainly on lizards (Thorstrom et al. 1990, Thorstrom 1993, del Hoyo et al. 1994).

The Collared Forest-Falcon (*M. semitorquatus*) also has a broad distribution, ranging from central Mexico to eastern Bolivia, northern Argentina, and Paraguay (Brown and Amadon 1989). It occupies dense primary and secondary forests from sea level to 2500 m. A recent sighting in Texas (Lasley et al. 1994) extended its northern distribution to the southwestern U.S. Food of the Collared Forest-Falcon includes birds, mammals, lizards, snakes, and insects (Brown and Amadon 1989, Thorstrom 1993).

In this paper, I compare the diet of Barred Forest-Falcons and Collared Forest-Falcons based on several years of nest observations of prey deliveries, and direct observations at and away from nests during breeding seasons from 1988–92 in northeastern Guatemala. My objectives were to compare prey frequency and biomass and to assess the amount of overlap in diet among the two species and compare food-niche parameters and differences as potential mechanisms for coexistence of these two forest-falcons.

STUDY AREA AND METHODS

I studied Barred and Collared Forest-Falcons in Tikal National Park, Petén, Guatemala from 1988–92. The park encompasses 576 km^2 in northeastern Guatemala and its center lies at 17°13′N, 89°36′W. Vegetation in the park is semideciduous tropical forest with lowland rolling hills ranging from 200–450 m elevation.

Schulze and Whitacre (1999) described several forest types that occur along topographical drainage, soil type, and moisture gradients within the park. The 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 is covered mostly by unbroken primary forest, except for some areas where light selective logging occurred prior to 1969.

The climate has pronounced wet and dry seasons with rains usually beginning in May or June and ending by December. Between 1989–95, monthly precipitation ranged from 1.0 mm in April to 302.5 mm during September with an annual mean rainfall of 1309 mm (pers. obs.). Mean monthly temperatures ranged from a low of 15°C in January to a high of 35°C in May.

The forest and known forest-falcon territories were searched daily from February through August to document nesting activity and potential breeding pairs. Nests of Barred Forest-Falcons were observed primarily from the ground and those of the Collared Forest-Falcon were occasionally observed from tree platforms. Observations were made using 7–10× binoculars at distances of 25–50 m. During the breeding season, observations of prey items were recorded during prey deliveries and away from nests during radiotracking sessions. All prey was identified to the most accurate taxonomic level possible with the exception of amphibians and insects, which were not identifiable to the species level and were assigned to larger taxonomic groupings. The resulting tabulation produced a total of 37 prey categories for both species. Only observed prey delivered and captured were included in biomass estimates to avoid possible bias from prey found in nests (Snyder and Wiley 1976, Wiley and Wiley 1981, Marti 1987). *Anolis* lizards were separated in small (<20 cm) and large catagories (>20 cm).

To estimate mean weight of prey (MWP), I multiplied each prey item by its average weight (Table 1), summed the products and divided the sum by the total number of prey observed. Mammal weights follow Emmons and Feer (1997), bird weights come from Smithe (1966) and Dunning (1993), and reptile weights were taken in the field.

Food-niche breadths (FNB) were calculated using Levins' (1968) equation: FNB = $1/\Sigma P_i j^2$, where P_i is the proportion of the ith prey category of species j. For comparison among raptors with different number of prey categories, a standardized niche breadth value (FNBs) was also calculated as follows: FNBs = (FNB − 1)/(n − 1), where n is the number of prey categories (Levins 1968) Niche overlap was calculated using Schoener's (1970) index of symmetrical overlap: overlap = 1 − (½)($\Sigma|P_{ij} - P_{ik}|$), where P_i is the proportion of the ith prey category for species j and k. Linton et al. (1981) found this overlap formula to be the only index that accurately measures real overlap between 7–85%.

