

BEHAVIOR, DIET, AND BREEDING BIOLOGY OF DOUBLE-TOOTHED KITES AT A GUATEMALAN LOWLAND SITE¹

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Abstract. We studied Double-toothed Kites (*Harpagus bidentatus*) in tropical lowland forest at Tikal National Park, Petén, Guatemala, documenting behavior and diet during the incubation and nestling periods. These 200-g kites are *Accipiter*-like in form and strikingly size-dimorphic for a kite. Modal clutch size was two, producing 0.63 fledglings per nesting attempt and 1.25 per successful nest. Nesting was largely synchronous among pairs, with hatching during the first month of the rainy season and fledging one month later. Incubation lasted 42–45 days and nestlings fledged at 29.5 days on average. A radio-tagged fledgling was fed near the nest for 35 days; 6–8 weeks after fledging it dispersed at least 10 km, presumably reaching independence. Males did not incubate or brood, and rarely fed nestlings directly. Males typically provided most but not all prey (mainly lizards) during incubation and early nestling periods. Insects in the nestling diet increased through the nestling period as females increasingly hunted, often bringing in insects. These kites hunted from perches, below and within the closed canopy of tall, mature forest, taking 60.5% insects, 38.1% lizards, and 1.4% other vertebrates; vertebrates comprised at least 75% of prey biomass. Most prey were taken from vegetation, but prey in flight also were captured. Active, adjacent nests averaged 1.35 km apart, for a maximum density estimate of 0.60 pairs km⁻² and a more likely estimate of 0.33–0.50 pairs km⁻² in homogeneous, favorable habitat and 0.29–0.44 pairs km⁻² for Tikal National Park as a whole.

Key words: behavior, breeding biology, diet, Double-toothed Kite, *Harpagus bidentatus*, Neotropical forest, raptor.

INTRODUCTION

The Double-toothed Kite (*Harpagus bidentatus*) inhabits tropical forest and woodland from southern Mexico to Rio de Janeiro, Brazil, and in Trinidad (Brown and Amadon 1968). Morphological similarities to the genus *Accipiter* as well as to other kites and even falconids have led to debate about the phylogenetic position of the Double-toothed Kite (Miller 1937, Amadon 1961, Holdaway 1994). It has been regarded as a “milvine kite” (Brown and Amadon 1968), but recent analyses suggest the milvine kites are polyphyletic and place *Harpagus*—in the case of Holdaway (1994), along with *Ictinia*—quite close to *Buteo*, *Accipiter*, and *Circus* (Kemp and Crowe 1990, Griffiths 1994, Holdaway 1994).

The natural history of the Double-toothed Kite is poorly known. Knowledge of the species’

breeding biology and diet stems mainly from scattered, fortuitous observations. Six nests are mentioned in the literature, but a few observations of adult behavior were made at only two of these (Laughlin 1952, Skutch 1965). These kites are best known through a series of published observations of kites following monkey troops in Central and South American forests. Here we present results from four years of study of the breeding biology, behavior, and diet of *Harpagus bidentatus* at a forested lowland site in northern Central America.

METHODS

STUDY AREA

We studied Double-toothed Kites in Tikal National Park at 17°N in Petén, Guatemala during the breeding seasons of 1992–1996, as part of The Peregrine Fund’s Maya Project. The forest here is tropical semi-deciduous (Pennington and Saruhkan 1968), with mean annual rainfall of 1,350 mm and a pronounced dry season from February to May or June. Forest throughout most of Tikal’s 576 km² area is structurally and floristically mature, despite the occurrence of scattered, low-intensity logging as recently as

¹ Received 5 January 1999. Accepted 13 October 1999.

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the 1960s, and probable regional deforestation ca. 1,000 years ago prior to the Maya collapse. Human-made clearings in the forest are limited to the park center around Mayan ruins and park facilities.

Vegetation of Tikal is described in detail by Schulze and Whitacre (1999). The terrain is gently rolling, 160–400 m in elevation. Mature forest varies in structure and composition from hill-tops to swales. Upland forest on hills and slopes is tall (mean canopy height 25 m), densely-canopied, and has relatively open understory, whereas hillbase and Sabal forest at the foot of slopes is lower (ca. 18 m) with more broken canopy, denser understory, and frequent emergents. A low (ca. 12 m), open-canopied thicket of vines and stunted trees (scrub swamp or “bajo” forest) occupies seasonally-flooded depressions known as “bajos.” Names of forest types used here follow Schulze and Whitacre (1999).

DATA COLLECTION

We studied 11 nesting attempts: 1 each in 1992 and 1993, 5 in 1995, and 4 in 1996. We obtained data on prey delivery rates and diet at six nests. Adult behavior was observed at five nests during the incubation period (one nest in 1993, two each in 1995 and 1996) for a total of 295 hr, and at four nests during the nestling period (two each in 1995 and 1996) for a total of 522 hr. During the nestling phase, observation periods were dawn to dusk except in a few instances of severe weather. During the incubation phase, partial- and full-day observations were employed.

We observed nests from tree-tops, Mayan temples, and in one case the ground, using a 30X spotting scope at 10–30 m. Double-toothed Kites at Tikal are sufficiently dimorphic in size (females larger than males) and coloration (females with more rufous on chest than males) that we distinguished sexes with a high degree of confidence. By comparison with the raptor's bill length, we estimated prey length in mm and rounded resulting statistics to 0.5 cm. Except to verify some clutch sizes and to measure and place radios on juveniles and adults at two 1996 nests, we delayed climbing to and measuring nests until after young had fledged. We used radiotelemetry (via direct pursuit on foot) to document dispersal of two fledglings and spatial use of an adult female. Radio transmitters, mounted as back-packs, were 216 kHz (model no. RI-2C,

Holohil Systems, Carp, Ontario, Canada) and weighed from 4–8.5 g (2.4–3.6% of Double-toothed Kite body weight). In characterizing nests, we used 10 nests as our sample size, as one nest was occupied in two years.

STATISTICAL ANALYSES

We used analysis of variance (ANOVA) and Kruskal-Wallis tests to examine between-nest variation in prey composition, adult behavior patterns, and prey delivery rates, and to document variation in adult activity with time of day and of nesting cycle. ANOVA was used for mean numerical, time, and rate data, and multiple comparisons utilized Tukey's HSD. For proportional data, we used Kruskal-Wallis tests. To analyze time-of-day effects, we divided observations into four time blocks: early morning (05:00–08:59), late morning (09:00–11:59), afternoon (12:00–14:59), and late afternoon (15:00–18:59). For tests involving portion of the nesting cycle, we grouped observations by week from the date of egg-laying or hatching.

