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Predation by Squirrel Monkeys and Double-toothed Kites on Tent-making Bats

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Central American squirrel monkeys *(Saimiri oerstedi)* appear to recognize the modified leaves that phyllostomid bats utilize for diurnal roost sites. The monkeys visually and manually search these bat tents for both bats and insects. Adult males are the most successful at capturing bats. Nonvolant juvenile bats are more vulnerable to monkey predation than are adults. Bats that escape monkey predation frequently are captured by double-toothed kites *(Harpagus bidentatus)* that tend foraging troops of monkeys. Predation by squirrel monkeys, coupled with that of double-toothed kites, may be a significant source of mortality for tent-making bats.

Key words: *Saimiri oerstedi*, squirrel monkey, bats, Costa Rica, double-toothed kites, foraging behavior, tent-making bats, wasps

INTRODUCTION

Squirrel monkeys eat a wide variety of foods including fruits, nuts, flowers, buds, seeds, leaves, gum, insects, and to a lesser extent smaller vertebrates [Fooden, 1964; Thorington, 1968; Mittermeier & Coimbra-Filho, 1977; Boinski, 1980]. Recently, we observed Central American squirrel monkeys *(Saimiri oerstedi)* apparently recognizing leaf roosts ("bat tents" constructed by phyllostomid bats for diurnal roosts) and actively searching them for animal inhabitants. These observations are of interest because they represent the first report of any predator recognizing the cut leaves that several species of tropical bats use as diurnal roosts. They also exemplify a complex and specialized foraging skill used by the omnivorous squirrel monkey. The bats involved have specialized predator avoidance tactics that certain squirrel monkeys attempt to thwart, although not always successfully.

Several species of Neotropical fruit-eating bats (Phyllostomidae; Stenoderminae) are known to modify leaves of various plants to produce daytime roosts termed "tents" [Barbour, 1932; Chapman, 1932; Foster & Timm, 1976; Timm & Mortimer, 1976; Timm, 1984, in press]. Three species of tent-making bats, Thomas' fruit-eating bat *(Artibeus watsoni)*, Peter's tent-making bat *(Uroderma bilobatum)*, and the little yellow-eared bat *(Vampyressa pusilla)* occur within our study area. The form, appearance, and size of the tents varies considerably. Each species of bat creates its own distinctive style of tent on from one to several plant species. The cryptic roost sites provided by tents are thought to protect bats from predators as well as sun and rain [Timm & Mortimer, 1976; Timm, 1984, in press].

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The objectives of this report are to describe foraging behavior of squirrel monkeys at bat tents, to document that the monkeys do obtain an array of animal protein from bat tents including both bats and insects, and to document that double-toothed kites routinely tend troops of squirrel monkeys and readily consume bats flushed by the monkeys.

METHODS

Squirrel monkeys *(Saimiri oerstedi)* were observed intensively from February through September 1982 and from June 1983 through September 1984 at Estación Sirena, Parque Nacional Corcovado, Costa Rica, by Boinski as part of a long-term study of their ecology. Timm studied tent-making bats at Corcovado in June and August in 1982 and in August of 1984.

The free-ranging monkeys are well habituated. Over 75% of the focal animal behavioral samples of squirrel monkeys during this study were at a distance of 10 m or less. This proximity to foraging animals permitted detailed observations on squirrel monkeys foraging and specifically what food items are consumed.

Corcovado National Park is located on the Osa Peninsula of southwestern Costa Rica (between 8°27′ N and 8°39′ N, and 83°25′ W and 83°45′ W); the elevation ranges from sea level to 400 m. Corcovado lies within the Tropical Wet Forest Life Zone, with lowland evergreen forest the dominant forest type. Mean annual rainfall is 3,800+ mm, with the wettest months being August–November; mean monthly temperatures range from 25.0°C to 26.5°C. Vegetation and habitat types at Corcovado have been described by Herwitz [1981] and Hartshorn [1983].

RESULTS AND DISCUSSION

Tent-making bats construct a tent by chewing the lateral nerves and interconnecting tissues radiating from the midrib, causing the sides of the leaf to collapse down around the midrib (Fig. 1). A tentlike structure is formed, and the bats hang from the midrib where they are well concealed from predators both from above and the sides [Timm, in press]. Tents also function to protect roosting bats from rain and intense sunlight. In addition to housing adult bats, tents serve as natal roosts. During the reproductive season, most adult females found in tents are accompanied by a single young. Bat tents are also occupied by a wide array of insects.