The Collared Forest-Falcon is the largest of the two species with a body mass of 467–511 g for males (Dickey and van Rossem 1938) and 556–750 g for unknown sexes (Haverschmidt 1968). Males I weighed averaged 587 ± 17.6 g (±SD, range = 563–605 g, N = 4) and females averaged 869 g ± 63 g (range = 792–940 g, N = 6) Barred Forest-Falcons averaged 167.8 ± 10.6 g (range = 144–184 g, N = 25) for males and 233.2 g ± 23.9 (range = 200–322 g, N = 34) for females.

RESULTS

Barred Forest-Falcon. I recorded lizards (*Anolis* spp., *Ameiva* spp. or *Cnemidophorus* spp., *Laemanctus* spp., and *Corytophanes* spp.), birds (*Momotus* spp., *Aulacorhynchus* spp., *Turdus* spp., *Leptotila* spp., *Dendrocincla* spp., *Thryothorus* spp., and Tyrannidae), amphibians, mammals, snakes, and insects (Blattidae) in the diet of Barred Forest-Falcons during the nesting season.

I observed a total of 600 prey items being delivered to females, nestlings, and fledglings from 1988–92. On a numerical basis, reptiles were the predominant prey comprising 61.5% of the diet (249 prey items), followed by birds 22% (89), insects 8.2% (33), mammals 5.9% (24), and amphibians 2.5% (10) (Fig. 1). Nearly one third (195) of

Table 1. Weights used to estimate prey biomass of Barred and Collared Forest-Falcons at Tikal National Park, Guatemala.

PREY	WEIGHT (g)	SOURCE
Insects		
Blattaria	1.5	This study
Reptiles		
Anolis <20 cm	3.9	This study
Anolis large >20 cm	13.8	This study
Ameiva or *Cnemidophorus*	25	This study
Laemanctus	15	This study
Corytophanes	45	This study
Birds		
Crypturellus	440	Smithe 1966
Penelope	600	Smithe 1966
Crax	500	Smithe 1966
Ortalis	450	Smithe 1966
Agriocharis	3000	Smithe 1966
Odontophorus	300	Smithe 1966
Leptotila	160	Smithe 1966
Ciccaba	240	Smithe 1966
Momotus	133	Dunning 1993
Ramphastos	350	Dunning 1993
Pteroglossus	220	Dunning 1993
Aulacorhynchus	150	Smithe 1966
Melanerpes	81	Dunning 1993
Celeus	85	Dunning 1993
Tyrannidae	15	Smithe 1966
Cyanocorax	200	Dunning 1993
Troglodytidae	15	Smithe 1966
Muscicapidae	75	Smithe 1966
Mammals		
Sciurus small	205	Emmons and Feer 1997
Sciurus large	400	Emmons and Feer 1997
Artibeus	50	Emmons and Feer 1997
Unidentified bat	20	This study
Unidentified mouse (*Heteromys*)	76	This study, Emmons and Feer 1997
Unidentified rat (*Rattus, Oryzomys, Sigmodon*)	150	This study, Emmons and Feer 1997

the items were unidentified, especially late in the nestling period, because male forest-falcons flew secretively into their nests without calling their mates to receive prey, and females flew into the nests quickly and directly without vocalizations. It was unlikely, however, that the unidentified prey items differed from those actually identified. The most detailed dietary information was obtained during 1989 when 267 of 380 items delivered to nests were identified. Again, most (64.0%, N = 171) were lizards and were represented by 57 small *Anolis* spp., 21 large *Anolis* spp., 28 teiids (most likely *Ameiva* spp. or *Cnemidophorus* spp.), 11 *Laemanctus* spp., 5 *Corytophanes* spp., and 49 unidentified lizards. Snakes included 1 coral snake or mimic (*Lampropeltis* sp. or *Micrurus* sp.) and 2 other snakes. Eleven of the 267 identified prey (4%) were frogs (*Rana* spp. and/or *Hyla* spp.). Only 21 arthropods (8 cockroaches and 13 other items including spiders and beetles, 8% of the diet) were identified. Birds contributed 52 prey items (19.5 % of the diet) and included five Blue-crowned Motmots (*Momotus momota*), two flycatchers (Tyrannidae), two Emerald Toucanets (*Aulacorhynchus pra-*