To estimate nesting density, we first calculated D , the mean distance between nests believed to be neighbors, using the minimum spanning tree method (Selas 1997), with n nests yielding $n - 1$ internest distances. Using $r = 1/2 D$, within CAMRIS GIS (Ecological Consulting, Inc., Portland, Oregon), we drew a convex polygon enclosing all nests that may have been neighbors, and extending to radius r beyond the outer nests. The area of this polygon was divided by the number of known territories within it to yield mean area per territory. This method underestimates density if undiscovered territories are within the polygon constructed. To set an upper bound on actual densities, we assumed nests are spaced similarly to a close-packed crystal lattice; hence area per nesting pair is given by πr^2 (where r is half the mean internest distance), adjusted by multiplying by 1.158 to account for the associated interstices. In all statistical tests we used a significance level of 0.05. Values reported are means \pm SD.

RESULTS

NESTING PHENOLOGY

Double-toothed Kite nesting took place between early April and late July, spanning the late dry season and early wet season. All study pairs ($n = 8$) initiated nest building in April or May (late dry season) with 8 April the earliest confirmed

TABLE 1. Breeding phenology of Double-toothed Kites at Tikal, Guatemala.

Territory and year	Laying date	Hatching date	Fledging date	No. young fledged
Barens				
1992	26–28 April ^a	8–10 June	na ^b	0
1996	9–10 April	21–22 May	18 June	1
Bajada de la Pina				
1993	14 May	na ^c	na	0
1995	6 May	na ^c	na	0
Parcela de Pajaritos				
1995	25–28 April ^a	7–8 June	na ^b	0
Temple III				
1995	21–22 May	2–3 July	29–31 July	1
1996	5–6 May ^a	17–18 June	19 July	1
Temple IV				
1996	5–6 April ^a	18–19 May ^a	18–19 June	2

^a Estimated based on hatching or fledging dates.

^b Nest failed during nestling phase.

^c Nest failed during incubation phase.

date of nest initiation and 25 May the latest observed date of nest building prior to incubation. Although at one nest incubation began on 9–10 April, at four others incubation began in May and continued to June or early July (Table 1). Incubation lasted 42–45 days at one nest and 42–44 days at another (Table 1). Nestlings hatched early in the wet season, with most hatching taking place between 6 June and 2 July. The nestling period ranged from 27–37 days (31.0 ± 3.9 days, $n = 4$), although three out of four nesting periods were 27–31 days (29.5 ± 1.1 days). Fledging occurred from mid-June to late July (Table 1).

NESTS AND NEST SITES

Nine of 10 nests (10 of 11 nesting efforts) were in areas of tall, closed-canopy, upland forest, and the tenth was in Sabal forest, a relatively tall, broken-canopied forest type occurring just below upland forest on the catena. Nests were built in live trees integral with, rather than emergent above, the canopy. Eight of 10 nests were adjacent to a canopy gap greater than 100 m². Double-toothed Kites nested in a variety of tree species; only three nests were placed in the same species (*Ceiba pentandra*). Four nest trees were dry-season-deciduous, but only one lacked leaves during any part of the nesting period, the first few days of incubation. All nests were at least partly shaded by upper branches of the nest tree. Nests were located in the upper third of

these trees, at heights of 20–27 m, typically in a fork of two or more major limbs (9–25 cm diameter), 0–12 m from the bole. Four of 10 nests were built upon bromeliads. Nests were shallow cups composed of small sticks ca. 1 cm in diameter and 20–40 cm long. Average diameter of four nests was 32 ± 6 cm, and mean external depth 10 ± 1 cm.

NEST SPACING, ALTERNATE SITES, AND REOCCUPANCY

Territory occupancy appeared relatively stable; of five territories active in 1995, courtship activity was observed in four during 1996, and active nests were located in three of these. One territory was known to be active in 1993, 1995, and 1996 (not checked in 1994). Within territories, alternate nest trees were on average 525 m apart ($n = 4$; range = 0–800 m), with one nest occupied in consecutive years. Nests simultaneously active in territories believed contiguous averaged 1.35 ± 0.76 km apart ($n = 3$; range = 0.76–2.20 km), yielding estimates of 1.64–2.80 km² per territory, with the best estimate probably being 2.0–2.65 km² per territory. We also calculated mean internest distance regardless of year; where two nest sites were used within a given territory, we used the mid-point between them. This version yielded a mean internest distance of 1.58 ± 0.67 km ($n = 5$, range = 1.04–2.09 km), and estimates of 2.09–3.13 km² per pair, with the best estimate, we feel, being 2.3–

3.0 km² per pair. Hence, our best estimates all fell within the range 2.0–3.0 km² per pair. Assuming a closed-packed nest arrangement, the maximum density consistent with the mean innermost distances we observed is one pair per 1.66 km².

CLUTCH SIZE

Seven nests at Tikal contained two 1-egg and five 2-egg clutches. At an eighth nest, behavior of the female indicated the presence of more than one egg; we assume this was a 2-egg clutch. The 1-egg clutches were laid in consecutive years in the same nest. The modal clutch at Tikal was 2 and the mean clutch 1.75 ($n = 8$).

REPRODUCTIVE SUCCESS

Four of 11 nesting attempts (36.4%) fledged young (Table 1). Of 14 eggs laid in eight nests, 10 hatched and 5 produced a fledgling; hence 36% of eggs resulted in fledglings. Productivity was 0.63 fledglings per nesting attempt and 1.25 fledglings per successful nest (Table 1). Three nests were abandoned during construction (two in the same territory in consecutive years) with no evidence of re-nesting. Of eight nests receiving eggs, two failed during incubation and two with nestlings. In addition, at one 1996 nest, one nestling was killed and carried off by an unidentified raptor 7–10 days prior to fledging and the other was discovered dead, with a head wound, 7 days after fledging. One nest fledged two nestlings; three other nests fledged one young each.

BEHAVIOR OF ADULTS

Pre-laying and nest-building period. Females conducted most nest-building, although males participated on several occasions. Typically there was a flurry of nest-building activity in early to mid-morning, prior to break-up of the chronic morning fog and onset of display flights. Males regularly brought prey (always lizards) to females in the nest vicinity during early to mid-morning. Arriving with prey in their talons, males typically landed in a tree 10–20 m from the nest, emitting a series of single-note chirping calls. Usually voicing a two-note *Cheee-weet* vocalization, the female would fly to the perched male, where the prey exchange would take place. On one occasion the Temple III male mounted and presumably copulated with the fe-

male while she ate a lizard he had brought her. Often no activity was observed around the nests from late morning until late afternoon, when activity occasionally resumed.

