OBSERVATIONS ON THE FORAGING ASSOCIATION OF DOUBLE-TOOTHED KITES AND WHITE-FACED CAPUCHIN MONKEYS

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ABSTRACT.—A 10-month study of the foraging association between white-faced capuchin monkeys and Double-toothed Kites was conducted in conjunction with a study of the behavior of three monkey species. Kites were observed 30 times more frequently in association with capuchins than with the other monkeys, and they were present for 19.3% of the capuchin contact time. Kite-capuchin associations were not subject to significant diurnal and monthly variation.

Associating kites normally stayed 5–30 m from capuchins, and they fed on large insects disturbed by the capuchins' activity. Kites were normally active on a plane horizontal with or below the monkeys but seldom above. Strata locations for the two species were significantly correlated.

Capuchins seemed minimally affected by the presence of the kites. The foraging association between the two species was interpreted as a product of the behavioral characteristics of the capuchins and the opportunistic feeding strategy of the kites. *Received 3 April 1978, accepted 25 September 1979.*

THE behavior and ecology of the Double-toothed Kite (*Harpagus bidentatus*), a small forest hawk of the Neotropics, remain poorly known because of the difficulty of observing a wide-ranging predator active in closed habitats. The limited literature includes notes on stomach contents (Haverschmidt 1962), a nesting attempt (Laughlin 1952), nesting and dietary habits (Skutch 1965), and foraging associations between these kites and white-faced capuchin monkeys (*Cebus capucinus*) in Panama (Greenlaw 1967, Ridgely 1976) and *Cebus* and squirrel monkeys (*Saimiri sciureus*) in Brazil (E. O. Willis, in Greenlaw 1967). These reports describe a diet of lizards and large insects.

In addition to the above, other workers have noted foraging associations between birds and monkeys. Stott and Selsor (1961) reported one between white-faced capuchins and Slaty-tailed Trogons (*Trogon massena*) in Panama. In the Old World, Chapin (1939) reported associations between Long-tailed Hornbills (*Berenicornis albocristatus*) and African monkeys, Greater Racket-tailed Drongos (*Dicrurus paradiseus*) and macaques, and Spangled Drongos (*Dicrurus hottentottus*) and Celebes black "apes" (*Cynopithecus niger*). Stott (1947) reported an association between Philippine Fairy Bluebirds (*Irena cyanogaster*) and crab-eating macaques (*Macaca fascicularis*). These studies cite a similar phenomenon: a unilaterally profitable "flushing" association in which the birds fed on insects stirred into visible activity by the travel of the monkeys. These accounts, however, make no reference to the long-term stability of the observed associations.

This report is an account of the foraging behavior of Double-toothed Kites (hereafter called kites) in association with white-faced capuchin monkeys (hereafter called capuchins) during 10 months on Barro Colorado Island (BCI), Panama. It supplements Greenlaw's (1967) 2-day study of this phenomenon by greatly lengthening the

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observational time period, thus providing insight into the role of this association in the natural history of the kites. I consider the specificity, frequency, and temporal-spatial characteristics of kite-capuchin associations and include new observations on the diet of the kites.

METHODS

I observed kite-capuchin foraging associations while studying the behavior of three cebid monkeys on BCI: capuchins, mantled howler monkeys (*Alouatta palliata*), and red spider monkeys (*Ateles geoffroyi*). As a control, I noted kite sightings during search periods when monkeys were absent on one randomly selected field day per week. I devoted about 80% of the time to capuchins with a habituated troop, the Tower Troop, while I spent the balance with other troops. Although I began preliminary observations in November 1976, I collected systematic data from February to December 1977. I also made unsystematized observations of kites at BCI's laboratory clearing.

