

FOLLOWING OF BROWN CAPUCHIN MONKEYS BY WHITE HAWKS IN FRENCH GUIANA¹

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Abstract. One group of brown capuchin monkeys (*Cebus apella*) was observed for 19 months in French Guiana. White Hawks (*Leucopternis albicollis*) were seen in association with these monkeys throughout the year. Our study revealed that: (1) hawks mainly followed capuchins in open forest types, and in this vegetation they mainly flew at the height of 10–20 m from the ground where horizontal visibility is better than in other strata of the forest, (2) hawks usually landed preceding the monkey troop spreading into an area, and they followed the capuchin troop when the monkeys were traveling, and (3) no predation of any capuchins by hawks occurred at any time during our study, and seven times it was observed that hawks captured arboreal snakes disturbed by the movement of capuchins. We propose that White Hawks followed brown capuchins in this Amazonian forest primarily for capturing arboreal snakes disturbed by monkey troop movements.

Key words: *brown capuchins, Cebus apella, French Guiana rainforest, Leucopternis albicollis, White Hawks.*

The White Hawk (*Leucopternis albicollis*) inhabits the tropical rain forest primarily from Colombia and the Guianas to Bolivia and Amazonian Brazil, and it primarily eats reptiles (Brown and Amadon 1968). The brown capuchin monkey (*Cebus apella*) is a medium-sized arboreal primate, with newborn infants weighing 220 g and adult males more than 3 kg (Napier and Napier 1967), distributed widely throughout the Neotropics in various forest habitats (Freese and Oppenheimer 1981). This species is considered to be frugivore-insectivore (Robinson and Janson 1986), and spends a major part of its daytime activity foraging for invertebrates and small vertebrates.

Although White Hawks and brown capuchins live in sympatry over large areas of South America, the only report of the association between these two species was made by Boinski and Scott (1988) in Costa Rica, where White Hawks were occasionally observed following brown capuchins. However, while studying

the feeding ecology of brown capuchins in an intact rainforest of French Guiana, we frequently saw White Hawks accompanying these monkeys. In this paper, we report the characteristics of the hawk-capuchin association and try to explain why the White Hawk follows these monkeys.

METHODS

The study area is located in an undisturbed primary forest around Nouragues (4°05'N, 52°40'W), an ecological station in French Guiana. The station is near a 411-m granite dome (Inselberg), 100 km from the Atlantic Coast (Erera et al. 1989). The climate is characterized by an annual dry season (mid-August to mid-November) and a long rainy season interrupted by a 3-week dry period between February and March. The average annual rainfall exceeds 3 m (Finkelstein 1982), and yearly minimum and maximum temperatures average 22.0°C and 31.2°C, respectively. The geography of the study site is described in Zhang (1995a).

The focal capuchin group consisted of 13 individuals (1 adult male, 2 adult females, 2 subadult males, 4 subadult females, 3 juveniles, and 1 infant) at the beginning of the study (Zhang 1994).

Two White Hawks had been observed following the capuchin troop. Primarily, a single hawk accompanied the capuchins and, on rare occasion, both individuals followed the monkeys together. As the two hawks were extremely similar, it was difficult to distinguish one from the other. We believe they were a pair as they were frequently seen resting on the tree branch side by side, particularly after a heavy rain.

The capuchin group was followed from dawn to dusk for a total of 132 days, from April 1991 to July 1993. Scan sampling (Altmann 1974) was employed to monitor their ranging pattern and activity. The study area included mapped and tagged trails, and a 1-ha grid was superimposed on the site map of 1:10,000 scale. For each 15-min sighting, the location of capuchins was assigned to the quadrat containing the center of the troop. The movement routes of the group were then drawn by joining the consecutive quadrats entered.

The activities of the capuchin group were divided into three speed-related categories: traveling, feeding, and resting. Traveling is the rapid locomotion of the whole group when the monkeys moved from one site

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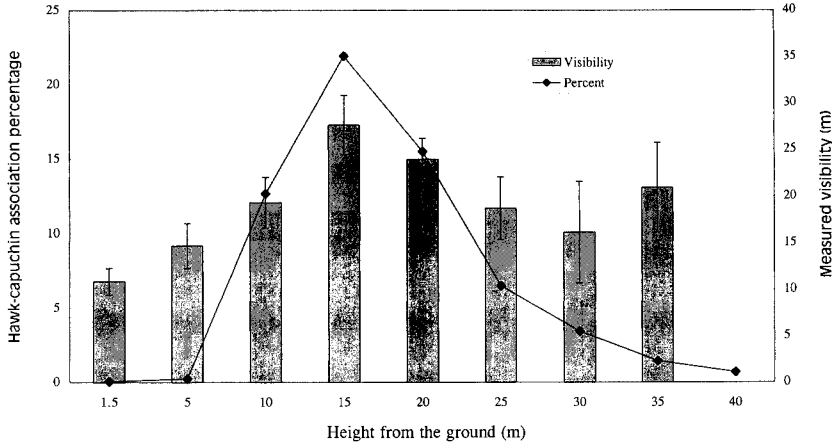


FIGURE 1. Percent of hawk-capuchin association and horizontal visibility (\pm SD) at different heights of the high forest.

to another. Feeding is the slow locomotion of the group when the animals searched, manipulated, and ingested all food material. Resting describes capuchins' sedentary state in which they were not traveling nor feeding, and included social behavior such as grooming and sleeping.