Double-toothed Kites frequently soared high over the forest in pairs, maintaining a distance of less than 20 m between the two. We observed no contact between soaring birds. The aerial display has been described as similar to that of an *Accipiter*; males made repeated short swoops or stoops which were interrupted periodically by rapid flapping to regain altitude. We frequently observed a soaring individual or pair to stoop from a height of >300 m down into the forest canopy. On two such occasions, the point of entry into the canopy was within 100 m of a nest under construction. The peak of aerial display activity occurred in mid- to late morning during April and May, prior to and during the nest construction phase; at such times, several pairs could often be observed from a single vantage point. After this time, we continued to observe soaring individuals but stooping activity was much reduced. To date, we have not observed Double-toothed Kites soaring over the canopy in the nonbreeding season.

Incubation phase. At all five nests we observed during the incubation phase, only females were seen to incubate. On average, females were on the nest $85.3 \pm 14.1\%$ of the observation period ($n = 38$ observation periods), either in incubation position or standing in the nest (standing included rolling and shading the eggs, preening, and stretching). This ratio was consistent between nests (range = 73.9–93.9%). In addition, the female was visible and within 40 m of the nest on average $10.7 \pm 11.1\%$ of the observation time. Only rarely was the female out of view ($4.1 \pm 9.0\%$ of observation time), and in many of these instances we lost contact as the female dropped into the canopy relatively near the nest tree; thus females often were near the nest. We did not see any change in female activity patterns as the incubation phase progressed ($P > 0.5$ in Kruskal-Wallis tests by week of incubation period for five females).

Incubation bouts at five nests averaged 42 ± 29 min ($n = 38$ observation periods), and were longer on average in the early morning and late afternoon than at mid-day (ANOVA, $F_{3,276} = 27.79$, $P < 0.001$; Tukey's HSD, early morning > late morning and early afternoon; late afternoon > late morning). The percent of total ob-

servation time that birds spent incubating also was greatest in early morning and late afternoon ($H_3 = 8.0$, $P < 0.05$, means = 87, 59, 66, 77%, respectively, for periods as above). Standing bouts, averaging 21 ± 52 min ($n = 38$ observation periods), were half as long as incubation bouts, and standing was marginally more frequent at mid-day, when shading became a dominant activity, than in the morning and late afternoon ($H_3 = 6.6$, $P = 0.09$). At one nest, standing/shading behavior accounted for 90% of total observation time during the heat of the day (10:00–14:00).

The ratio of time females spent incubating to time standing on the nest (shading) varied greatly between nests, from 12:1 to 1.1:1, averaging 4.8:1. Variation in this behavior was best explained by the degree of canopy cover above each nest. In the four nests with high ratios of incubation to shading, the nest was relatively protected by higher branches of the nest tree, probably resulting in cool temperatures for longer periods of the day, while the nest with more shading relative to incubation received more sun due to a more exposed location. Females were rarely out of sight of the nest during early morning, mid-day, and late afternoon, the times when temperatures presumably can reach dangerous extremes for unprotected eggs. Unlike several other accipitrid hawks studied at Tikal, we did not observe these kites to bring green sprigs of foliage to the nest at any time.

Males were rarely seen in the nest vicinity during the incubation period except during infrequent prey deliveries, which were generally of large items (61% lizards). During the incubation period, males delivered on average 2.3 ± 0.7 prey items day^{-1} ($n = 5$ nests), but this varied between nests from a high of 1 item 4.4-hr^{-1} of observation to slightly more than 1 item day^{-1} (1 item 9-hr^{-1}). Prey exchanges were like those described for the nest-building period. Receiving prey 10–20 m from the nest, females usually consumed it before returning to the nest, although on several occasions, particularly in the case of lizards, the female brought the prey item to within a few meters of the nest before eating it.

Of 48 prey items recorded at nests during the incubation period, 40 were delivered by males and 8 were apparently captured by females during incubation breaks. We regularly observed females leaving the nest on what appeared to be

foraging excursions. Although it is possible females sometimes retrieved prey cached by the male nearby, in several cases we witnessed females launch attacks from the nest. Hence males supplied the majority but not all of the food for incubating females.

Nestling phase. After nestlings hatched, adult females spent progressively less time on the nest as they increased time spent hunting (Kruskal-Wallis test by week after hatching, $H_3 = 20.2$, $P < 0.001$, $n = 40$ observations; median for week 1 = 71.2%, for week 4 = 15.7%). Overall during the nestling phase, females were on the nest for an average of only $34.5 \pm 23.6\%$ of the total observation time ($n = 40$ observation days). Only $24.2 \pm 18.3\%$ of the time on the nest was spent in a brooding position, with the remainder spent standing on the nest (including shading or feeding nestlings, preening, and stretching). Brooding was the dominant female behavior in the early morning and late afternoon throughout the nestling phase (Kruskal-Wallis test by time of day, $H_3 = 11.4$, $P = 0.01$; early morning and late afternoon > late morning and early afternoon), and individual brooding bouts were longer on average during these times of day than at midday ($F_{3,12} = 6.6$, $P < 0.01$; Tukey's HSD: early morning > late morning). After the nestlings were more than 7 days old, brooding by females was largely restricted to early morning (05:00–08:00), late afternoon beginning 16:00–18:00, and hours of darkness. Exceptions to this pattern occurred mainly on rainy days, when females covered nestlings in a brooding posture.

Female activity patterns varied considerably among nests. At one nest (Pajaritos) the female spent substantially more time out of sight and/or away from the nest vicinity (mean = 61%, $n = 10$ observation days) than did females at other nests: mean = 22 ($n = 8$), 40 ($n = 9$), and 32% ($n = 13$). At all nests except this one, males provided the majority of prey during the nestling phase. Whereas at other nests females were observed hunting only sporadically and captured an estimated 13–35% of the prey items fed to nestlings, at the Pajaritos nest, the female consistently hunted in the nest vicinity, and captured at least 70% of the prey items delivered to the nest. On only eight occasions (1.4% of total deliveries) did males feed chicks directly. In all other cases, males delivered prey to the female, who then fed the nestlings. As during the incu-

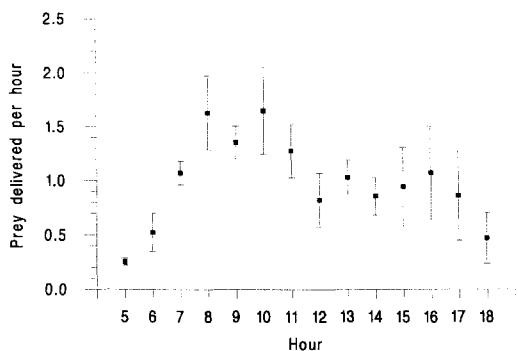


FIGURE 1. Diel pattern of prey deliveries (mean \pm SE) at four Double-toothed Kite nests at Tikal, Guatemala. 5 = 05:00–06:00, etc.

bation period, prey transfers usually took place at least 10 m from the nest tree. Prior to all observed prey exchanges, the female emitted a two-note call; we sometimes heard males vocalizing as well.

