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# BREEDING BIOLOGY AND BEHAVIOR OF THE PLUMBEOUS KITE

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ABSTRACT.—We studied Plumbeous Kites (*Ictinia plumbea*) in Tikal National Park, Petén, Guatemala, from 1991–1996. We documented productivity of 19 nesting attempts and studied behavior at six nests each during incubation and nestling periods. Nesting was highly synchronous among pairs, with eggs hatching late in the dry season and young fledging at the onset of the rainy season, a time of maximal prey abundance. Kites built stick nests high in exposed situations in living or dead trees, often reusing the same nest or a nearby alternate site in subsequent years. We observed only clutch sizes of one. Based on museum records, latitudinal variation in clutch size occurs, with single-egg clutches the norm except at the northern- and southernmost limits of the species' range, where two-egg clutches have been found. Fifty-eight percent of eggs hatched, and 64% of those resulted in fledged young, producing 0.37 fledglings per nesting attempt. Pair members shared incubation duties in a 60:40 ratio, and each adult caught its own food throughout the nesting cycle, differing from most raptors in these respects. We hypothesize that these patterns result from prey characteristics that make it inefficient for the male to provision the female at the nest. During incubation, one adult or the other was on the nest 97.8% of the time, and incubation shifts averaged 1.99 h. Two incubation periods were 32 and 33 days, and four nestlings fledged at an average age of 38.5 days. Similar to Mississippi Kites (*Ictinia mississippiensis*) in most regards, Plumbeous Kites laid a smaller clutch, and, unlike Mississippi Kites, held regularly-spaced breeding sites 0.5 km apart and exhibited intraspecific territorial behavior. *Received 17 July 1997, accepted 3 Nov. 1997.*

The Plumbeous Kite (*Ictinia plumbea*) forms a superspecies or is conspecific with the Mississippi Kite (*I. mississippiensis*; Sutton 1944, American Ornithologists' Union 1983, Parker 1988). Plumbeous Kites inhabit humid lowlands from eastern Mexico to Bolivia, Argentina and Paraguay, while Mississippi Kites breed widely across the southern U.S.A. and winter in South America (Brown and Amadon 1968). Migratory at the southern and northern limits of their range, Plumbeous Kites vacate Mexico and Central America to winter in South America (Eisenmann 1963). Breeding biology of the Mississippi Kite is relatively well studied (Skinner 1962; Parker 1974, 1988; Evans 1981; Glinski and Ohmart 1983; Shaw 1985), but that of the Plumbeous Kite is known from only one nest (Skutch 1947). Here we present data collected during a six-year period on the breeding biology and behavior of Plumbeous Kites at a Central American lowland site.

## STUDY SITE AND METHODS

We studied Plumbeous Kites in Tikal National Park, Petén, Guatemala from 1991–1996 as part of The Peregrine Fund's "Maya Project." Tikal National Park covers 576 km² in NE Guatemala (17° 13′ N, 89° 38′ W). Elevation is 160–450 m amsl, topography gently rolling, and the climate tropical with annual rainfall of about 1350 mm. The rainy season begins between mid-May and late June, and lasts through January, with highest rainfall in September, and a pronounced dry season occurs from February until May or June.

Tikal National Park is covered mostly by unbroken primary forest. Some areas experienced light selective logging prior to 1969, but were practically indistinguishable from primary forest. Vegetation is semideciduous tropical forest, which varies along a subtle topographic continuum; in well-drained sites it is 25–30 m tall with closed canopy, open understory, and diverse tree species, while in low-lying areas it is lower (10–15 m) with more open canopy, dense understory, and differs in tree species composition. Vegetation, climate, and land-use patterns of the Tikal area were described by Lundell (1937), Schulze (1992) and Whitacre and coworkers (1993, 1995). Clearings in the forest existed around Maya ruins and facilities near the park center.