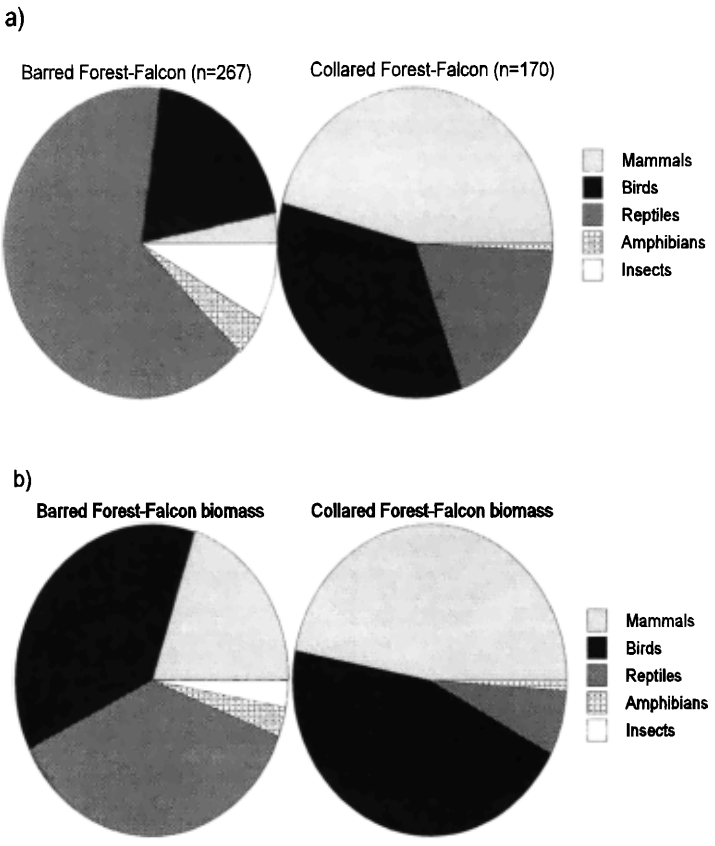

Figure 1. Comparison of the diets of Barred Forest-Falcons and Collared Forest-Falcons as (a) the percent prey of individuals and (b) the biomass composition (% weight of prey individuals).

sinus), one Gray-fronted Dove (*Leptotila rufaxilla*), one woodcreeper (*Dendrocincla* sp.), one Spot-breasted Wren (*Thryothorus maculipectus*), and one Clay-colored Robin (*Turdus grayi*). Birds taken ranged in size from an unidentified warbler (*Dendroica* sp.) at 9 g to a Gray-fronted Dove at 160 g (Smithe 1966, Dunning 1993). The nine mammals I identified represented only 3% of the diet. Among them were seven rodents, one bat, and one other mammal. The rodents were possibly members of the genera *Heteromys* and *Oryzomys*. Snakes accounted for 3 prey items or 1.1% of the diet.

Biomass estimates were made for 267 identified prey items delivered during the 1989 breeding season. On a biomass basis, reptiles (37.3%), birds (36.8%), and mammals (20.2%) comprised 94.3% of the estimated biomass (Fig. 1). Males delivered more prey items and prey biomass than females during the breeding season. Of the 267 identified prey delivered in 1989, five males brought in 3.8 kg (75.7%) and five females delivered 1.2 kg (24.3%) of the biomass during the breeding season.

Collared Forest-Falcon. I found squirrels (*Sciurus* spp.), bats (*Artibeus* spp.), rats (*Sigmodon* spp.), mice (*Heteromys* spp.), birds (*Crypturellus* spp., *Penelope* spp., *Crax* spp., *Ortalis* spp., *Agriocharis* spp., *Odontophorus* spp., *Leptotila* spp., *Ciccaba* spp., *Momotus* spp., *Ramphastos* spp., *Pteroglossus* spp., *Aulacorhynchus* spp., *Melanerpes* spp., *Celeus* spp., *Cyanocorax* spp., Dendrocolaptidae), snakes (*Coluber* sp.), and lizards (*Corytophanes* spp.).

