VOCALIZATIONS, FOOD HABITS, AND NESTING BIOLOGY OF THE SLENDER-BILLED KITE WITH COMPARISONS TO THE SNAIL KITE

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ABSTRACT. — We studied the vocalizations, food habits, and nesting biology of the Slenderbilled Kite (Rostrhamus hamatus) in the llanos of Venezuela and made comparisons with its sympatric congener, the Snail Kite (R. sociabilis). Two types of structurally simple vocalizations were identified, and both occasionally were given as duets. Slender-billed Kites fed mostly on Pomacea doliodes snails (91.9%), captured by still-hunting, but they also ate aquatic crabs (Dilocarcinus dentatus). Although Slender-billed Kite diet composition was similar to that of the Snail Kite, Snail Kites fed on significantly larger snails. Slender-billed Kites extracted snails in the same manner as Snail Kites. Slender-billed Kite aerial displays, courtship feeding, and copulation sequences are described and resemble those of Snail Kites (R. sociabilis). Ten Slender-billed Kite nests were found and they usually were built in the crotches of slanting limbs in large trees in the flooded gallery forest. Nest height averaged 14 m above ground, and some sites were reused in subsequent years. Minimum distances between known active pairs ranged from 1.0-1.2 km. Both sexes incubated, brooded, and fed the young. Slender-billed Kites delivered food to nestlings at a significantly higher rate than did Snail Kites. No mate desertion was observed at a Slender-billed Kite nest of two young monitored for this behavior, although desertion occurred at one-third of the Snail Kite nests fledging two young. Slender-billed Kite nestlings stood by two weeks of age, swallowed whole snails by 17 days, fledged by 35 days, and were capable of sustained flight by 40 days. Nesting occurred in the wet season (July-October) and the duration of a nesting cycle was estimated to be 98-112 days. Only 37.5% of the nests found before hatching were successful, fledging 1 or 2 young. Differences between Slender-billed and Snail kite behavioral ecology are related to differences in habitat utilization and the potential effects of hydroperiod on snail size and abundance. Received 3 Dec. 1987, accepted 30 Mar. 1988.

The Slender-billed Kite (Rostrhamus hamatus) is a South American hawk with plumage coloration and bill morphology superficially resembling its congener, the Snail Kite (R. sociabilis). However, Slender-billed Kites are broader winged and about 15% heavier, and the sexes lack plumage dimorphism (Bangs and Penard 1918, Haverschmidt 1959, Brown and Amadon 1968). Another striking difference between these two raptors is that Slender-billed Kites frequent flooded forests or wooded plantations (Haverschmidt 1959, Thomas 1979a), while Snail Kites are usually found

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in a variety of open freshwater marshes (Haverschmidt 1970, Beissinger 1983, Beissinger and Takekawa 1983, Bourne 1985).

Little else is known about the ecology and behavior of the Slender-billed Kite. Few nests and only one set of eggs have ever been described (Haverschmidt 1959, Mader 1981). Like the Snail Kite (Haverschmidt 1962, Snyder and Snyder 1969, Beissinger 1988), Slender-billed Kites are thought to feed almost entirely on freshwater snails (Haverschmidt 1959, Voous 1969), but little information on their food habits and no description of their methods of snail capture or extraction exist. Although it is patchily distributed and sometimes locally abundant (Haverschmidt 1959, Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986), the Slender-billed Kite is uncommon throughout much of its range. Phelps and Phelps (1957) suggested that this kite had only recently extended its range northward into Venezuela.

This paper presents new information on the vocalizations, food habits, and nesting biology of the Slender-billed Kite in the llanos of Venezuela. We also compare the behavior and ecology of this species to a concurrently studied Snail Kite population (Beissinger unpubl. data).

STUDY AREA AND METHODS

We studied Slender-billed Kites on the ranch "Fundo Pequario Masaguaral" 45 km south of Calabozo in Guarico, Venezuela (8°34′N, 67°35′ W). The ranch is composed of nearly 7000 ha of natural savanna and gallery forest (Troth 1979) that are lightly grazed by cattle. The nearly flat terrain is 60 to 75 m above sea level. Many parts of the gallery forest and savannah are flooded during the wet season (May–November) but dry out completely during the dry season (December–April). A few areas remain wet throughout the dry season, including two small lagoons that are flooded by pumping. The vegetation is intermediate between the well-drained high llanos, about 60 km to the north, and the lower, more flooded low llanos, about 60 km to the south (Troth 1979, Sarmiento 1984).