Adults fed insect prey to nestlings in small pieces torn off with the bill as the adult held the prey against a branch with its foot. Most lizards were fed whole to nestlings, following removal of the head. However, several observations of adults feeding larger lizards, birds, bats, rats, and a snake to young in pieces, showed that these birds were capable of tearing apart vertebrate prey.

Overall, a mean of one prey item was delivered per hour of observation during the nestling phase. At the two nests observed in 1995, prey delivery rates during the nestling phase followed a strongly bimodal pattern throughout the day, the largest peak in deliveries occurring in the mid- to late morning (08:00 to 11:00, mean = 1.6 hr⁻¹, $n = 40$ observation days), with a second peak in the afternoon between 15:00 and 17:00 (mean = 1.4 hr⁻¹). In 1996, prey delivery rates peaked from mid-morning through early afternoon, decreasing in late afternoon. Overall, delivery rates in late morning were higher than at any other time, and significantly higher than late afternoon ($F_{3,155} = 3.2$, $P = 0.02$; Tukey's HSD mid-morning > late afternoon; Fig. 1).

The mean number of prey deliveries per day varied considerably between nests, and was correlated with two factors: the number of chicks in the nest and percent of total prey contributed by lizards and other vertebrates. The mean prey delivery rate for four nests during the nestling phase was 13.6 items day⁻¹. The Pajaritos pair,

with two chicks, averaged nearly twice this number of prey deliveries (24.3 \pm 5.8, range = 22–31, $n = 10$ observation days), a significantly higher delivery rate than recorded at any other nest ($F_{3,36} = 125.1$, $P < 0.001$; Tukey's HSD: nest 1 > nests 2, 3, and 4). However, when rates were adjusted for the number of chicks in the nest, only one nest had a significantly lower delivery rate per chick than that recorded for the Pajaritos nest ($F_{3,36} = 12.2$, $P < 0.05$; Tukey's HSD: nest 1 > nest 3; nest means ranged from 7.8–12.1 feedings chick⁻¹ day⁻¹). Daily prey delivery rates across all four nests showed a non-significant increase from week 1 to week 4 of the nestling phase ($F_{3,36} = 4.7$, $P = 0.16$; range = 7.4 deliveries chick⁻¹ in week 1 to 11.1 chick⁻¹ in week 4).

Nests differed in both the number of vertebrate prey items delivered per day ($F_{3,36} = 39.5$, $P = 0.007$; range = 2.4–5.4 nestling⁻¹ day⁻¹), and in the proportion of total prey accounted for by vertebrates ($H_3 = 13.7$, $P = 0.003$, based on 40 observations days), with the Pajaritos chicks receiving the fewest vertebrates per day. Across nests, vertebrate prey items were less important at the end of the nestling phase than at the beginning, both in terms of the number delivered per day ($F_{3,36} = 17.4$, $P = 0.02$; Tukey's HSD: week 1 > week 4), and percent of total items brought to nests ($H_3 = 14.2$, $P = 0.003$).

NESTLING DEVELOPMENT AND BEHAVIOR

Upon hatching, chicks were covered in white down, with dark eyes and bill, and yellowish cere and legs. By day 10, nestlings had wing feathers in pin but no body or tail feathers visible. By 12 days, eyes had begun to lighten to a dark yellow-orange. By day 16, chicks were estimated to be 1/2 the size of the attending female, wing feathers were 1/4 to 1/3 grown, tail feathers were emerging from feather tubes, and some body feathers had emerged on the back, forming a V-shaped pattern. After 23 days, chicks were typically full-sized or nearly so, fully plumed on the body except the head and part of breast, with flight feathers nearly or fully grown. Less developed birds at this age had flight feathers about half grown, and only sparse feathering dorsally and ventrally. At fledging, chicks appeared fully feathered.

Initially chicks were quiet at the nest, and spent most of the day prostrate. Within a week of hatching, chicks became more active, stand-

TABLE 2. Frequency (%) of prey items delivered to four Double-toothed Kite nests (nestling phase only) at three territories in Tikal National Park, Guatemala. Percentages based on identified prey items.

	Parcela de Pajaritos	Temple 3		Barens	Total
	1995	1995	1996	1996	
Homoptera	149 (70.6)	28 (44.4)	24 (23.8)	26 (29.6)	227 (49.0)
Coleoptera	2 (1.0)	0 (0.0)	2 (2.0)	0 (0.0)	4 (0.9)
Orthoptera	4 (1.9)	4 (6.4)	2 (2.0)	4 (4.6)	14 (3.0)
Lepidoptera	0 (0.0)	0 (0.0)	0 (0.0)	1 (1.1)	1 (0.2)
Hymenoptera	1 (0.5)	0 (0.0)	0 (0.0)	0 (0.00)	1 (0.2)
Unidentified insects	15 (7.1)	2 (3.2)	3 (3.0)	7 (8.0)	27 (5.8)
Total insects	171 (81.0)	34 (54.0)	31 (31.0)	38 (43.2)	274 (59.2)
Lizards	39 (18.5)	27 (42.9)	69 (68.3)	50 (56.8)	185 (40.0)
Snakes	1 (0.5)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.2)
Bats	0 (0.00)	1 (1.6)	0 (0.0)	0 (0.0)	1 (0.2)
Birds	0 (0.00)	1 (1.6)	0 (0.0)	0 (0.0)	1 (0.2)
Rats (Rodentia)	0 (0.00)	0 (0.00)	1 (1.0)	0 (0.0)	1 (0.2)
Total vertebrates	40 (19.0)	29 (46.0)	70 (69.3)	50 (56.8)	189 (40.8)
Unidentified prey	1	20	27	6	54
Total identified prey	211	63	101	88	463
Total prey	212	83	128	94	517

ing and stretching periodically. At this time we also began hearing more frequent vocalizations from the chicks, primarily soft begging calls upon the arrival of an adult at the nest. At one of the two-nestling nests we noticed a very uneven distribution of food items, with the larger of the two chicks consuming 38% more prey than the smaller, including 28 of 39 lizards. This chick was not observed attacking the smaller one, but aggressively pursued prey morsels, often obtaining bits that initially appeared destined for the second chick's crop. At other nests with two chicks we observed much less dominance of one nestling over the other.