During the incubation period, we studied adult behavior at two 1994 nests and four 1995 nests, for a total of 133 h of observation on 17 days. On 9 days observations were dawn-to-dusk or nearly so (Table 1). During the nestling period we documented prey deliv-

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TABLE 1. Incubation roles of pair members at six Plumbeous Kite nests.

| Site/pair | Date | Duration of nest observation session | Percent of time one adult or other was on nest | Percent of time on nest contributed by | |
|---|---|---|---|---|---|
| | | | | Bird 1[a] | Bird 2[a] |
| Mundo Perdido | 9 April, 1994 | 4.12 h | 98.4 | 60.5 | 39.5 |
| Mundo Perdido | 25 April, 1994 | 6.0 | 97.8 | 61.1[b] | 38.9[b] |
| Temple 1 | 17 April, 1994 | 12.87 | 97.4 | 52.6[c] | 47.4[c] |
| Temple 1 | 2 April, 1995 | 12.58 | 99.5 | 75.5 | 24.5 |
| Temple 1 | 4 April, 1995 | 10.57 | 98.0 | 56.4 | 43.6 |
| Mundo Perdido | 3 April, 1995 | 11.50 | 98.4 | 51.7 | 48.3 |
| Mundo Perdido | 5 April, 1995 | 12.82 | 93.8 | 56.2[d] | 43.8[d] |
| Bajada la Pina | 6 April, 1995 | 10.25 | 74.8 | 65.7 | 34.3 |
| Bajada la Pina | 18 April, 1995 | 12.88 | 64.8 | — | — |
| Grupo G | 21 April, 1995 | 13.03 | 99.0 | 75.8 | 24.2 |
| Grupo G | 24 April, 1995 | 12.75 | 85.9 | 56.2[e] | 43.8[e] |
| Mean | | 10.85 | 91.6 | 61.2 | 38.8 |
| Median | | 11.5 | 97.8 | 58.45 | 41.55 |
| SD | | 3.05 | 11.7 | 8.7 | 8.7 |

[a] Distinction between Bird 1 and Bird 2 is valid only within each observation session.
[b] Mean of two possible extremes: Bird 1 = 64.05 or 55.11; Bird 2 = 32.95 or 44.89.
[c] Based on 8.58 hours of observation period.
[d] Mean of two possible extremes: Bird 1 = 59.1 or 53.4; Bird 2 = 40.9 or 46.6.
[e] Based on 7.3 hours of observation period.

eries at six nests—two each in 1991, 1992, and 1994. Behavioral data during the nestling period were taken at the two 1992 nests, in mostly day-long observation periods totalling 184 h, and at the two 1994 nests (171 h), where most observations were 2–6 h, distributed throughout the day.

Nests were observed from Mayan temples or the ground, using 30× spotting scope and binoculars at a distance of 15–30 m. Plumbeous Kites were not sufficiently dimorphic for us to distinguish males and females. However, we were able to keep track of individual pair members (designating them as "a" and "b") for long periods. Except to verify some clutch sizes and laying and hatch dates, we avoided climbing to nests until after fledging. To determine clutch sizes, we climbed to nests at least twice, the second time a few days after the first, to verify whether additional eggs had been laid in the interim. In calculating mean heights of nests and nest trees, each was used only once, though some were occupied in multiple years. Values given are mean ± standard deviation except as stated; the median is used where distributions were notably asymmetric.

Statistical tests employed SYSTAT (Wilkinson 1990). To examine the likelihood that the population of nests from which clutch sizes were recorded contained two-egg clutches that were undetected, we conducted Monte Carlo simulations (Crowley 1992) using Resampling Stats software (Simon 1995). We simulated the 43 documented clutches from tropical populations (all of which were 1-egg clutches), testing the probability that this observed sample was taken from a population of nests that in reality included 2-egg clutches in proportions 0.5, 0.3, 0.1, 0.07 and 0.05. In each simulation we conducted 15,000 repetitions in order to estimate probabilities.

## RESULTS

### Nesting Biology

*Migration and nesting phenology.*—Plumbeous Kites began nesting in March, soon after their arrival at Tikal in late February–early March (Vásquez et al. 1992; Whitacre et al., unpubl. data). We recorded three laying dates, six hatching dates and seven fledging dates, estimating additional dates based on incubation and nestling intervals (Table 2). The earliest laying date observed was 18 March and the latest fledging date was 11 June. Two incubation periods were 32 and 33 days, and the nestling period was 38.5 ± 1.5 days ($n = 4$; range = 36–40). Ten pairs laid eggs between 18 March and 5 April (mid-to-late dry season) and six of these did so during the last week of March (Table 2). Eggs hatched in late April and early May (late dry season), and young fledged in late May and early June (onset of rainy season). Plumbeous Kites departed Tikal in August (Vásquez et al. 1992; Whitacre et al., unpubl. data).

