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FOOD DELIVERED TO NESTS OF SWALLOW-TAILED KITES IN TIKAL NATIONAL PARK, GUATEMALA

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Abstract. In 1990 and 1991, we studied Swallow-tailed Kite (*Elanoides forficatus yetapa*) diets by recording food delivered to nests in northern Guatemala. Kites delivered primarily vertebrates to incubating mates. During the nestling period, 62% of 1496 prey deliveries were insects, 18% nestling birds, and 10% lizards; frogs and fruit were brought infrequently. Coleopterans and hymenopterans were the most frequent insects delivered. Birds comprised most of the biomass. Lizard deliveries were most frequent early in the nesting season, whereas insect prey were infrequent until after the first rains, in late May. Compared to *E. f. forficatus* in Florida, *E. f. yetapa* provided more insects and fewer frogs, and did not adjust feeding rates based on brood size. Swallow-tailed Kites delivered more vertebrates, particularly birds, than sympatric Plumbeous Kites (*Ictinia plumbea*), and used different foraging space and hunting techniques than sympatric Double-toothed Kites (*Harpagus bidentata*) and Gray-headed Kites (*Leptodon cayanensis*).

Key words: Elanoides forficatus, *food habits, Guatemala, nestling diet, Swallow-tailed Kite, Tikal National Park.*

Alimento Llevado a los Nidos de *Elanoides forficatus* en El Parque Nacional Tikal, Guatemala

Resumen. En 1990 y 1991, estudiamos las dietas del milano *Elanoides forficatus yetapa* en el norte de Guatemala, registrando el tipo de alimento que fue llevado a los nidos. Los milanos llevaron principalmente vertebrados al miembro de la pareja que incubaba. Durante el período de crecimiento de los polluelos, 62% de las 1496 presas llevadas fueron insectos, 18% polluelos de otras especies de aves y 10% lagartijas; en raras ocasiones llevaron frutas y ranas. Los coleópteros e himenópteros fueron los insectos más comúnmente utilizados. Las aves formaron la mayor parte de la biomasa. Los milanos llevaron largatijas más frecuentemente al principio de la nidificación, mientras que los insectos no fueron frecuentes sino hasta después del inicio de las primeras lluvias en mayo. En comparación con *E. f. forficatus* en Florida, *E. f. yetapa* llevó más insectos y menos ranas, y no ajustó la tasa de alimentación con relación al tamaño de la nidada. *E. forficatus* llevó más vertebrados, especialmente aves, que la especie simpátrica *Ictinia plumbea*, y utilizó diferentes espacios de forrajeo y técnicos de cacería que las especies simpátricos *Harpagus bidentata* y *Leptodon cayanensis*.

Two subspecies of Swallow-tailed Kites (*Elanoides forficatus*) are recognized. The northern, *E. f. forficatus*, which breeds in the southeastern United States and winters in South America, has received a good deal of research attention (e.g., Snyder 1974, Cely and Sorrow 1990, Meyer and Collopy 1995). By contrast, little is known of the southern subspecies, *E. f. yetapa*, which breeds from southern Mexico through south-central South America (Meyer 1995).

The North American subspecies underwent a sharp decline in numbers and a significant decrease in its breeding distribution between 1880 and 1940 (Cely 1979); the remaining populations face a variety of threats on the breeding grounds and during migration and wintering (Meyer 1995). Several studies have examined the breeding-season feeding habits of this subspecies (Sutton 1955, Snyder 1974, Meyer and Collopy 1995, Meyer et al. 2004). For the Mesoamerican subspecies, knowledge of feeding habits comes only from anecdotes (Haverschmidt 1962, Skutch 1965, Voous 1969, Buskirk and Lechner 1978, Lemke 1979). The extent to which this subspecies differs from the northern one in its status, ecology, and conservation needs remains unstudied (Meyer 1995).

We examined the breeding ecology of Swallow-tailed Kites in northern Guatemala, near the northern edge of the subspecies' range (Gerhardt et al. 1997). Herein, we report our findings with regard to food delivered to nests, and compare their diet with those of the northern subspecies and with those of three sympatric kite species.