Kites and monkeys were judged to be "in association" if I could see them simultaneously. Observation conditions limited recorded associations, however, to those in which less than 50 m separated the two species. The term "sighting" refers to a period of relatively continuous visual contact with a kite. Sightings varied in duration from less than 5 min to several hours. I recorded the following data at the instant of initial kite detection in each sighting: time, forest type, estimated distance between kite and nearest capuchin, location of kite with reference to nearest capuchin (above, horizontal, below), and stratum location (<4 m, 4–12 m, 12–22 m, >22 m) of kite and nearest capuchin. Because continuous observation was normally impossible in the forest, I calculated an estimate of total kite association time by summing the durations, including sets of successive sightings and the time estimates for single sightings. Membership in a set was determined by the condition that intervals between sightings within a set must be less than 20 min. For example, on 8 August 1977, kites were observed with capuchins in 5 sightings from 1055–1111, 1116–1137, 1204–1246, 1302–1305, and 1629–1638. These data yielded 3 sighting sets—1055–1137, 1204–1305, and 1629–1638—for a total estimated kite-capuchin association time of 1 h 52 min. Note that when adjacent sightings were within 20 min of each other, intervals between sightings were also included in computing estimated association time.

The restricted view available in the forest rendered the identification of food items fortuitous, yielding unstandardized data.

RESULTS

Specificity and extent of association.—The sighting rate in the presence of capuchins was 30 times that observed in the presence of spider monkeys and howlers and 15 times that observed in the absence of monkeys (Table 1). Kites associated with capuchins for 19.27% of the total contact time with this species—an estimated percent association more than 80 times greater than that of the other conditions listed in Table 1. Only two kite-spider monkey associations were noted in the clearing, which both species frequent. I never saw trogons and capuchins in association as reported by Stott and Selsor (1961). This suggests that, although capuchins may flush prey suitable for other birds, only kites exploit this condition on a regular basis.

Both juvenile and adult kites were observed in association with capuchins, but juveniles normally appeared to be accompanied by one or more birds in adult plumage.

Temporal-spatial characteristics of kite-capuchin associations.—Monthly values (n = 10) for estimated association with capuchins varied from 10.2% (October and November) to 35% (May), with a mean of 17.07% (SD = 8.02%). The sighting rate with capuchins varied from 0.19 (November) to 0.87 (May) with a mean of 0.51 (SD = 0.21). (These values differ from the overall means reported in Table 1 because of unequal monthly capuchin contact time). Variations in monthly values for both

TABLE 1. Kite-capuchin association in comparison with other observational conditions.

	Observational condition			
Association data	Capuchin monkeys	Spider monkeys	Howler monkeys	No monkeys
Total hours observed (T)	268	177	200	79
Estimated hours of kite association (E)	51.65	0.42	0.25	0.17
Number of kite sightings (*n*)	161	4	4	3
Sighting rate (*n*/T)	0.60	0.02	0.02	0.04
Estimated percent association = (E/T) × 100	19.27%	0.24%	0.13%	0.22%

measures were not significant (χ^2, One-sample Test, Siegel 1956), suggesting that kite-capuchin associations are a relatively stable feature of the kite's mode of life.

Bihourly values ($n = 7$) for estimated association with capuchins varied from 8.1% (1600–1759) to 22.5% (1200–1359), with a mean of 15.7% (SD = 5.74). The sighting rate with capuchins varied from 0.31 (800–959) to 0.78 (600–759) with a mean of 0.55 (SD = 0.17). Variations in bihourly values for both measures were not significant, suggesting that kites follow capuchins rather than other large cebids because both kites and capuchins share a tendency to remain rather continuously active throughout the day.

Examination of the percentage distribution of ranges of distance estimates between kites and nearest capuchins at the instant of initial sighting reveals that 85.7% of these values lie between 5 and 30 m. Kites very rarely perched within a few meters of capuchins; most kites observed less than 5 m from them were active, either seizing prey or flying.

The kites' position relative to the nearest capuchin at initial sighting seemed consistent with their hunting method. Kites were above nearest capuchins in 10.8% of initial detections, while they were below in 40.5% and horizontal in 48.6% of these events. The last two positions probably facilitated prey detection, because prey dislodged by the monkeys usually flew or fell toward the ground. Because this relationship held at all stratum levels, stratum locations for both species were significantly correlated (Contingency coefficient = 0.478, $\chi^2 = 49.6$, $P < 0.001$; Bruning and Kintz 1977).

The diet of kites.—It was impossible to quantify differences between the foraging behavior and diet of capuchin-associated kites and nonassociated kites, because meager unstandardized data were available for the latter.