From 1990–92, 222 prey items were delivered to females, nestlings, and fledglings and 170 of these were identified. On a numerical basis, 45.9% were mammals (78 prey items), 34.7% birds (59), 18.8% reptiles (13 lizards and 19 snakes), and 0.6% amphibians (1 frog) (Fig. 1). The 52 unidentified

prey items were presumed to have been similar to those that were identified. In addition, 36 items were given to two fledglings by an extra adult believed to be a male. This male specialized in catching toucans so I calculated the diet of Collared Forest-Falcons both with and without this male's contribution.

Prey of Collared Forest-Falcons ranged in size from a frog estimated at 20 g to an Ocellated Turkey (*Agriocharis ocellata*) weighing about 3 kg. The two largest prey were the adult female turkey and a young Crested Guan (*Penelope purpurascens*). Of the 13 lizards taken, 12 were in species belonging to the genus *Corytophanes*. The 19 snakes I observed were most likely colubrids. The 78 mammals identified included 42 Deppe's squirrels (*Sciurus deppei*; 190–220 g), 11 Yucatan squirrels (*S. yucatanensis*; 420 g), two fruit bats (*Artibeus* spp.), 14 unidentified bats, 7 rat-sized rodents including the hispid cotton rat (*Sigmodon hispidus*), and 2 mice believed to be spiny pocket mice (*Heteromys* spp.). Among the 59 birds identified, the most numerous were Collared Aracari (*Pteroglossus torquatus*, $N = 9$), Plain Chachalaca (*Ortalis vetula*, $N = 7$), Great Curassow (*Crax rubra*, $N = 7$), Keel-billed Toucans (*Ramphastos sulfuratus*, $N = 6$), Ruddy Woodcreepers (*Dendrocincla homochroa*, $N = 4$), Tinamous (*Crypturellus* spp., $N = 3$) , and Brown Jays (*Cyanocorax morio*, $N = 3$).

In 1990, a third adult forest-falcon, probably a male, began delivering prey items to two young, 4 wk after they fledged. We observed this adult deliver 36 prey items until 11 weeks after fledging. It appeared to prefer Keel-billed Toucans delivering 27 toucans, two Collared Aracari, two unidentified birds, four squirrels (*S. deppei*), and one unidentified prey item. Sometimes it delivered two Keel-billed Toucans a day. When this contribution was included in the overall diet of Collared Forest-Falcons, the diet was dominated by birds (43.9%, 90 individuals) followed by mammals (40.0%, 82), reptiles (15.6%, 32), and amphibians (0.5%, 1). In terms of biomass, this extra adult delivered 12.6 kg of prey during the post-fledging period.

Biomass estimates were based on the 170 identified prey items delivered during the breeding seasons. On this basis, 47.0% of the prey were mammals, 45.4% birds and 6.5% reptiles (Fig. 1). Squirrels represented 66.7% of the mammalian biomass. Males delivered 11.4 kg (65.7%) and females 5.9 kg (34.3%) of the biomass.

Food-niche Parameters. Lizards, especially *Anolis* spp., dominated the Barred Forest-Falcon diet and, as a result, it had a narrower niche breadth than did the Collared Forest-Falcon. Collared Forest-Falcons took a higher richness of bird and mammal species (Table 2). The standardized FNB of the Barred Forest-Falcon was lower (0.33) than the Collared Forest-Falcon (0.49). Dietary overlap between the two forest-falcons was 0.49. Estimated MWP captured by Collared Forest-Falcons was significantly heavier than that of Barred Forest-Falcons (Table 2). The larger Collared Forest-Falcon captured larger avian ($\bar{x} = 373.9 \pm 49.5$ g, ±SE, $N = 59$) and mammalian ($\bar{x} = 179 \pm 12.5$, $N = 78$) prey than did the Barred Forest-Falcon which took mostly lizards ($\bar{x} = 13.8 \pm 0.6$, $N = 122$) and birds ($\bar{x} = 62.1 \pm 4.9$, $N = 52$).