Within 5–7 days prior to fledging, chicks began to leave the nest cup to clamber on supporting limbs. Chicks often flapped while perched on the nest, and several days prior to fledging began making short hop-flights from branch to branch. Occasionally, after a long hiatus in prey deliveries, chicks began vocalizing, but in general, begging calls appeared to be instigated by visual contact with, or a vocal cue from, an approaching adult, usually the female.

DIET AND HUNTING BEHAVIOR

Although Table 2 presents only those prey observed during the nestling phase at four nests, overall we recorded 622 prey items (of which 550 were identified) during observations at seven nests from courtship through the nestling phase, and including a few observations during

nest-searching and radio-tracking. Insects and lizards comprised 99% of identified prey items, but more than 15 taxa were recorded, and variation in prey composition between nests and years was considerable. Taking all kite pairs together, insects comprised 53% of the prey items (60.6% of identified prey) and lizards 34% (38% of identified prey), with bats, birds, rats, and snakes all recorded but together comprising only 1.4% of identified prey. The majority of identified lizards were arboreal *Anolis* spp., with geckos (Gekkonidae), four *Corytophanes* spp. (Iguanidae; also arboreal), and a skink (Scincidae) also recorded. Cicadas (Homoptera: Cicadidae) and Orthopterans (mainly grasshoppers and katydids) constituted the majority of insect prey—81.7 and 8.7%, respectively. Other insects taken were beetles (Coleoptera), caterpillars (Lepidoptera), cockroaches (Blattidae), and wasps (Hymenoptera). In general, it was more difficult to identify insect than vertebrate prey items, and we suspect that most unidentified items were insects.

Considering the diet in terms of biomass substantially increases the importance of lizards and other vertebrates. Insect prey averaged 4 ± 1 cm in length ($n = 333$, range = 1.5–9.5 cm), with an estimated weight of 1–3 g. Most lizards were small, with 76.7% of 211 lizards estimated at <10 g, whereas lizards estimated at 10–15 g accounted for 18.6% of lizard prey. However, lizards with estimated weights up to 30 g were re-

corded, and lizards >15 g comprised 4.6% of the 211 lizards. Hence, a conservative estimate is that vertebrate prey items were on average five times the mass of insect prey items. Based on this estimate, vertebrate prey items accounted for at least 3/4 of the total prey biomass.

Different nests within the same season showed significant differences in prey composition, especially during the nestling phase (Table 2). In 1995, at the Pajaritos nest, insects comprised 81.0% of identified prey items, whereas at the Temple III nest insects (54.0%) were only marginally more frequent than lizards (42.9%). The Temple III pair took far fewer cicadas than did the Pajaritos pair, despite a high degree of temporal overlap between these two nesting efforts. At the two 1996 nests, insects formed less than half the identified prey items (43.2 and 31%), whereas lizards accounted for the majority (56.8 and 68.3%) of identified prey and at least 85% of prey biomass.

Although combined data from 1995 and 1996 showed no correlation between time of day and the type of prey delivered to nests, 1995 data showed a strong diel pattern in prey composition. In the early morning (06:00–09:00), kites brought in many cicadas (accounting for 94% of prey deliveries at one nest), with the importance of this resource declining through the mid-day hours and increasing again in late afternoon. Conversely, lizards were more common as prey during the hot, late-morning and early-afternoon hours. Other insects and non-lizard vertebrates showed no apparent correlation with time of day.

We observed 51 hunts, all initiated from a perch; 45% were level, or nearly level, powered flights at flying quarry or culminating in contact with vegetation, 49% were hard glides or swoops at steep angles (25–45°) downward from a perch to snatch prey from the air or vegetation with a quick turn, and 6% were fluttering “parachute” drops straight down to the surface of a lower tree crown. Parachuting flights were at times an obvious, direct attack on prey, and at other times preceded active visual scanning for prey from sub-canopy perches. Attempts at quarry perched on vegetation were twice as common (63%) as those at quarry in flight (31%).

No significant differences were detected in success rates between hunting methods. Overall hunting success was 73%. However, this figure

may be artificially high, as we could only record those hunts occurring within view of our observation platforms, and most of these were attempts on insect prey. We did, however, witness four captures of lizards, using both straight, powered flight to the vegetation surface and hard swoops culminating in a crash into a tree crown. We also frequently observed individuals on extended, erratic flights through tree crowns—apparent hunting attempts on quarry unseen by us.

INTERSPECIFIC INTERACTIONS

Double-toothed Kites aggressively defended their nests from Brown Jays (*Cyanocorax morio*), Keel-billed Toucans (*Ramphastos sulfuratus*), Collared Aracaris (*Pteroglossus torquatus*), Pale-billed Woodpeckers (*Campephilus guatemalensis*), Roadside Hawks (*Buteo magnirostris*), spider monkeys (*Ateles geoffroyi*), a Montezuma's Oropendola (*Psarocolius montezuma*), and a Crane Hawk (*Geranospiza caerulescens*). They swooped on intruders, calling aggressively and occasionally making contact, and tail-chased fleeing interlopers. At one nest, the female was repeatedly harassed by Brown Jays and even driven from the nest in what may have been an attempt at nest predation. This interference with the female's shading activities may have been lethal to the eggs, which never hatched at this, the most exposed of 11 nests. At several nests, Keel-billed Toucans repeatedly harassed female kites and we consider it likely this species takes Double-toothed Kite eggs on occasion, as Laughlin (1952) observed for Swainson's Toucan (*Ramphastos swainsonii*) in Panama. We often observed subdued defensive behavior by incubating or brooding females when vultures or raptors soared near the nest. The females' typical response was mantling and fluffing of the feathers while standing over the nest; only occasionally did the female vocalize. We never observed Double-toothed Kites pursuing soaring raptors.

AGONISTIC BEHAVIOR

We observed only one obviously aggressive encounter between conspecifics in the vicinity of a nest. On one occasion an immature Double-toothed Kite landed within 3 m of a nest, and was rapidly driven off by the returning female. In a second event at the same nest, a nestling was killed and carried off by another raptor, probably a conspecific. Soaring individuals fre-

quently appeared to follow, or on a few occasions, to actively pursue conspecifics soaring in the vicinity. These encounters resembled ritualized displays more than outright attacks, and were similar to those of Plumbeous Kites (*Ictinia plumbea*) in Tikal (Seavy et al. 1998).