*Nests and nest sites.*—All study nests were associated with forest openings ranging from a narrow dirt roadway to clearings of several

TABLE 2. Breeding phenology of Plumbeous Kites at Tikal, Guatemala.

| Territory and year | Egg laid | Egg hatched | Nestling fledged |
|---|---|---|---|
| Airstrip 1992 | 18 March | 20 April | 28–29 May |
| M. Perdido 1996 | 22-25 March[a] | 23–26 April[a] | 1–3 June |
| Bodega 1991 | 22-23 March[a] | 24–25 April[a] | 3–4 June |
| Temple 1 1991 | 26 March[a] | 28 April | na[b] |
| M. Perdido 1992 | 27 March | 28 April | 3 June |
| M. Perdido 1994 | 28 March[a] | 29 April | 7 June |
| Champon 1996 | 28 March[a] | 29 April[a] | 6 June |
| Airstrip 1991 | 29 March[a] | 30 April | na[b] |
| Temple 1 1994 | 1 April[a] | 1–3 May | 11 June |
| Champon 1994 | 5 April | na[c] | na[c] |

[a] Estimated dates based on hatching or fledging intervals.
[b] Nest failed during nestling period.
[c] Nest failed during incubation period.

ha. Nests were in live trees isolated from or emerging above surrounding forest, with no or minimal crown contact with neighboring trees. In addition, we noted six nests in open farming landscape near Tikal in similarly isolated trees, three of which were dead. Tree species used for nesting were *Cedrela mexicana* (4 trees used 1, 2, 2 and 3 times), *Bernoulia flammea* (2 trees used 1 and 2 times), *Ceiba pentandra* (4 trees used once each), *Aspidosperma megalocarpon* (1 tree used once) and *Swietenia macrophylla* (1 tree used once). Nest trees were dry season deciduous. Because nest building and incubation took place late in the dry season, the trees were usually leafless making the nests conspicuous. Nests became less conspicuous during the nestling period when nest trees leafed out at the onset of the rainy season.

Nests averaged 25.5 m above ground (SD = 7.1 m, $n$ = 12, range = 13–36 m), while nest trees averaged 30.0 m tall (SD = 7.9, $n$ = 10, range = 17–40 m). Nests were in forks created by two or more limbs, usually against the bole or on major limbs ($n$ = 8), but sometimes in slender limbs toward the outer part of the crown ($n$ = 4). Nests were high and exposed to sun and wind. Three of 12 nests were built on large clumps of bromeliads. Nests were of dry sticks, lined with sprigs of green leaves; both sexes participated in construction. Throughout incubation and nestling periods adults periodically added green sprigs to nests.

*Nest spacing, alternate sites and reoccupancy.*—Kites nested in the same nests or in other nearby trees from year to year. Alternate nest trees within a given territory were less than 150 m apart. When nesting areas were thoroughly checked in years subsequent to discovery, they rarely lacked a current nesting attempt. Six territories had known occupancy status over 2–4 year periods, totaling 20 territory-years. Birds nested in 18 territory-years, were present but non-nesting in one territory-year, and absent in another. In both the latter instances, they may have nested in an adjacent site. Contiguous, active nests averaged 500 m apart (SD = 52 m, $n$ = 4, range = 453–570 m).

*Clutch size.*—We documented clutch size for eight nests at Tikal; each had a single egg. Nine other Tikal nests each contained a single nestling. We collated data on 38 *Ictinia plumbea* egg sets, apparently the total holdings of U.S. museums. Most were from Venezuela (19), Brazil (7) and Veracruz, Mexico (7), with one each from Trinidad and El Salvador, and three from Paraguay. All were one-egg clutches except for three from the Tropic of Capricorn near Horqueta, Paraguay, which were two-egg clutches. In addition, published accounts indicate two-egg clutches at the northern extreme of the species' range; Belcher and Smooker (1934) reported a clutch of one and a clutch of two from Trinidad, while Sutton and coworkers (1950) observed a nest with two nestlings in Tamaulipas, Mexico. All other primary accounts we examined mentioned only single-egg clutches and broods of one (e.g., Dickey and van Rossem 1938, Thurber et al. 1987).