We conducted field work as part of other projects (Thomas 1979b, 1986; Strahl 1985, in press; Beissinger unpubl. data) in all months from 1975–1978 (Thomas); from July-August 1981, May-October 1982, and May-December 1983 (Strahl); and from July through November 1985 and 1986 (Beissinger). Observations of Slender-billed Kites were made with binoculars and spotting scopes from 13–15 m tall towers placed at canopy level in the gallery forest or from the ground. Because of the difficult placement of the nests, they were inaccessible by climbing and were too high to reach with our extension ladder. However, nest contents could often be inferred by adult behaviors or, after hatching, by direct observations. Mader (1981) reported on two of the ten nests that we describe here but we give additional details.

Data were gathered incidentally from 1975-1985. But from August-October 1986 one nesting pair was observed approximately one or two mornings a week for periods of 2-5 h (usually 3 h) from mid-incubation through fledging (for a total of 25 h) from a blind constructed 50 m from the nest site. The behavior of the adults and nestlings, and the types of food fed to the young were noted. Usually the adults at this nest could be differentiated by the size of the orange cere extending upwards from the bill toward the eye, which was much more extensive in one bird than in the other. However, their sexes were not determined.

Empty snail shells were collected from beneath the nest or nearby feeding perches, and standard shell length was measured with calipers. A Marantz tape recorder and Gibson sound parabola were used to record vocalizations which were analysed on a Kay Elemetrics Corporation Sona-Graph 7800 in the National Zoological Park's sound laboratory.

RESULTS

Vocalizations.—Two distinctive adult vocalizations were recognized. Type I (Fig. 1A) is richly harmonic and tonal in quality. It increases rapidly in frequency followed by a slow decrease, and then a sudden downward shift in frequency leading to a slow decline and another sudden downward shift near the end. We paraphrase this call as "KE-EE-AAY-AAY-" This is probably Haverschmidt's (1959) "mewing" call. It was the most frequently used call and was given by birds flying or soaring, approaching the nest, or responding to potential predators or intruders. Type II (Fig. 1B) was often given by one member of the pair as it approached its mate near the nest. It is a frequency-modulated whistle, with abrupt ups and downs followed by a slow up and down frequency modulation at the beginning of the last half of the call. We paraphrase this as "KER-AH." It is usually given three or four times in succession, sometimes repeating the "AH-AH" phrase several times.

Both calls were sometimes given as duets (sensu Farabaugh 1982). One member of the mated pair called in a syncopated manner usually just after but rarely during the other's vocalization. Sometimes the mate joining in the duetted type II call would syncopate the "AH-AH-AH" syllables with the same part of its mate's call. This was particularly striking because (in at least two pairs) one member of the pair had a much lower pitched voice than the other.

Nestlings rarely vocalized, even when their parents returned with food. Once a nestling directed a soft "peeping" call toward a nearby adult after its sibling had been fed. The only true call uttered by a young Slenderbilled Kite was given by a fledgling about seven weeks of age in answer to a type I call given by its nearby parent. The call sounded like the type I adult call but was much higher and more whistle-like in quality.

Food and feeding behavior.—We saw adult Slender-billed Kites eat or feed to their chicks 77 food items and all but three prey items (4%) were identified. Aquatic *Pomacea doliodes* snails comprised 91.9% of the food items identified (68) while freshwater crabs (*Dilocarcinus dentatus*) composed the remainder (6). All unidentified food items appeared to be either snails or crabs. In September and October 1986, parents fed nestlings (N = 57) a diet of 89.5% snails and 10.5% crabs. Watches at Snail Kite nests during the same period also revealed that crabs composed 10% of the diet and snails the remainder (Beissinger unpubl. data). However, Slender-

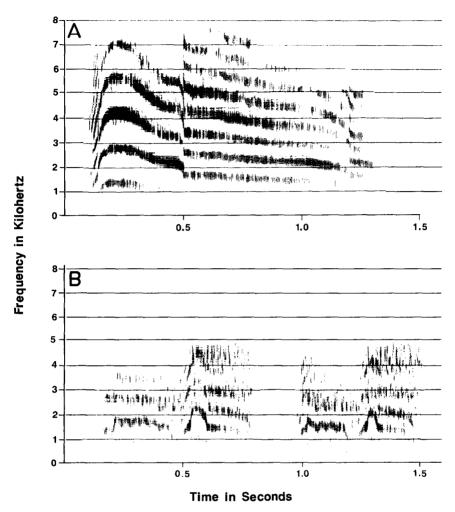


Fig. 1. Spectrograms of two vocalizations of the Slender-billed Kite: (A) type I "KE-EE-AAY-AAY" call; and (B) type II "KER-AH" call given twice.