METHODS

This research was conducted in Tikal National Park in the Department of El Petén in northern Guatemala (17°13'N, 89°38'W). The forest is tropical semideciduous (Pennington and Sarukhan 1968). The area has

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an average annual rainfall of approximately 1.4 m (Smithe 1966) and experiences distinct wet and dry seasons, the latter occurring from February to June. Vegetation was described by Schulze and Whitacre (1999). The main Maya ruins around which the park was established are on a limestone hill that is the highest point (250 m elevation) for a considerable distance. Our observations were conducted on this hill, which supported a dense concentration of Swallow-tailed Kite nests (12 in approximately 1 km^2). Although some areas were seasonally inundated, very little permanent water existed in the vicinity of these nests.

DATA COLLECTION

In 1990 and 1991, we used Maya ruins as observation points from which to locate and observe nests. Because these birds were both vocal and conspicuous, courtship and nest construction were easily observed. Swallow-tailed Kites consistently remained above the canopy and placed nests in the tops of the tallest trees (Gerhardt et al. 1997). We observed nests using binoculars and 30× spotting scopes from distances ranging from 30 to 60 m. We observed each focal nest approximately every third day from the time located until fledging or failure. Observations began 30 min before dawn and ended 30 min after sunset; because these times varied only slightly through the season, a day's observation averaged 13 hr. We verified clutch sizes, brood sizes, and hatching dates by climbing to nests (Gerhardt et al. 1997).

We recorded the date and time of each food delivery and identified food items to the lowest possible taxonomic level. We estimated the length of each item at the time of observation. To estimate biomass, we compared this size estimate with mass data collected from both living and dead local specimens of the appropriate taxon. Because the sexes were not dimorphic, we were unable to reliably sex the individuals delivering food.

We conducted observations at nine nests, four in 1990 and five in 1991. We present data for eight nests for the incubation period, representing 58 days or approximately 754 hr of observation. Four of the nine nests failed soon after hatching, and were excluded from posthatching analyses of diet because of small sample sizes. Data reported herein for food delivered to nestlings are from three nests in 1990 and two nests in 1991, each of which resulted in the fledging of a single young. These results represent 88 days, and approximately 1144 hr, of observation. Unidentified food items, which comprised only 7% of all observations, were excluded from all analyses except those dealing with delivery rates. Such unidentified food items were generally small, and ingested in a single bite; most were likely insects, though fruit and small lizards could not be ruled out.

STATISTICAL ANALYSES

We used log-likelihood ratio (G) tests (Wilks 1935) to analyze year effects, nest effects, and to compare among sample sets (i.e., results of similar studies of other kite species at Tikal and of *E. f. forficatus*). We used Kolmogorov-Smirnov goodness-of-fit tests (Zar 1984) to determine whether diel patterns differed from uniformity. Results are reported throughout as means ± SD, and the significance level used is $\alpha < 0.05$.

RESULTS

Swallow-tailed Kites arrived during the first week of February. As elsewhere, several pairs at our Tikal study site nested in loose association, defending only a very small area immediately around the nest from conspecifics. We did not observe nonbreeding kites associated with nests, as was frequently seen in Florida (Meyer and Collopy 1995). Although a single brood was the norm, we observed renesting after the failure of first nesting attempts. Indeed, one of the focal nests of this food-habits study was a renesting that took place following loss of a first brood, albeit a very young brood.

Foraging adults delivered food to incubating mates at a rate of 1.0 ± 1.3 items per day (range 0–5). Both adults incubated and foraged during this period, but one individual (presumably the female) performed the majority of incubation at each nest. Forty-seven identifiable food items were delivered during observations at this stage of nesting. Most of these were vertebrates, including 22 lizards, 1 snake, and 15 nestling birds. Only five insects were identified, with four deliveries of fruit documented. There was a significant difference ($G = 54.1$, $P < 0.001$) between incubation and nestling periods in proportions of the different classes of food (insect, amphibian, reptile, bird, fruit) delivered to nests.

At each of the five nests studied during the nestling stage, clutch size was two and both eggs hatched. Hatching interval ranged from 3–5 days, and siblicide occurred early (by five days after hatching of the second egg; Gerhardt et al. 1997). We did not see second chicks receive any food; thus, our observations for the nestling period reflect the delivery of food to single nestlings. Food was delivered to nestlings at a rate of 15.9 ± 10.8 items per day (range 1–45, $n = 91$ days). Rates (deliveries per day) peaked between 38 and 44 days after hatching, decreasing thereafter until fledging at 51–58 days posthatching.