Kites appeared to detect prey from an exposed perch. Once they spotted a prey item, they flew directly toward it and seized it in their talons. I recorded 34 captures of positively identified prey items, presumably dislodged by Tower Troop capuchins, and 32 incomplete feeding observations lacking details such as prey identity, capture, etc. The 34 positively identified items included 10 katydids, 8 cicadas, 5 cockroaches, 4 dragonflies, 2 beetles, 2 grasshoppers, 1 mantis, 1 walkingstick, and 1 lizard (*Anolis* sp.). All these items had an estimated length in excess of 4 cm. The kites took smaller items as well, but I could rarely identify them.

Although the kite-capuchin relationship seemed to favor the kites entirely, this study cannot provide a demonstration of increased foraging efficiency in kites as a result of their association with capuchins, because the small size of the data pool for kites not in association with capuchins (0.84 estimated h) rules out a definitive comparison of the benefits of association vs. nonassociation.

DISCUSSION

What behavioral characteristics of a monkey species might contribute to its effectiveness as an insect flusher? A partial list would include its range size, daily travel distance, activity budget, diet, and travel mode. Milton (1977) reported a home range size of 31 ha and a mean daily travel distance of 443 m for howlers. Richard (1970) plotted a home range of 125 ha for spider monkeys. My own observations suggest a home range of at least 400 ha for this species. Richard reported daily travel distances for spider monkeys ranging from 320 to 2,740 m, figures that accord with my own observations. Capuchins occupy home ranges varying from 50 ha (Freese 1976) to 85 ha (Oppenheimer 1968). They travel about 1,600 m daily, displaying conspicuously less daily variation in travel distance than spider monkeys. These three species differ markedly in their activity budgets. The most critical aspect of this variation to foraging kites is resting time, because no insects can be flushed by a motionless animal. The inactivity of howlers is well-known; Smith (1977) and Milton (1977) reported 79% and 65.5% of the day devoted to rest, respectively. Richard (1970) reported that spider monkeys devoted 54% of their day to rest. Capuchins, on the other hand, are far more active; only 14% of their day is spent resting (Oppenheimer 1968). A high level of activity within a relatively confined area may induce kites to follow capuchins. The importance of activity to this relationship is further emphasized by the fact that the single observation of a kite feeding in the absence of capuchins involved an association between a kite and a troop of rapidly traveling howlers. Perhaps any active moving monkey troop has flushing potential. Thus, kites may follow capuchins because of the capuchins' high activity level, while they may break off contact with *Ateles* and *Alouatta* when these monkeys take their frequent extended rests.

Field workers have noted conspicuous contrasts in the diet and foraging behavior of these three monkeys. Smith (1977) reported a seasonally variable diet of 41.5–65.9% leaves, 46.1–31.5% fruit, and 8.7–2.5% flowers for howlers. Milton (1977) and Smith described the howler monkey's consistent, single-file, goal-directed travel to definite food trees over repeatedly used routes. This strategy, although consistent with leaf-eating, limits the number of occasions when insects may be disturbed. Both Richard and Carpenter (1935) wrote that fruits are about 90% of the spider monkey diet, with the balance consisting of leaves and flowers. They reported that these monkeys follow consistent routes to fruit-bearing trees. Spider-monkey groups also fragment widely over their range in the course of a day (Klein and Klein 1975, 1977). As a result, a kite associating with a group would soon end up following only a small fraction of it. Capuchins incorporate quantities of insects (perhaps as much as 25% of the weight intake) into their diet (Oppenheimer 1968), and they have adopted highly active foraging behaviors, which contrast with those of the more vegetarian howler and spider monkeys. Spreading out in a long fragmented front, different capuchins use different paths each day. They remain more or less continuously active, regularly engaging in activities that disturb hiding insects. Capuchins make frequent strata changes, they readily move into dense vine tangles, and they frequently tear apart dead wood and leaf accumulations, an activity that frequently flushes large insects or causes them to drop to the ground.

Kites readily exploit these prey items made available by capuchin foraging activities. Because they also exploit insects made available by a human-maintained edge habitat, however, we may conclude that their regular attendance upon capuchins is but one aspect of an alert predator's highly opportunistic feeding strategy.

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