billed Kites ate significantly (t = 7.2, df = 210, P < 0.001) smaller snails ($\bar{x} = 43.9 \pm 5.0$ [SD] mm, N = 21) than did Snail Kites ($\bar{x} = 55.8 \pm 7.4$ mm, N = 191). This difference in snail size selection represents a 1.5 times greater caloric intake per snail for Snail Kites than Slender-billed Kites (Beissinger unpubl. data).

On seven occasions we saw Slender-billed Kites extract snails from their shells in a manner similar to Snail Kites (Snyder and Snyder 1969, Snyder and Kale 1983). Grasping the snail in one or both talon(s) against a limb, the kite inserted its bill, presumably between the shell and operculum, and twisted its neck back and forth to pull off the operculum. We were unable to see the initial orientation of the mollusk but after the operculum was removed, the snail was positioned with the aperture facing up and the spire sideways. Then placing its upper mandible inside the shell and the lower one outside, the kite cut the columellar muscle with a few strokes of the bill. The body mass was freed from the shell, which fell to the ground. The kite discarded the digestive tract before tearing pieces from the body and eating the snail, or delivering it to a nestling. We were unable to see if albumen glands were discarded, which Snail Kites usually do when eating gravid female snails (Snyder and Snyder 1971). Extracting a snail from its shell required less than a minute.

On three occasions we saw Slender-billed Kites capture snails. The kites had been still-hunting (Snyder and Snyder 1969, Beissinger 1983) and flew down to the water's surface from overhanging branches to pluck the snail from the water with their talons.

We did not observe Slender-billed Kites capturing or dismembering crabs. But when feeding nestlings, adults tore pieces of meat from crabs and passed them bill-to-bill to the chicks. Apparently the adults had removed the crabs' carapaces before arriving at the nest.

Group movements and displays.—Slender-billed Kites were often observed soaring in groups of two to five birds. Typically, the group circled about 100–300 m in the air but sometimes as high as 500 m. Usually one or two members of the group gave the type I call. Group soaring occurred during the nesting season, from July through October.

Often at least one member of the group, and sometimes two, displayed while circling. The displays, lasting up to 40 min, consisted of a series of repeated swooping dives in which the bird would fold its wings and plummet about 5 m before opening them again and rising. When two members of a soaring group displayed, they sometimes chased each other. On one occasion we saw a lone adult give an undulating flight display about 5 m above the ground while returning toward its nest site. While soaring in groups or alone, Slender-billed Kites joined or were joined by Turkey Vultures (*Cathartes aura*), Black Vultures (*Coragyps atratus*), and King Vultures (*Sarcoramphus papa*).

Courtship.—We observed courtship and copulation behavior of two pairs of Slender-billed Kites. The sequence of events appeared very similar to that of the Snail Kite (Beissinger 1987a, 1988). In one pair, the presumed male brought snails to a female perched on a dead snag along an old drainage canal at the edge of the gallery forest. However, no known

nest site was within 300–400 m of the pair. The female remained perched in the same vicinity throughout most of the observation period (1.75 h) while the male left, presumably to hunt, and returned with a snail five times. As the female begged vociferously giving rapid type I calls, the male extracted the snail on a perch 1–2 m away. Often the female began calling when the male was first seen approaching with food. The male would pass the snail to the female bill-to-bill after she had shuffled along the branch to within 0.5 m of him. Twice the male fed the female pieces of the snail instead of relinquishing the whole mollusk to her.

Four copulation sequences were observed. Two occurred just after or while the female ate a snail recently delivered by the male. In the typical copulation sequence, the female crouched, opened and quivered her wings (quarter open at the wrist), lowered her head, and arched her back. The male mounted the female, with wings spread two-thirds to full, and pushed his tail around to the left and beneath the female's to make cloacal contact. Using a pumping motion, the male copulated for 5–6 sec. Sometimes during mounting, the female arched her back forward and held her head back, looking at the male with her mouth open, and softly made a high nasal call or a low pitched rattle-like "BRAH." At the conclusion the male remained on the female's back for 3–4 sec, and then hopped off and perched 0.5 m away. Twice type I calls were uttered by the female before and after copulation.