Food delivered to young ($n = 1496$ items at five nests) consisted primarily of insects, nestling birds, and lizards. Four unidentified fruits were delivered. By frequency, insects comprised 62% of the nestling diet, with birds and herpetofauna contributing 18% and 10% of observed prey, respectively (Fig. 1a). Insects were the most frequent food item at all but one nest, and the composition of food items was relatively constant among the five nests (Fig. 1a). As far as we could ascertain, all birds delivered to kite nests were altricial young taken from their nests and incapable of flight. Four hylid frogs constituted the only amphibians, and lizards all the reptiles, delivered to nestlings.

Although insects were the most numerous prey, biomass estimates suggested that vertebrates, particularly nestling birds, composed a larger portion of the diet of nestling Swallow-tailed Kites (Fig. 1b). Indeed, at all five nests avian biomass represented more of the diet than all other food combined.

The insect component of the nestling diet comprised six orders (Fig. 1c). Nests differed greatly from one another in frequency of delivery of these orders ($G =$

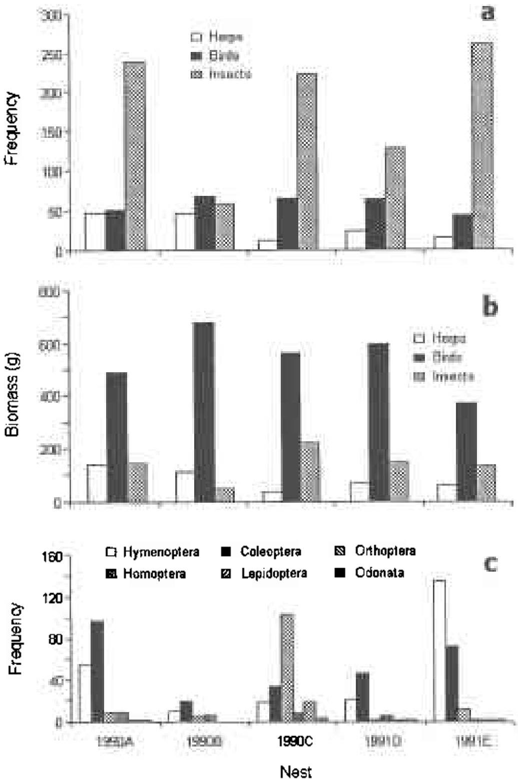

FIGURE 1. Composition of the diet of Swallow-tailed Kite nestlings at five nests in Tikal National Park, Guatemala, 1990–1991. Diet as (a) frequency of total prey by class, (b) biomass of total prey by class, and (c) frequency of insect prey by order. "Herps" consisted mostly of lizards but included four frogs.

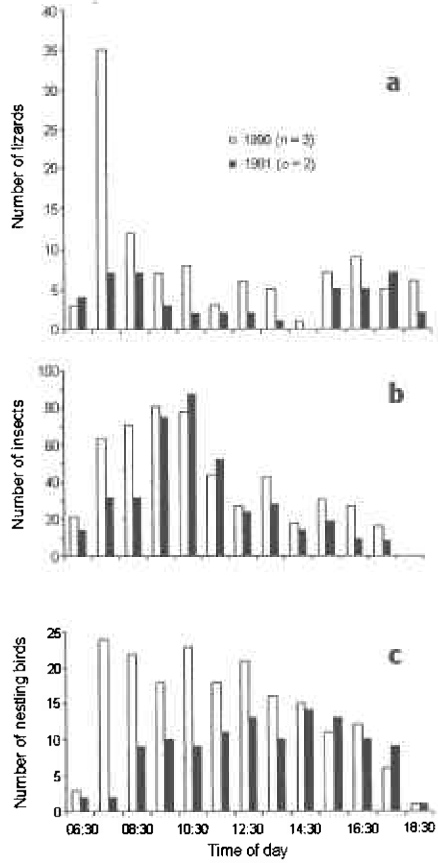

FIGURE 2. Diel patterns of prey delivered to Swallow-tailed Kite nestlings at five nests in Tikal National Park, Guatemala, 1990–1991. Frequency of deliveries by time of day of (a) lizards, (b) insects, and (c) nestling birds.