The hawk-capuchin interactions were recorded whenever one or both hawks were observed in the vicinity of the troop. When the hawk could not be located in two successive 15-min sampling sequences, it was thought to be away at the sequence following the last hawk observation. The following information also was recorded: (1) perching sites of White Hawks with reference to the capuchin troop, (2) the monkeys' alarm responses relative to the behavior and the spatial locations of the hawk (above, same height, or below the troop), and (3) antagonistic reactions of capuchins to hawks.

In order to avoid mistaking the coincident presence of hawks near the monkey troop for the hawk's active monkey-following behavior, they were judged "in association" (Fontaine 1980) only when the hawk was seen in a minimum of two successive sample sequences. It was usually easy to detect White Hawks in the forest because of their prominent white color.

The visibility at different heights in the high forest was measured as follows. We reached to the given height of the platform system (Zhang and Wang 1995) by using the climbing technique described by Perry (1978), and looked at eight directions which were 45°C from each other (north, north-east, etc.). The longest distance clearly observed from the platform was measured by another person on the ground. A total of six platforms were used, and the visibility at a given height was obtained by averaging all distances measured.

RESULTS

The home range size of the capuchin group was 355 ha, of which 322 ha were seen entered by the capuchin troop (Zhang 1995b); the hawk-capuchin association

occurred in 212 ha of the monkeys' range. The area used by the capuchin troop covered five forest types: high forest, pina swamp forest, liana forest, low forest, and transition forest. The hawk-capuchin interaction only occurred in the first three forest types, but the association occurring in liana was significantly less than expected ($\chi^2_1 = 8.8$, $P < 0.05$).

The capuchin troop usually was spread over an area of about 80×80 m during their movement. White Hawks showed a relatively regular flying pattern when following monkeys, they flew soon after most capuchins started moving and usually perched toward the leading quadrant area occupied by the moving monkey troop. White Hawks mostly (66.8%) perched in front of the moving capuchin troop, and rarely (4.1%) behind it. The preference of perching in the front was significant ($\chi^2_1 = 68.9$, $P < 0.001$).

White Hawks mainly (80.2%, $n = 281$) perched on branches 10–25 m high when following monkeys, and capuchins spent 65% of their daytime in the middle height stratum, 15 to 30 m above the ground. In most cases (66%, $n = 231$), hawks remained under the troop, and in fewer cases they were sighted above (15.8%, $n = 55$) or horizontal to (18.2%, $n = 64$) the capuchins. Rarely did the hawks fly from a low position to a high position or vice versa in relation to the monkey troop.

In high forest, the measured horizontal visibility distance varied considerably at different heights. Maximum horizontal visibility is around the height of 15 m above the ground (Fig. 1), because the crowns of short trees do not reach this height and the branches of high trees exceed it. A significant correlation ($r = 0.86$, $P < 0.01$, $n = 8$) was found between perching frequency by hawks and the visibility distance at various heights, signifying that hawks preferred perching at high-visibility sites when following monkeys.

The hawk-capuchin association occurred throughout the year, covering 11% of the activity time of the capuchin troop. The association events varied widely throughout the day ($\chi^2_{12} = 76.2$, $P < 0.001$), with

peaks at 10:00–11:00 ($\chi^2_1 = 7.8$, $P < 0.05$) and 14:00–15:00 ($\chi^2_1 = 5.0$, $P < 0.05$). In early morning and late afternoon, hawks rarely followed capuchins.

A hawk's flight often elicited capuchins' alarm calls, which were short and clear, sounding much like a dog's bark. Only one direct agonistic episode was observed: the adult male capuchin descended carefully near the ground, as a hawk flew directly toward it. As the hawk neared the monkey, the monkey jumped on the ground, then returned rapidly to the canopy and scurried from one tree to another. Shortly after, the monkey quietly ate a toad (*Bufo* sp.) on a branch near the hawk. Twenty minutes later, it threw away the remains of the dead toad and climbed slowly upward. Suddenly, it leapt towards the hawk which flew away before being touched by the monkey.