Nest sites.—We discovered 10 nests, eight in gallery forest and two in shrub woodland bajio (terminology of Troth 1979). All nests were in habitat that flooded during the wet season, with standing water 5–60 cm in depth, but dried nearly completely during the dry season. Most nests were positioned over heavy brush, although sometimes nests were located over open water (pools or borrow-pit pools).

Nest sites were situated 9–20 m above the ground ($\bar{x} = 14$ m) in large trees (up to 25 m in height) usually in the middle of long, horizontal, or gently sloping limbs. Nests were found in the following trees: Albizia aff. polycephala (2), Pterocarpus acapulcensis (3), Bombacopsis sp., Spondias mombin (2), and unidentified (2). All nests were small platforms approximately 50–60 cm in diameter, constructed of bulky dead twigs, and most were placed in bifurcating crotches. Often nests were surrounded by green leafy twigs that stuck into the air at an angle. At least some leafy twigs were gathered and stuck into the side of the nest by the birds, perhaps to assist in camouflage. Nests were usually well-shaded by the tree canopy but easily visible from the ground.

Slender-billed Kite nests were well dispersed and some were traditional sites. Distances between pairs of simultaneously active nests in 1976 and

1978 were approximately 1–1.2 km. In two instances, the same nest sites were used by kites in successive years, and in one case evidence suggested two years of prior occupancy of the site (Ernest Stevens pers. comm.).

Parental behavior and mate desertion.—Both sexes incubated as do Snail Kites (Beissinger 1987b). When relieving its mate during incubation, the approaching bird often gave the type I call. Unlike Snail Kites which fly directly onto the nest or hop on from a nearby perch but never walk, Slender-billed Kites usually landed a few m away from the nest, and shuffled or slid along the tree limbs to the nest site.

At the 1986 nest, both parents fed and brooded the two young. Snails or crabs were torn into small pieces and passed bill-to-bill from parent to chick. The food delivery rate increased through the first three weeks (Fig. 2). From weeks three through six, delivery rates averaged 3.92 \pm 1.50 (N = 4) per h for Slender-billed Kites, significantly higher (t = 2.09, df = 32, P < 0.05) than the rate at which concurrently active Snail Kite nests with two chicks were being fed by both parents ($\bar{x} = 2.51 \pm 1.25$ [SD], N = 32). Neither Slender-billed Kite parent in 1986 deserted its mate and both fed the fledglings until at least 7 weeks of age.

Nestling development and behavior.—The young hatched approximately 2–4 days apart at all three nests that we could observe. Haverschmidt's (1959) plate 2 depicts a light grey, downy nestling that resembled our chicks at about 7–10 days of age. At this stage, the nestlings strongly resembled those of Snail Kites (see Bent 1937 for a photograph). By four weeks of age, however, nestling plumage became a dark grey and looked similar to the immature in Haverschmidt's plate 1. In this plumage, a standing nestling resembled the adult except that its iris was dark brown instead of yellow and its cere was bright yellow (resembling R. sociabilis young) instead of orange.

The young were nearly always tranquil and quiet in the nest. When the adults landed near the nest with food, the chicks remained quiet and did not give begging screams. We never observed any fighting between the two nestlings, except once (1.5% of the feedings) when the young engaged in a tug of war over snail meat.

Nestling development appeared to be rapid. By two weeks of age the parents no longer brooded. Nestlings stood frequently during the second week after hatching and by the third week stood consistently. Nestlings were capable of taking extracted snails from adults and swallowing them whole by 17 days after hatching. Fledging occurred at 35 days of age, but the young were not capable of sustained flight until 40 days of age and remained perched in trees adjacent to the nest site.

Nesting phenology and success. —In Venezuela, the nesting season extended from July through October. The earliest nest records were on 22

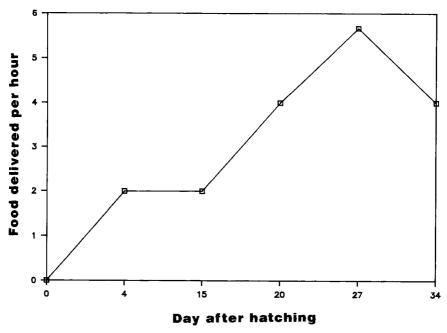


Fig. 2. Food delivery rates by Slender-billed Kite parents to a nest with two young.