Parker (1988) concluded that most 1-egg clutches in Mississippi Kites resulted from loss of an egg from a 2-egg clutch. Using Monte Carlo simulations, we found that the probability of drawing 43 single-egg clutches from a population of nests comprised partly of 2-egg clutches is as follows for specific assumed frequencies of 2-egg clutches in the population. For 50% and 30% 2-egg clutches in the population, $P < 0.001$; for 10% 2-egg clutches, $P < 0.012$, for 7% 2-egg clutches, $P < 0.05$, and for 5% 2-egg clutches, $P > 0.05$. Hence, it is unlikely that the underlying population of nests contained as many as 7% 2-egg clutches at the time they were documented. We conclude that, except at the northern- and southern-most extremes of the species' range, the modal clutch size of Plumbeous Kites is a single egg.

*Reproductive success.*—We documented the fate of 19 nestings in which eggs were laid. Eight nests failed during incubation, while 11 hatched a single egg each. Four of the latter nests failed during the nestling period, and seven nests fledged a single young each. Assuming that the 11 nests where laying was inferred from behavior received single-egg clutches, 11 of 19 eggs (58%) hatched, 7 of 11 young (64%) fledged, and 7 of 19 eggs/nests (37%) produced a fledgling, for a productivity of 0.37 fledglings per nest and 1.00 per successful nest. Two nestlings fell from nests during windstorms, and two were believed killed by predators.

## Behavior of Adults

*Incubation period.*—During the incubation period, one adult or the other was on the nest nearly constantly (median = 97.8% of the time; $n$ = 11 observation days at 6 nests; Table 1). When no kite was on the nest, adults remained vigilant, with one usually perched in or near the nest tree or soaring nearby. Both sexes incubated, switching roles periodically throughout the day. On average, one adult provided 61% of incubation and the other 39% (SD = 8.7%, $n$ = 11 observation days at six nests; Table 1). Pair members caught their own prey throughout the incubation phase; we witnessed only two prey exchanges between adults (cicada-sized insects) during 133 h of nest observation.

Periods on the nest averaged 1.99 h (SD = 1.31, $n$ = 24, range = 0.17–4.93). Switches appeared to be initiated by the arriving bird, which typically perched in the nest tree or nearby, occasionally calling as it approached or landed. The incubating bird then stepped off the nest, walked up a limb a short way, and flew off as the arriving bird hopped to a perch near the nest and walked down the limb to settle on the nest. At 5 of 30 switches observed, the arriving bird brought material to add to the nest.

While on the nest, adults alternated between incubating and standing in the nest cup—preening, stretching, rolling or shading the egg. Egg shading (standing over the egg with wings drooped and partly spread) occurred mainly during periods of direct sunlight. Incubation bouts averaged 15 min (SD = 13; $n$ = 100), and standing bouts averaged 3 min (SD = 3; $n$ = 99; range = 1–10). During the mid-day hours, incubation bouts were interrupted more frequently by bouts of standing in the nest, mostly shading the egg. As a result, incubation bouts were significantly longer prior to 09:00 CST (21.6 ± 3.7 min, $n$ = 15, $P$ = 0.002; Tukey HSD test) and marginally longer after 14:00 (17.5 ± 3.7 min, $n$ = 15, $P$ = 0.078; Tukey HSD test), than during mid-day (09:00–14:00; 11.1 ± 0.9 min, $n$ = 67). Duration of standing bouts did not differ significantly with time of day (ANOVA; $F$ = 1.85, $n$ = 98, $P > 0.05$), although the briefest intervals (1 min) occurred mostly in early morning and late evening.

*Nestling period.*—Hatchlings were covered with white down and had dark eyes, yellow cere, and black bill. Most aspects of behavior were as described by Skutch (1947). In flight, adults carried prey in the bill or feet, but transferred it to the bill before landing near the nest. The adult would often lift the prey in its foot and, using its bill, feed small pieces to the nestling.