ADULT MOVEMENT PATTERNS AND JUVENILE DISPERSAL

We radio-tracked one adult female regularly from 21 July to 18 September 1996, beginning one week after a fledgling left the nest. In 15 independent sightings, the female was within an area of 2 km², ranging from 150 m to 2 km from the nest tree. The female was found in a 75° wedge to the north of the nest on all but one occasion, when she was located 500 m to the southeast. In 80% of detections the female was in upland forest, with only one detection (6%) in lowland scrub swamp forest (remaining detections were in transitional forest types).

One of two juveniles outfitted with radio transmitters was found dead with a head wound within a week of fledging, still in the immediate nest vicinity. The other juvenile remained within 250 m of the nest for 35 days. During this period we observed the adults feeding the fledgling. On 30 July, 41–42 days after fledging, the juvenile had moved >2 km from the nest site. Over the next two weeks we repeatedly detected the juvenile roughly 4–8 km northeast of the nest. The last detection, 52–53 days after fledging, was at ca. 6–8 km northeast of the nest. Repeated telemetry efforts thereafter suggested the fledgling had moved yet farther from its natal nest.

DISCUSSION

As nesting habitat, Double-toothed Kites displayed a preference for tall, dense-canopied, open-understoried upland forests relative to the lower, broken-canopied, densely-understoried lowland or scrub swamp forest types occurring at Tikal. None of 11 nests were in lowland forest despite the fact that this forest type covered ca. 20% of the area we intensively searched for nests. Hence, Double-toothed Kites do not fit the pattern documented for a number of raptor species at Tikal: preferential selection of transitional and lowland forest for nesting sites (Madrid et al. 1992, Panasci 1995). Raptors that commonly nest in lowland habitats at Tikal are those that nest in canopy-emergent trees, which are relatively abundant in lowland forest types due to

the characteristically low or broken canopy structure in these areas. Emergent trees are thought to provide a measure of safety from climbing nest predators.

Given that Double-toothed Kites nested in trees integral with the forest canopy, proximity to favorable foraging habitat presumably was a more important criterion in nest-site selection than was the abundance of emergent trees; that females often hunted near the nest, with prey obtained in the immediate vicinity contributing importantly to the provisioning of nestlings, supports this hypothesis. Double-toothed Kites also may reduce the risk of nest predation through nest-site selection. For species nesting within the canopy, upland forest may provide safer nest sites than does lowland forest, as vine densities are considerably lower in upland than lowland forest, resulting in fewer travel routes for climbing predators. All nest trees were relatively vine-free, and seven bordered on a canopy gap. Nests were situated such that overhead foliage provided camouflage and partial protection from the elements, factors that likely facilitated females leaving the nest to hunt.

The affinity for upland forest displayed by Double-toothed Kites was not limited to nest placement. An adult female we studied via radio telemetry was detected mainly in such forest, and rarely in the shorter, more open-canopied forest types. Moreover, we observed soaring Double-toothed Kites descending into upland forest on dozens of occasions, but never into a lowland forest stand (these forest types were easily distinguished from our observation points). Whitacre et al. (1990) also found these kites were significantly associated with structural variables indicative of tall, closed-canopy, upland forest at Tikal. The basis for this apparent preference of hunting habitat is unknown. Upland and lowland forest types at Tikal differ in terms of vegetation structure, flora, and avifauna (Schulze and Whitacre 1999, Whitacre et al., unpubl. data), and the butterfly community (N. Haddad and C. Méndez, pers. comm.); we do not know whether they differ in abundance of the small lizards and large insects on which these kites mainly fed.

There are many allusions in the literature to the frequent presence in, or even preference of Double-toothed Kites for forest edge or second-growth habitats (e.g., Slud 1964, Skutch 1965). The perception that these kites favor such hab-

itat may be largely an artifact of the ease of observing them there. In contrast, published accounts of Double-toothed Kites engaged in foraging are predominantly of individuals in the forest interior (Laughlin 1952, Skutch 1965). Although these kites no doubt use forest edge and other somewhat open habitat at times, we saw no indication that our study pairs sought out such habitat. Indeed, such habitat was not available to our study pairs, except in the form of natural tree-fall gaps.

Timing of nesting was relatively synchronous among nests, with eggs at five of six nests hatching less than two weeks prior to, or soon after, the onset of the wet season, a period of high insect abundance at Tikal (Whitacre et al., unpubl. data), and in Central American forests in general (Wolda 1982). The proportion of insects in the nestling diet increased as the nestling period progressed. We speculate that such timing of nesting serves to take advantage of high insect abundance early in the wet season, thereby increasing hunting efficiency of adult kites at a time when energy demands are highest. Such timing conforms with a pattern prevalent among insectivorous birds in Central America (Skutch 1950).

Double-toothed Kites in Tikal laid one or two eggs. The only other report of a 1-egg clutch is by Laughlin (1952) in Panama; however, that nest failed at the onset of incubation and the clutch may not have been complete. Skutch (1965) observed a nest in Costa Rica with two nestlings. Although Euler (1900) gave the clutch size in Brazil as three or four eggs, the only actual record of a clutch larger than two eggs that has come to our attention is a 3-egg clutch from Trinidad (Western Foundation for Vertebrate Zoology, #16,323). Thus clutch size apparently ranges from one to two or three eggs.

During incubation and nestling periods, the role of males was limited to prey acquisition. Males rarely fed nestlings, and were never seen to incubate or brood. However, neither were males the sole providers. During incubation, females only rarely were observed hunting, but regularly left the nest for several minutes to half an hour, possibly to hunt. During the nestling phase, females hunted more consistently, particularly after chicks were more than a week old. Such a pattern is common in raptors, but the fact that the female at one nest provided the majority of prey during the nestling period is noteworthy.

Because males did not incubate or brood, Double-toothed Kites depart from the commonest pattern among raptors, in which males relieve the female periodically from incubation duty; they also depart from the pattern exemplified by Plumbeous and Swallow-tailed (*Elanoides forficatus*) Kites, some small insectivorous falcons, and vultures, in which pair members share incubation duties relatively equally and meet their own food demands throughout the nesting cycle (Seavy et al. 1998). These kites conformed more closely to the accipiter/harrier pattern, in which males provide most food for the female and young nestlings, and commonly play no role in incubation and feeding young (Newton 1979). Skutch (1965), in 12 hr of observation at a Double-toothed Kite nest in Costa Rica, observed both adults brooding and feeding nestlings; it is unknown whether parental duties are more evenly shared between the sexes in that portion of the species' range.