July 1983, when a pair was found but the nest contents were unknown, and on 29 July 1982 when a pair was located with a half-built nest. While Slender-billed Kites have been sighted occasionally in our study area as late in the year as December, we have not seen this bird from January through April, the height of the dry season.

We could not determine the exact length of a nesting cycle. Our best data are from the intensively studied nest in 1986. If we assume that egg laying had begun (as judged by adult defensive behaviors) when the nest was found on 30 July and that the young were about 4 days old when discovered on 5 September, the incubation period would be about 30 days. The nestling period at this nest was about 35 days, but the fledglings were still receiving food from their parents in the nest area a week later. This suggests that the nesting cycle of the Slender-billed Kite has a minimum length of 72 days. Assuming an estimate of two weeks for nest-building and another 2–4 weeks of parental care before the young become independent (no observations but see Beissinger [1987b] and Beissinger and Snyder [1987] for *R. sociabilis*), a nesting cycle would be closer to 98–112 days.

We were able to determine the fates of nine of ten nests found during

this study. Four (44.4%) successfully fledged young. If, however, we exclude one nest found after the young had hatched, nesting success was 37.5%. In three nests we were sure of the number of young fledged; two fledged two young and one fledged a single young. In the other nest, one young fledged but we could not be certain whether the second nestling had fledged successfully.

Interspecific interactions.—On two occasions we saw R. hamatus defend a nest site. Once a family unit of red howler monkeys (Alouatta seniculus) was foraging on leaves in the nest tree about 3–20 m from the nest. After a trip to feed the young, a Slender-billed Kite parent perched near the monkeys and began vocalizing type I calls towards the group. Then after diving once at the monkey group, the kite departed and the monkeys moved to another tree. Red howler monkeys are folivorous and are not known to eat vertebrates (Crockett and Eisenberg 1987).

Nest-site defense also occurred when a pair of Laughing Falcons (*Herpetotheres cachinnans*) called about 50 m from a Slender-billed Kite nest. The kite parent, perched nearby, flew to the top of the nest tree and gave type I calls. Then it gave chase in the direction of the Laughing Falcons.

DISCUSSION

One of the most interesting discoveries in this study was that Slender-billed Kite pairs can give calls as duets. To our knowledge, the Slender-billed Kite is the only falconiform for which duetting has been documented (Thorpe 1972, Farabaugh 1982). Duets were given when the pair was perched on the territory, when a member of the pair approached its mate near the nest or in response to human intruders. Although the function of these duets is not known, they may be used as a broadcast call for territorial defense, directed toward nearby nesting pairs, and/or in pair-bond maintenance. Voices of mates differed in pitch and this may be a sexually dimorphic characteristic.

Slender-billed Kites were thought to have a specialized diet solely of freshwater snails (Haverschmidt 1959). In this study they fed mostly (about 90%) on *Pomacea* snails but the remainder of their diet was comprised of crabs, which were also taken by a nearby population of Snail Kites at a similar rate. Neither species (Beissinger 1988) should be considered solely snail eaters but clearly they are snail specialists.

Slender-billed Kites extracted and ate snails in the same manner as *R. sociabilis* (Snyder and Snyder 1969, Voous and van Dijk 1973, Snyder and Kale 1983). However, Slender-billed Kites were observed on three occasions catching snails by still-hunting and have not been seen coursing for food as Snail Kites frequently do (Snyder and Snyder 1969, Beissinger 1983). This could be due to the paucity of observations on this species

but is more likely a constraint imposed by the closed forest habitat hunted by Slender-billed Kites. Here many perches are suitable for still-hunting but it is probably difficult for kites to maneuver in flight through the dense forest while searching for snails. Also, still-hunting may be more profitably employed in the forest if snail availability is higher there than in open marshes (Beissinger 1983). There is some evidence supporting this hypothesis since Slender-billed Kites fed their nestlings at a higher rate than did Snail Kites.

Alternatively, a higher rate of food delivery by Slender-billed Kites to their nestlings may have compensated for feeding smaller snails to their young than did Snail Kites. Differences in the sizes of snails captured by these two hawks probably reflected a different distribution of snail sizes in the two habitats that they hunted (see Bourne and Berlin 1982 for an example). Rice fields in Venezuela hunted by Snail Kites can be artificially flooded year round, even during the dry season, and may permit increased growth and survival by snails. The snail populations of the gallery forest, however, must aestivate throughout the dry season when the water disappears.