An adult arriving with prey either fed the nestling directly or transferred the item to the brooding adult, who then fed the nestling. Such transfers between adults were common while nestlings were newly-hatched, and decreased significantly in incidence thereafter (Fig. 1; $F$ = 12.9, $n$ = 49, $P < 0.001$ in ANOVA comparing weeks). Week one differed from all other weeks (df = 43; $P < 0.001$; Tukey HSD test). This pattern indicated that a shift of parental roles occurred during this period, with one pair member performing

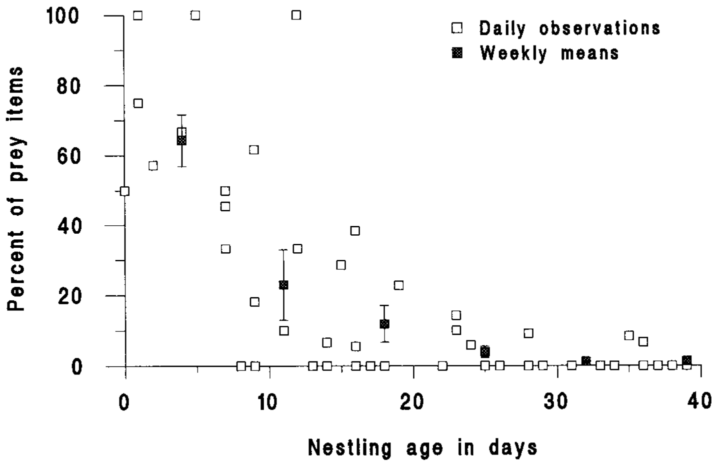

FIG. 1. Percent of prey items transferred to adult at nest before being fed to nestling, versus nestling age, at four Plumbeous Kite nests. Each data point represents one daily observation period. Mean ± SE is given for each week since hatching, for four nests.

most brooding and feeding while nestlings were newly-hatched, and pair members sharing these tasks more evenly as nestlings grew older. Throughout the nestling period each adult captured its own food.

Overall, prey were delivered to nests at the rate of 1.75 ± 1.64 items per hour ($n = 49$ observation periods; range = 0.25–11 items/h). Prey delivery rates did not differ significantly with nestling age ($F = 1.69$, $n = 49$, $P > 0.05$ in ANOVA comparing weeks since hatching). However, the six highest delivery rates (3.7–11.0 prey/h) were noted between nestling ages 16 and 32 days, and all occurred during sessions when prey was never transferred between adults at the nest, that is, when both adults appeared to be bringing prey. During the week prior to fledging, instances of both adults being away from the nest vicinity, presumably hunting, were more frequent.

*Interspecific interactions.*—During the incubation phase, defense of the nesting area was confined to the nest tree and occurred most often when potential avian predators approached within a few meters of the nest. During the nestling period, however, kites were aggressive toward certain bird species within a 100–200 m radius of the nest. Typically the kite voiced a loud, two-note call as it chased or swooped repeatedly at the interloper. Species most commonly eliciting such a reaction were the Roadside Hawk (*Buteo magnirostris*), Bat Falcon (*Falco rufigularis*), and American Swallow-tailed Kite (*Elanoides forficatus*). Keel-billed Toucans (*Ramphastos sulfuratus*) and Brown Jays (*Cyanocorax morio*) were also chased when in the nest tree or immediate vicinity. Black Vultures (*Coragyps atratus*) and Short-tailed Hawks (*Buteo brachyurus*) were chased once each. In contrast, parrots were commonly in the nest tree but rarely chased. Plumbeous Kites and Bat Falcons chased one another, especially in a case where the two nested less than 100 m apart.

Plumbeous Kites were often harassed by songbirds including Sulphur-bellied Flycatchers (*Myiodynastes luteiventris*), Melodious Blackbirds (*Dives dives*), Social Flycatchers (*Myiozetetes similis*) and Brown Jays. Intense mobbing sometimes turned back a kite approaching the nest with prey, and songbirds sometimes struck a kite or clung to its back momentarily. We saw no evidence of Plumbeous Kites depredating bird nests.

*Agonistic behavior.*—We observed seven interactions among Plumbeous Kites involving more than the mated pair; two of these appeared territorial while the others suggested a subdued form of territoriality. In one interaction a kite left the nest vicinity to make an aggressive tail-chase at a conspecific that had approached the nest tree. In another case, a nesting kite flew from the nest tree toward a conspecific perched within 100 m. It flushed the perched bird, and remained perched in that tree as the interloper withdrew. In the remaining five cases when Plumbeous Kites other than the mate approached a nest tree, one or both of the nesting birds flew to meet the approaching kite(s) and then followed behind at a constant distance of 10–15 m, until the conspecific was out of sight of the nest (often >1 km). The nesting kites appeared to escort rather than pursue the interlopers.