Table 2. Food-niche breadth, dietary overlap, and estimated mean weights (g) of prey (MWP) and of birds (MW) of Barred and Collared Forest-Falcons during the nesting season. All calculations based on prey at the generic or family level. Mean ± SE (*N*).

Food-niche Parameters	Barred Forest-Falcon	Collared Forest-Falcon
Total identified prey items	267	170
Mammal species richness	3	6
Bird species richness	7	15
Lizard species richness	5	1
MWP	23.7 ± 2.5 (267)	238.9 ± 18.9 (170)
MW birds	62.1 ± 15.3 (52)	373.4 ± 49.5 (59)
FNB	7.9	13.8
FNBs	0.33	0.49
Dietary overlap	0.49	

Discussion

Barred and Collared Forest-Falcons are moderately dimorphic with Collared Forest-Falcons 3–4 times larger than Barred Forest-Falcons. Optimal foraging theory predicts that larger predators should have a wider food niche than smaller ones (Schoener 1970). I found this to be true for these two forest-falcons. Collared Forest-Falcons captured a higher proportion of medium-sized mammals, especially squirrels, and they had a greater diversity of birds in their diet giving them a broader food-niche breadth (13.8) compared to Barred

Forest-Falcons (7.9). Barred Forest-Falcons preyed predominantly on lizards, mainly *Anolis* spp., contributing to its narrower food-niche breadth, and birds were of secondary importance in their diet. Collared Forest-Falcons preyed on a wider range of animal sizes, ranging from a small frog (20 g) to large birds (3 kg) whereas Barred Forest-Falcons caught prey ranging in size from insects (1.5 g) to a dove (160 g).

In terms of biomass, Barred Forest-Falcons captured nearly equal proportions of lizards (37.3%) and birds (36.8%) during the breeding season. This was attributed to the smaller mean weight of lizards (13.8 g) vs. the mean weight of birds (93.5 g). Birds were approximately seven times heavier but three times fewer in numbers. Prey biomass of Collared Forest-Falcons was distributed nearly equally between mammals (47%) and birds (45.4%), but the mean weight of birds (368 g) was twice that of mammals (179 g). However, fewer birds (59) than mammals (78) were delivered during the nesting season, contributing to the nearly equal frequency of prey biomass of Collared Forest-Falcons.

The food-niche overlap was relatively high between these two congeners and almost near the competition threshold level of 0.6 which was proposed as biologically significant by Zaret and Rand (1971). Schoener (1984) and Temeles (1985) predicted that similar morphological features of raptors can be found among congeners which affect their hunting ability and food habits. However, Bosakowski and Smith (1992) showed that larger differences in body size limit food overlap below the competition threshold. Thus, while the two forest-falcons exhibited overlap on a few prey species, I suspect that the effect on overall prey availability was probably insignificant. Both species have a broad diet with Barred Forest-Falcons relying more on lizards and Collared Forest-Falcons preying mainly on squirrels.

The Barred Forest-Falcon is dependent on mature forests while the Collared Forest-Falcon occupies mature forests, forest edge, and secondary woodlands and thickets. Both species use a short stay "perch-hunting" technique, a common method found in forest or woodland-adapted species (Kenward 1982, Newton 1986). The higher consumption of avian prey by the Collared Forest-Falcon may be enhanced by its great maneuverability, owing to its long legs and long-arched tail which are morphological adaptations for chasing prey by foot. Collared Forest-Falcons were observed chasing prey by running on the ground, around tree trunks, and along large branches, whereas Barred Forest-Falcons usually attacked prey by surprise from concealed perches.

The information provided here is limited to observations during the nesting season and may not accurately reflect the overall diet of these two species. There may be seasonal shifts in the diet of these forest-falcons or certain prey types may be taken preferentially due to experience or ability as observed in the extra adult Collared Forest-Falcon that delivered 75% of its prey as Keel-billed Toucans. This particular bird apparently had a special ability or learned behavior for capturing toucans. More information is needed from other regions in the Neotropics and during the nonbreeding season to determine the extent of niche breadth and dietary overlap between these two species.

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