Double-toothed Kites took larger prey relative to their body size than did Plumbeous and Swallow-tailed Kites (Gerhardt et al. 1991, Seavy et al. 1997), which may make it more energetically efficient for one *Harpagus* adult to provision the nest than is the case in the latter two species. The regularity with which Double-toothed Kite females obtained insect prey in the nest vicinity appeared to allow females to combine nest-care with limited hunting activity, a compromise that would not be possible for a raptor specializing in larger vertebrates or other prey types requiring extended foraging excursions.

Males delivered mostly lizards rather than insects to the nest, especially early in the nesting cycle, suggesting that it was energetically more efficient for these kites to provision the nest with lizards than with insects. Males were not observed hunting near nests, and probably brought prey from some distance, emphasizing the energetic advantage of delivering few, large items rather than many small ones. That females delivered proportionally more insects than did males need not indicate that they used different foraging "rules;" females tending nests are under different time constraints than are males, likely causing them to remain nearer the nest and quickly catch whatever they can. At the one nest where the adult female provided most of the food for the nestlings, she fed them mainly on insects, especially cicadas she captured nearby, between bouts of brooding and shading the nest-

lings. At all other nests, males brought most prey, and lizards comprised a majority of prey biomass. Adults fed the young increasingly on insects toward the end of the nestling period, when large-insect abundance increased dramatically early in the rainy season, and when both adults spent much of their time foraging.

Reports of Double-toothed Kite hunting behavior in other tropical areas are consistent with our conclusion that this species is primarily a perch hunter, but add three additional hunting methods: (1) pursuing lizards along branches by hopping with outstretched wings (Laughlin 1952, Wetmore 1965), (2) taking bats on the wing near a presumed roost site (A. Baker, unpubl. data), and (3) attending troops of capuchin (*Cebus capucinus*), squirrel (*Saimiri sciureus* and *S. oerstedii*), and tamarin (*Saguinus mystax* and *S. fuscicollis*) monkeys, opportunistically capturing prey flushed by the primates (e.g., Fontaine 1980, Boinski and Scott 1988, Heymann 1992).

The primate species most regularly followed by kites in these studies were small species that include a fair number of invertebrates in their diet and that travel extensively, traits that make them effective at flushing quarry for the kites (Fontaine 1980). The only primates occurring at Tikal are the Mexican black howler monkey (*Alouatta pigra*) and Central American spider monkey (*Ateles geoffroyi*), which are inactive for long periods of the day and eat few insects; in the studies cited above, monkeys of these genera were only occasionally followed by Double-toothed Kites (Fontaine 1980). Boinski and Scott (1988) also noted a seasonal component to Double-toothed Kite monkey-following behavior in Costa Rica, with twice the frequency of *Harpagus* sightings around squirrel monkeys during the peak of the wet season (a period of low insect abundance), than in more bountiful times of year. In Tikal we have not observed Double-toothed kites hunting in association with monkeys, a result probably attributable to two factors: (1) the absence of highly active, partially insectivorous monkey species, and (2) our observations have been mostly during the late dry and early wet season, when insect prey is abundant and kites are nesting. We suspect that monkey-following behavior is not a commonly used foraging technique of Double-toothed Kites in our study area.

One radio-tagged kite dispersed >10 km from

its natal site 6–8 weeks after fledging, and we tentatively conclude that young typically reach independence within two months or so after fledging, unlike several larger raptor species at Tikal that show protracted (year-long) post-fledging dependency. Nor was there evidence that Double-toothed Kite pairs skipped a year between nesting efforts as do several species with prolonged dependency periods at Tikal. However, observations of multiple adult kites attending squirrel monkey troops sometimes accompanied by a juvenile (Boinski and Scott 1988), and that juveniles attending monkeys were normally accompanied by one or more adults (Fontaine 1980), suggest that juvenile kites and parents may at times associate for a longer period than suggested by our radio-tagged fledgling.

The breeding biology and hunting behavior of Double-toothed Kites differed markedly from those of two other kites studied at Tikal—the Plumbeous Kite and Swallow-tailed Kite. These three kites all fed nestlings mainly large insects and small lizards; however, their diets also differed importantly. Whereas the nestling diet of Double-toothed Kites was 59% insects, 40% lizards, and 1% other vertebrates, that of the Plumbeous Kite was 93% insects, 5% lizards, and 2% other vertebrates (Seavy et al. 1997). Among the insect portion, *Harpagus* used cicadas more heavily than did *Ictinia*, which preyed more heavily on beetles, dragonflies, and Lepidoptera than did *Harpagus*. The nestling diet of Swallow-tailed Kites at Tikal, based on 1,350 identified prey items, resembled that of *Harpagus* in terms of percent insects (69.0%) and lizards (11%), but these highly aerial kites also took many nestling birds (20%; Gerhardt et al. 1991). Swallow-tailed Kites, like Plumbeous Kites, took a wider variety of insects than did *Harpagus*, especially beetles, wasps, and locusts (Orthoptera), with dragonflies, butterflies, cicadas, and others figuring less prominently.

Hunting behavior of the three kite species differed considerably. Double-toothed Kites hunted mainly from perches within the forest, taking prey from canopy, sub-canopy, and occasionally ground level, whereas the other two kites snatched prey from the upper canopy surface and the air above. Part of the observed difference in diet is linked to differences in hunting methods. For example, no dragonflies were taken by *Harpagus* in our study, because these rap-

tors did not forage in open airspace. Vertical stratification of hunting may provide a degree of resource partitioning among these kite species, to the extent that insect and lizard prey below the canopy and those in the upper canopy and air above represent different populations. Overlap of Double-toothed Kite diets with that of Barred Forest-Falcons (*Micrastur ruficollis*) also is potentially significant, because these forest-falcons also hunt below the canopy, with their diet biomass at Tikal comprised of 37% lizards, including many *Anolis* (Thorstrom et al. 1992).

These three kites differed also in timing of nesting. On average, Double-toothed Kites at Tikal laid eggs six weeks later than did Plumbeous and Swallow-tailed Kites (Gerhardt et al. 1991, Seavy et al. 1998), and most Plumbeous and Swallow-tailed Kite nestlings fledged by the time Double-toothed Kites hatched or soon thereafter. Whether this phenological difference is related to seasonal abundance patterns of the partly different prey of these kite species, and whether such a difference holds true elsewhere in their large zone of sympatry, would be interesting to know. Although this pattern may result from chance, it also could result from natural selection to minimize simultaneous reliance on prey resources used in common.