## DISCUSSION

Plumbeous Kites at Tikal were notably synchronous in nesting phenology, with 7 of 10 laying dates falling within the last week of March and 5 of 7 birds fledging during the first week of June. These kites, which were largely insectivorous at Tikal, fledged at the onset of the rainy season, a time of maximal insect abundance (Seavy et al. 1997). Such reproductive phenology conforms to a pattern prevalent among insectivorous birds in Central America (Skutch 1950).

Nests were positioned high in open-canopied trees, making them accessible to kites without entering the forest canopy, and visible, perhaps facilitating defense by adults perched or soaring nearby. Nest trees were isolated from or emergent over the forest canopy, which may reduce nest predation by climbing predators.

One of our most noteworthy results was the relatively even sharing of incubation duties by pair members (a 60:40 ratio of incubation effort), with each pair member providing its own food needs during this period. A similar pattern was noted in Mississippi Kites (Parker 1988), with males only occasionally delivering prey to incubating females (Glinski and Ohmart 1983). This is in marked contrast to the majority of raptor species, in which females conduct most incubation and males are often sole providers for female and nestlings until the latter are partly grown (Newton 1986). The pattern shown by Plumbeous Kites, with pair members sharing about equally in incubation, and foraging for themselves during this time, does occur, however, in the *Gyps* vultures (Houston 1976, Newton 1979), in all three U.S.-breeding cathartids (Jackson 1998a, b; Snyder 1988), and in some small, largely insectivorous falcons, e.g., the Lesser Kestrel (*Falco naumanni*) and Western Red-footed Falcon (*F. vespertinus*; Cade 1982).

We propose that this near-equal sharing of incubation duties, with each pair member capturing its own food, results from the small size of prey taken by Plumbeous Kites. It would not be energetically efficient for the male to provision the female at the nest with such small items. Furthermore, we hypothesize that any factor that makes it energetically more efficient for each pair member to forage than for one to provision the other at the nest will promote evolution of shared incubation and self-feeding during incubation. Predisposing factors should include not only a diet of small prey, but also reliance on prey that are sparsely and patchily distributed, ephemeral, or of unpredictable occurrence in time and space. These characteristics of prey place a premium on the ability of individual adults to remain away from the nest for substantial periods, and to consume prey where it is found rather than carrying it to an incubating mate. These descriptors apply to large animal carrion—the principal food of vultures—and to many concentrations of airborne insects, e.g., mating swarms of ants, termites, mayflies, and others (Whitacre 1992).

The hypothesis outlined above is supported by a study of American Swallow-tailed Kites (Snyder 1974), whose aerial hunting and diet resemble those of the Plumbeous Kite. In American Swallow-tailed Kites, males performed about 36% of incubation (Snyder 1974), similar to our results for Plumbeous Kites. In a year when hylid frogs (a predominant prey item) were abundant, males fed females during incubation about once every 2.5 h, but in a year when kites subsisted mainly on insects, such feedings were rare (2 in 85 h), and the female studied that year provided essentially all of her own food during incubation (Snyder 1974).

The incubation intervals we documented (32 and 33 days) were similar to the 29–32 day period reported for the Mississippi Kite (Parker 1988). Our inference that one parent assumed primary brooding responsibilities while nestlings were young also parallels the Mississippi Kite, for which Evans (1981) reported that females with nestlings 10 days old spent twice as much time at nests as did males. Despite this pattern of females apparently spending more time than males in nest attendance during the first 2–3 weeks of the nestling period, females continued to meet nearly all of their own food demands by hunting while males brooded nestlings. Though highest prey delivery rates occurred on days when it appeared both adults were bringing prey to the nest, the occurrence of such high rates was sporadic, and delivery rates were no higher during the week prior to fledging than during the first two weeks after hatching.

Plumbeous Kites at Tikal consistently nested about 500 m apart, with pairs utilizing the same nest trees or nearby alternates repeatedly over a 6-yr period. This regular, substantial spacing, along with our observations of intraspecific aggression, suggest that territorial behavior influenced nesting dispersion and density at Tikal. Dispersion of Plumbeous Kite nests differed greatly from that of American Swallow-tailed Kites, which are similar in diet, hunting style, and choice of nest site. The area occupied by our Mundo Perdido and Temple 1 Plumbeous Kite territories often supported up to 12 nests of American Swallow-tailed Kites, some as close together as 35 m (R. Gerhardt, pers. comm.). Nests of the latter species were grouped into loose colonies, while extensive areas of forest had few or no nests (pers. obs.).