491.0, $P < 0.001$). Beetles, most of which appeared to be scarabs, ranked either first or second in frequency among insect orders at all five nests. Bees and wasps were easily the most numerous insect order at one nest, and were second to beetles at another nest. Bee and wasp nests were delivered frequently, providing numerous larvae in a single delivery. Orthopterans (i.e., katydids and grasshoppers) were only a small part of the diet at most nests, but were easily the most numerous insects delivered to one nest in 1990. This nest (1990C; Fig. 1) was a renesting initiated much later in the season than other nests. Butterflies were rarely delivered, but the adults at the late nest brought a number of caterpillars on a single day. Cicadas (Homoptera) were delivered to all nests infrequently. Dragonflies (Odonata) were not observed at one nest and were not numerous at any nest.

Most lizards delivered to nests were identified only as such. Of those that were identifiable to genus, most belonged to the genus *Norops* (Middle American anoles). *Sceloporis variabilis* (rosebelly lizards) were also taken rather frequently, and a small number of young *Corytophanes* (helmeted basilisks) were identified.

There was no year effect upon diel pattern of lizard deliveries ($G = 13.4$, $P > 0.2$), which differed from uniformity (1990 and 1991 combined, $d_{max} = 32.5$, $P < 0.001$). Two peaks were observed in the daily delivery of lizards (Fig. 2a), a large peak between 07:00 and 11:00, and a smaller peak in late afternoon. Daily delivery of insects differed among years ($G = 30.2$, $P < 0.01$), but in each year, deliveries did not occur uniformly through the day (1990, $d_{max} = 119.1$, $P < 0.001$; 1991, $d_{max} = 110.1$, $P < 0.001$). Insect deliveries peaked later in the morning (between 09:00 and 11:00), and then tapered gradually thereafter (Fig. 2b). Diel pattern of avian deliveries differed among years ($G = 22.6$, $P < 0.05$). In 1991, the delivery of nestling birds remained high throughout the day ($d_{max} = 13.4$, $P > 0.05$), although in 1990 more arrived in the morning ($d_{max} = 28.5$, $P < 0.01$; Fig. 2c).

Seasonal patterns were observable in the types of food brought to nests. In 1990, deliveries of insects were infrequent prior to 20 May, after which we noticed a sharp increase. Delivery of lizards, by contrast, was most frequent early in the breeding season, dropping off sharply by early June (both years). Deliveries of nestling birds exhibited two peaks in 1990; this reflected the asynchrony of the kite nests, and is likely associated more with the behavior of the kites than with abundance or availability of this prey.

DISCUSSION

DIEL PATTERNS

Diel patterns of prey deliveries likely reflect both the availability of prey and the hunger of nestling kites. Overall, more prey were delivered during the morning, during which chicks were more vocal and persistent in their begging. During the early afternoon, young kites were less vocal, apparently having been temporarily sated. The early-morning and (smaller) late-afternoon peaks in lizard deliveries probably reflect periods during which these prey are more exposed, easily caught, or both. A similar pattern of lizard deliveries was found among *E. f. forficatus* in Florida (Meyer and Collopy 1995). For Double-toothed Kites (*Harpagus bidentata*) at Tikal, however, this diel pattern was reversed, with most lizards delivered to nests during the middle of the day (Schulze et al. 2000). This difference may be explained by the difference in foraging zone of the two kites: Swallow-tailed Kites caught lizards basking on the upper edges of the canopy, and Double-toothed Kites hunted below and within the canopy. Delivery rates of insects to Swallow-tailed Kite nests peaked in late morning, when young kites were still hungry and flying insects were most active (RPG, pers. obs.). Availability, to foraging kites, of nestling birds is expected to vary little throughout the day. In 1991, nestling prey were delivered equally throughout the day, although in 1990 greater numbers arrived in the morning.

INTERSPECIFIC COMPARISONS

A comparison of Swallow-tailed Kite diet and hunting with that of three sympatric kite species suggests prey-resource partitioning, a result, at least partially, of differences in hunting behavior and foraging habitat. Of the many species of raptors that breed in Tikal, the species most ecologically similar to the Swallow-tailed Kite is the Plumbeous Kite (*Ictinia plumbea*). Plumbeous Kites are migratory, are of similar size, nest high in trees, and raise only a single young (Seavy et al. 1998). Like Swallow-tailed Kites, this species also hunts above the canopy in groups, and is largely insectivorous, at least outside the breeding season (Seavy et al. 1997). Plumbeous Kites at Tikal delivered primarily insects (92% of 653 prey items at six nests in three years); some lizards were eaten, but deliveries of other vertebrates, including birds, were few (Seavy et al. 1997). Type of prey delivered to Swallow-tailed Kite nests (this study) differed greatly from prey delivered to Plumbeous Kite nests (Seavy et al. 1997; $G = 250.7$, $P < 0.001$). Seavy et al. (1997) never observed Plumbeous Kites capturing or delivering nestlings as prey. Whereas most observed Plumbeous Kite hunts were initiated from soaring flight, 31% of capture attempts were from perches (Seavy et al. 1997). Although the two kite species delivered the same kinds of insects to their young, they did so in different proportions. Both kite species delivered numerous coleopterans to young; but homopterans were important and hymenopterans unimportant in the diet of Plumbeous Kites. Hence, even at the ordinal level, there appears to be some prey partitioning between these sympatric species.