Finally, these kite species also differed in the relative length of incubation and nestling periods. Incubation in *Harpagus* (42–45 days) was at least 10 days longer than in *Ictinia* (32–33 days) and *Elanoides* at Tikal (31.5 days; Gerhardt et al. 1991, Seavy et al. 1998). In contrast, duration of the nestling period in *Harpagus* (27–31 days) was shorter than in *Ictinia* (38.5 days) and *Elanoides* (52.3 days at Tikal, two weeks longer than in U.S. populations). Hence, time from laying to fledging of *Harpagus* (70–75 days) was similar to that of *Ictinia* at Tikal (70–72 days), whereas the equivalent figure for *Elanoides* at Tikal was substantially greater: ca. 83–84 days.

Internest distances for Double-toothed Kites in Tikal (1.3 km) were substantially greater than for Swallow-tailed Kites (as little as 35 m at times) and Plumbeous Kites (500 m; Seavy et al. 1998). Moreover, nests of Double-toothed Kites were distributed evenly within areas of tall, closed-canopy forest. In contrast, Swallow-tailed Kites nested in colonies, often on hilltops or other situations creating high availability of emergent trees, leaving large areas of forest with

few or no nests. Plumbeous Kite nests, although evenly spaced within local areas, appeared to occur in loose neighborhoods and were often associated with human-made or other forest clearings. The more homogeneous spacing of Double-toothed Kite nests may be facilitated by these kites' use of nest trees within the forest canopy, rather than in intrinsically less abundant emergent trees in association with clearings or other special landscape features. In addition, the prey-base of Double-toothed Kites may be more homogeneously distributed and perhaps more defensible than that of *Ictinia* or *Elanoides*, whose diets included some prey types that are temporally and spatially irregular in occurrence (Gerhardt et al. 1991, Seavy et al. 1997). Despite the closer spacing of *Ictinia* and *Elanoides* nests within local areas, we expect that in Tikal as a whole, *Harpagus* nesting densities are substantially higher than those of these other kites.

Using our density estimate of 0.33–0.5 territories km⁻² for the Double-toothed Kite, and assuming these kites do not nest in the scrub swamp forest types comprising at least 11.5% of the park's total 576 km² area, we estimate the remaining 510 km² of the park may support as many as 168–255 pairs of Double-toothed Kites, or 300 pairs if our maximum density estimate is attained. This is the third or fourth greatest density of any forest raptor studied in Tikal, behind the ubiquitous Mottled Owl (*Ciccaba virgata*; 3.5–4.4 pairs km⁻²; Gerhardt et al. 1994) and Barred Forest Falcon (*Micrastur ruficollis*; 1 pair km⁻²; Thorstrom et al. 1992); Vermiculated Screech-Owl (*Otus guatemalae*) densities were not ascertained and may rival those of this kite. Our density estimate for Double-toothed Kites at Tikal is much higher than the 1 pair per 14-km² estimated by Thiollay (1989) for a site in French Guiana.

These kites are *Accipiter*-like in shape but with wings relatively longer and more tapered than in *Accipiter*. Using Bierregaard's (1978) data, the ratio of wing to tail length for the Double-toothed Kite is 1.43—the same as in the American Kestrel (*Falco sparverius*; 1.42), less than in all or most North American buteos (1.55–1.88), Plumbeous Kite (2.04), and White-tailed Kite (*Elanus leucurus*; 1.73), and greater than in the three North American *Accipiters* (1.16–1.32; based on data in Palmer 1988). The magnitude of this ratio in the Double-toothed Kite appears to reflect adaptation to its largely

sub-canopy lifestyle, but not to the degree typical of *Accipiter*.

In addition to possessing somewhat *Accipiter*-like flight morphology, Double-toothed Kites are strikingly size-dimorphic for a kite. For *H. bidentatus fasciatus*, the race occurring at Tikal, Brown and Amadon (1968) gave male weights as 175–198 g (median = 187 g) and female weights as 190–229 g (median = 210 g). Hence these females weighed 12% more than males; using cube root of body weight, this yields a dimorphism index (Storer 1966) of 3.9%. For the South American *H. b. bidentatus*, Haverschmidt and Mees (1994) gave the mean weight as 167.5 g for males ($n = 11$) and 201.5 g for females ($n = 5$), for a (cube root) body weight dimorphism of 6.2%. The latter value, based on a known sample size, is probably more reliable than that based on Brown and Amadon's (1968) sample. For seven males and six females, Bierregaard (1978) calculated the following dimorphism indices: wing 9.8%, tail 8.7%, tarsus 6.5%, middle toe 5.5%, middle talon 3.1%, hind talon 8.6%, and for three mandibular dimensions, 2.1–2.5%. In comparing this kite's degree of dimorphism to that of other raptors, it is safest to use wing chord length, because the sample size underlying the weights given above is unstated and presumably small. Based on wing chord length, this kite's 9.8% dimorphism is similar to that of Merlin (*Falco columbarius*, 10.0%), less than that of Cooper's Hawk (*Accipiter cooperii*; 12.7%) and Sharp-shinned Hawk (*A. striatus*; 17.7%), greater than that of all North American *Buteos*, and far greater than that of the Swallow-tailed (1.8%) and Mississippi Kite (*Ictinia mississippiensis*, 2.2%; Snyder and Wiley 1976). The Double-toothed Kite's degree of size dimorphism is relatively large compared to that of other raptors taking a diet of insects and reptiles (Newton 1979). This and other ecological comparisons between this kite and other raptors will become more meaningful when this species' phylogenetic position is better resolved.

ACKNOWLEDGMENTS

This is a contribution of The Peregrine Fund's Maya Project. Portions of field work were conducted by T. Dubón, M. Córdova, and M. Vásquez. The Maya Project, begun by W. Burnham, has received funding from Ruth Andres, Robert Berry, Crystal Channel Foundation, Fanwood Foundation, Gold Family Foundation, KENNETECH/U.S. Windpower, the John D. and Catharine T. MacArthur Foundation, Mill Pond Press, Na-

tional Fish and Wildlife Foundation, Norcross Foundation, Henry and Wendy Paulson, Pew Charitable Trusts, Andrés Sada, Joe and Flinda Terteling, the U.S. Agency for International Development, and U.S. Man and the Biosphere Program/Tropical Ecosystems Directorate. We are grateful to T. J. Cade, D. Ellis, L. F. Kiff, and R. Gliński for helpful comments on the manuscript.

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