The social organization we observed in Plumbeous Kites falls at one end of a spectrum displayed by the Plumbeous/Mississippi Kite superspecies. Mississippi Kites show a clear tendency toward colonial nesting in the Great Plains (Parker 1988), where kites often aggregate nests in a single shelterbelt, leaving similar nearby sites unoccupied, and where colonies sometimes relocate en masse to other shelterbelts. Within shelterbelts, density approached 1 nest/ha, with most nests less than 100 m apart, and once as close as 13 m (Parker 1988). The tendency toward colonial nesting is apparently somewhat reduced in areas of extensive woodland in the eastern U.S. and in expanses of oak savannah and mesquite, where kites tend to nest farther apart (Parker 1988, pers. comm.), but published literature does not present clear evidence of regular and substantial internest spacing like that we observed at Tikal.

In light of the variable social organization of the superspecies, it is interesting to consider the subdued agonistic interactions we observed. Parker (1988, pers. comm.) stated that intraspecific territorial defense is unknown in the Mississippi Kite. In Plumbeous Kites at Tikal, we observed intraspecific aggression, but it was not strong. We speculate that the degree of tolerance toward conspecifics near the nest is facultative in this superspecies, and varies depending on conditions, which sometimes favor gregarious nesting, and other times favor dispersed nesting. Though much Plumbeous Kite hunting occurred within 200 m of the nest, much also occurred farther afield (Seavy et al. 1997). The extent to which the prey base of Plumbeous Kites is economically defensible is uncertain. Cicadas, beetles and lizards comprised at least 45% of the diet at Tikal (Seavy et al. 1997). These seem uniformly distributed throughout the forest, and hence may represent a defensible prey resource. In contrast, ephemeral aggregations of dragonflies and other flying insects probably are not defensible, but formed only 10% of the identified diet at Tikal. In the Great Plains, the clumped distribution of Mississippi Kite nesting habitat amidst large expanses of foraging habitat may result in high intruder pressure near the nest and in a spatial separation of nest and foraging sites. Together these may inhibit the development of all-purpose territories and high inter-nest distances. In comparison, the more homogeneous distribution of prey and potential nest sites in areas of extensive forest such as Tikal may permit the expression of a tendency toward wide inter-nest spacing and defense of nest and foraging areas.

Mississippi Kites in the Great Plains, Arizona, and Illinois respectively showed productivity of 0.60, 0.61, and 0.63 young fledged per nest, and 1.00, 1.29, and 1.29 per successful nest (Evans 1981, Glinski and Ohmart 1983, Parker 1988). In comparison, Plumbeous Kites at Tikal had lower productivity, fledging only 0.37 young per nesting attempt, though the number of young fledged per successful nest (1.00) was similar.

In Mississippi Kites, the modal clutch size is two, with clutches of three being very rare and probably in error, and single-egg clutches occasional and also largely artifactual (Sutton 1939; Parker 1974, 1988). In contrast, throughout most of its range, the only clutch size documented for the Plumbeous Kite is one, with two-egg clutches known from the northern and southern extremes of the species' range. Parker (1974, 1988) found that the frequency of 1-egg clutches in Mississippi Kites reached nearly 50% in some years, and presented evidence that most or all of these resulted from partial loss of clutches. It is possible that some partial clutch loss is represented in the museum and field data reported here for Plumbeous Kites. However, Monte Carlo simulations showed that it is unlikely that a high frequency of 2-egg clutches existed in the population from which the 43 single-egg clutches reported here were taken. We conclude that the modal clutch size of Plumbeous Kites in tropical regions is a single egg, but only further data can verify whether 2-egg clutches occur in tropical populations of this species. The difference in clutch size noted here between Plumbeous and Mississippi Kites, as well as the latitudinal variation in clutch size documented for the Plumbeous Kite, fit the latitudinal gradient in clutch size well-known for many birds (Moreau 1944).

In summary, the breeding biology and behavior of the Plumbeous Kite at Tikal bear strong resemblance to those of the Mississippi Kite. The smaller clutch size and greater manifestation of regular nest-spacing and territorial behavior in the Plumbeous Kite are the greatest differences in nesting biology of these two species now known.

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