At Tikal, the smaller Double-toothed Kite hunted below and within the forest canopy rather than above it, generally initiating capture attempts from a perch (Schulze et al. 2000). Insects comprised 60% of the diet at nests of this species, with homopterans and orthopterans (82% and 9%, respectively, of the insect component) being the most important insect orders. The remainder of the diet was almost exclusively lizards (primarily *Norops* spp.), and these were believed to be the major prey in terms of biomass (Schulze et al. 2000). Thus, although both Double-toothed Kites and Swallow-tailed Kites ate insects and lizards, they exhibited little overlap in foraging space, hunting techniques, or types of insects eaten. Moreover, nestling birds, the most important prey by biomass at Swallow-tailed Kite nests, were not delivered to Double-toothed Kite nests.

The sympatric Gray-headed Kite (*Leptodon cayanensis*) is also believed to be primarily insectivorous (Haverschmidt 1962, Brown and Amadon 1989), although this species remains little studied. Breeding-season observations found that this species hunted from perches in and below the canopy (Thorstrom 1997), thus using different foraging space and methods than Swallow-tailed Kites.

INTRASPECIFIC COMPARISONS

These data allow a quantitative comparison of the nestling diets of the northern and southern subspecies of Swallow-tailed Kites. The *E. f. yetapa* birds in our study and *E. f. forficatus* in Florida were quite different ($G = 923.7$, $P < 0.001$) in proportions of prey types in the diet (1092 items at 8 nests; Meyer 1995, Meyer et al. 2004). Both delivered a similar percentage of nestling birds to their nests. Lizards represented only 3% of the diet in Florida (as compared to 10% in our study), and snakes were delivered more frequently there than were lizards. Florida kites delivered far fewer insects (27% versus 62% of the nestling diet), whereas frogs (42% of prey) were the most numerous prey items. Although wasp nests and many of the same insect orders were observed in the diets of both subspecies, dragonflies appeared to be much more important to kites in Florida. The relative absence of frogs and dragonflies in the diet of Swallow-tailed Kites in Tikal reflects the difference in habitat: kites in the southeastern United States were associated with wetlands and rivers, but those in Tikal nested far from any significant sources of water.

The most significant difference between *E. f. forficatus* and *E. f. yetapa* was in reproductive success: 1.6 young per successful nest in South Carolina (Cely and Sorrow 1990) and 1.4 in Florida (Meyer and Collopy 1995); 1.0 in Guatemala (Gerhardt et al. 1997). This difference was underscored, though not explained, by differences in prey delivery. In Florida, adult Swallow-tailed Kites adjusted their feeding rates to the demands of larger broods (Meyer and Collopy 1995). In Guatemala, obligate siblicide occurred within the first week after hatching of the second chick (Gerhardt et al. 1997). We did not observe second chicks receiving any food, nor was there evidence of any change in provisioning rates based on number of young in the nest. For Swallow-tailed Kites at Tikal, we believe that prey delivery was not directly associated with prey availability. That is, we have no reason to believe that adults could not procure sufficient food for feeding more than one nestling, at least during the seasons of our study. Among birds, there is a well-documented trend toward smaller clutches and broods in the tropics (Moreau 1944, Lack 1966, Ricklefs 1969); obligate siblicide is the reproductive strategy currently employed by *E. f. yetapa* to achieve an apparently optimal brood size, just as Plumbeous Kites lay only a single egg (Seavy et al. 1998). Explaining this temperate-tropical difference in brood sizes remains a fertile field for theoretical discussion. The ability to adjust feeding rates to accommodate larger broods, as occurs in *E. f. forficatus*, is only one of the adaptations involved in allowing increased reproductive success in more temperate regions.

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