The Slender-billed Kite and the Snail Kite (Beissinger 1987a, b, 1988) have very similar nesting behaviors. Copulation and courtship feeding sequences appear identical. Aerial displays are also similar but Slender-billed Kites usually perform them high above the tree canopy while male Snail Kites nesting in open habitat give them most frequently at low elevations and near nest sites. In both species, the sexes share the duties of incubation and feeding the young. The duration of incubation, nestling, and fledgling periods of the two kites appears similar, although Slender-billed Kites apparently have a shorter breeding season (July-October) than Snail Kites (May-December).

One aspect of the nesting behavior of the Slender-billed Kite that may differ from the Snail Kite is territorial defense. Snail Kites usually defend only a small area near the nest site (see Snyder and Snyder 1970 for an exception). Our study did not determine whether Slender-billed Kites do the same or defend larger parts of their home ranges. We witnessed few aggressive interactions and, because Slender-billed Kites are not plumage dimorphic, the context of displays often could not be clearly understood. Territoriality is suggested by the large distance between nests. The frequency with which we saw Slender-billed Kites soaring over the forest suggests that this activity might have been territorial patrolling. However, we sometimes saw Slender-billed Kites soaring in groups and it may be that the large home ranges of *R. hamatus* pairs overlap.

In Florida, most Snail Kite nests are deserted by a parent, if food is abundant, when the young are between three and six weeks of age (Beis-

singer and Snyder 1987). At the only Slender-billed Kite nest checked for mate desertion, neither parent deserted their brood of two. In Venezuela, Snail Kite broods of two young were deserted only about a third of the time, whereas broods of one young were nearly always deserted (Beissinger unpubl. data). Therefore, we do not have enough evidence to determine if Slender-billed Kites ever desert their mates. Comparisons of food delivery rates to young suggest that the food base of *R. hamatus* might be large enough for mate desertion to occur: Slender-billed Kites fed their young 1.5 times more frequently than did Snail Kites. However, this difference was offset by a difference in size and total caloric value of the snails fed, which was 1.5 times greater for Snail than Slender-billed kites. However, the smaller-sized snails fed by Slender-billed Kites and the larger body size of their nestlings could necessitate biparental care because two parents are needed to make additional trips to the nest with food to yield nestling food intake equivalent to *R. sociabilis*.

Other evidence suggests that mate desertion might not be expected for Slender-billed Kites. Mate desertion would be surprising in this species if it is territorial or does not raise more than one brood in a breeding season (suggested by the relatively short breeding season compared to the length of the nesting cycle). Thus, it would be difficult for potential deserters to secure new mates and nest sites or have enough time to attempt to nest again, perhaps the most important benefit of mate desertion (Beissinger and Snyder 1987). That exact nest sites can be used several years in succession suggests that pairs may mate more permanently.

Slender-billed Kite young sit quietly in the nest and rarely fight over food delivered by the parents. In contrast, Snail Kite young scream loudly at parents approaching with food and may continue screaming at the parent, even after the food has been eaten, until the parent departs from the nest area. The silence of Slender-billed Kite nestlings, and the semicamouflaged nest of this species probably help to prevent detection from predators, which are common in the gallery forest (Strahl, in press). Young of both kite species were rarely observed fighting. Nestling fights are uncommon in medium-sized raptors, occurring only during times of obvious food shortage (Newton 1979).

Slender-billed Kite populations appear to be highly localized and restricted to flooded gallery forest or semiforest habitats. The species has been designated as rare or uncommon (Haverschmidt 1959, Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986). Although Slender-billed Kites are easily detected because their calls are unique and because they vocalize frequently, we believe that it is unlikely that this hawk recently expanded its range into Venezuela (Phelps and Phelps 1957). Instead, it probably was overlooked due to its irregular and seasonal

distribution. In the llanos of Venezuela, gallery forests are rapidly being destroyed and replaced by rice agriculture or human settlements. Because of its strong dependence on one prey species and its needs for a large forested territory for foraging and nesting, the Slender-billed Kite may be especially sensitive to tropical deforestation. Further study of its population biology is needed.

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WILSON SOCIETY ANNUAL MEETINGS

The 1989 annual meeting of the Wilson Ornithological Society will be held 25-28 May, at St. Mary's College, Notre Dame, Indiana. Doris J. Watt will chair the Committee on Arrangements. Richard C. Banks will chair the Scientific Program Committee.