DISCUSSION

The following of monkey troops by bird species is a widespread phenomenon. It has been reported in the Neotropics (Terborgh 1983, Boinski and Scott 1988), African (Chapin 1939), and Asian (Scott 1947, Oppenheimer 1977) forests. Birds usually were considered to be the principal beneficiaries of this association. They benefit from the disturbance created by the monkeys' movement through the foliage to harvest flushed prey; primates were thought to neither gain nor lose (Terborgh 1983).

For the association between White Hawks and the brown capuchin in French Guiana rain forest, we propose that the principal benefit to the hawks is to capture arboreal snakes based on the following reasons:

(1). Hawks usually followed capuchins in high forest and pina swamp forest. Compared with the three other forest types in the home range of the studied monkey troop, the common characteristics of these two forest types are that they are open, and the hawks while perched can see a greater distance in these two forest types than in the other three. In fact, in the low forest and the liana forest, capuchins are often conspicuously exposed in the canopy when exploiting fruits and flowers or foraging on insects. The following by the hawk should have been more intensive in these habitats than in the others if its goal was to seize the monkeys.

(2). Hawks perched ahead of the troop when following capuchins. This could be very advantageous for the raptor as it presented the possibility of detecting arboreal snakes disturbed by the movement of any monkey. Obviously, the hawk could be easily detected by most monkeys in such a position. This behavior was quite different from the feeding strategy of most other raptors, which usually capture prey (particularly arboreal mammals) by a sudden attack.

(3). For the same reason, hawks significantly preferred to follow the monkeys at tree heights which allowed the monkeys to be seen at a distance.

(4). Throughout a day, hawks intensively followed capuchins when the monkey troop moved, and they rarely associated with capuchins when the monkey troop rested. This implies that hawks profited directly from the movements of the troop.

(5). Although *Cebus apella* exhibited a short series of low frequency loud calls when a hawk flew near

the troop, this did not mean the raptor was a real danger to these monkeys, because other nonpredatory birds of large size, such as toucans (*Ramphastos* sp.) and macaws (*Psittacula* sp.) sometimes evoked the same calls. Conversely, a genuine aerial predator such as the Guiana Crested Eagle (*Morphnus guianensis*) typically elicited "mob" behavior by the troop. Furthermore, no member of the capuchin group was lost during our field study. If the hawks had followed the capuchin troop to capture young, we would expect a stronger response by the monkeys.

(6). We observed seven instances of a hawk having captured a tree snake in proximity to the monkeys.

We conclude that following of capuchins by White Hawks is for capturing arboreal snakes disturbed by the movement of the monkey troop in the French Guiana rainforest.

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LONG-TERM PAIR BONDS IN HARLEQUIN DUCKS¹

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Abstract. We documented the frequency of pair reunion in Harlequin Ducks (*Histrionicus histrionicus*) on breeding streams in Alberta, and at a molting/wintering area in southwestern British Columbia. As long as their mate is alive, Harlequin Duck pairs reunite on the wintering area and return to the breeding stream together. Pairs reunite even if the female is unsuccessful at breeding the previous season, which suggests that reuniting with the same mate year after year is important. Some males that have lost their mate and fail to re-pair on the wintering area show fidelity to their former breeding site.

Key words: *breeding site fidelity, Harlequin Duck, Histrionicus histrionicus, mate fidelity, pair reunion.*

New pair formation in many of the annually monogamous migratory duck species takes place at the non-breeding area, often months ahead of the breeding season (Bluhm 1988, Rohwer and Anderson 1988). With-

in the sea ducks (Mergini), timing of pairing varies from September in Common Eiders (*Somateria mollissima*) (Spurr and Milne 1976) to March in Buffleheads (*Bucephala albeola*) (Erskine 1972). In Harlequin Ducks (*Histrionicus histrionicus*), pairs detected in a previous winter reunite in the fall and new pair bonds (including those with young females) form in the spring, both events occurring at the wintering area (Gowans et al. 1997, Robertson et al. 1998).

Although it has been assumed that pairs that formed or reunited in the winter continue through to the breeding season, there has only been one incident recorded for a migratory duck species: one pair of Barrow's Goldeneye *Bucephala islandica* was observed in both locations (Savard 1985).

Given that Harlequin Ducks show long-term pair bonds (Gowans et al. 1997, Robertson et al. 1999), we examine whether: (1) reuniting is the rule rather than the exception, (2) reuniting during the winter results in the pair breeding together in the following summer, (3) pairs reunite even when breeding was unsuccessful, and (4) some males that fail to re-pair in the winter return to their previous breeding area.

The following definitions are used in this paper. A *long-term pair bond* between a male and a female lasts for two or more breeding seasons, but may be interrupted during the breeding season (Fowler 1995). *Reuniting* is pairing with the same mate for a second or subsequent season. *Mate change* refers to pairs that terminate, or fail to reunite for any reason, including death, disappearance, or divorce (Black 1996), followed by *re-pairing* with a new partner (Rowley 1983).

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