The three species of tent-making bats found at Corcovado are obligate tent-makers [Timm, in press]. They construct a series of tents scattered through a relatively restricted area of forest. A tent may be used from one to several days in succession before a shift is made to the next tent. Bats disturbed from a roost tent take flight immediately and may either attempt to return to the same tent or fly directly to another. As each bat or colony of bats uses a series of tents scattered throughout the forest, only a fraction of the cut leaves are occupied by bats on any given day.

We have observed tents of *Artibeus watsoni* constructed of leaves of the following plants: *Anthurium ravenii* (Araceae); *Asplundia* sp. and *Carludovica palmata* (Cyclanthaceae); *Asterogyne martiana, Geonoma* sp., *Welfia georgii*, and juvenile coconut palms, *Cocus nucifera* (Palmae); *Heliconia imbricata, H. latispatha, Heliconia* sp., and *Musa x paradisiaca* (Musaceae); and *Calathea insignis* (Marantaceae). Of tents used by *A. watsoni*, only approximately one in 20 tents is occupied. Leaves that have been cut by bats represent only a small fraction of the leaves available on any given plant. Depending on the species of bat and plant, and type of habitat involved, roost leaves may constitute from less than 1% up to 5% of the leaves of plant species.

The number of bats found in an individual tent varies considerably depending upon the season and the social system of that species. For solitary species, tents are

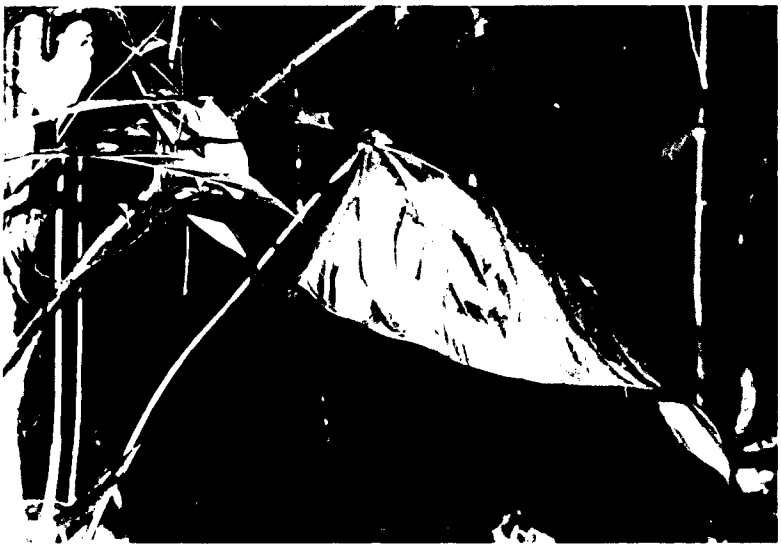

Fig. 1. Tent of *Artibeus watsoni* on *Anthurium ravenii* (Araceae). The basal lateral nerves of the leaf have been severed by the bats, causing the sides of the leaf to collapse around the midrib, forming a tentlike roosting structure. (Photograph by R.M. Timm.)

occupied by only single individuals or a female with offspring. In monogamous bats, mated pairs are usually found together and may be accompanied by a single young. In a harem species such as *Uroderma bilobatum*, colony size averages 10–15 individuals but may include as many as 50 [Timm, in press].

At Parque Nacional Corcovado, squirrel monkeys eat a wide array of plant and animal material, including larval, pupal, and adult insects, flower nectar, fruits, frogs, anole lizards, bird eggs and nestlings, earthworms, and occasionally bats [Boinski, personal observation]. Most food items are small and widely scattered. In contrast to reports from Peru [Terborgh, 1983], large, discrete fruit patches such as a fig tree are not a major food source.

A foraging squirrel monkey troop is best described as an aggregation of individual foragers. Aside from small infants (< 3 months), each troop member must be able to recognize, harvest, and appropriately process its own food items. Squirrel monkeys recognize from distances exceeding 20 m leaves that have been altered by bats to form tents. Bat tents and naturally formed cavities in both live and dead foliage are used by a diverse fauna including frogs, orthopterans, hymenopterans (both ants and wasps), and lepidopterans. Altered leaves and leaf cavities indicate suitable, more productive foraging substrates. The most ubiquitous foraging technique used by squirrel monkeys is scanning foliage for these microhabitats and stationary and or cryptic insects.

Squirrel monkeys were observed on 24 separate occasions leaping on bat tents and in five additional instances stalking the tent's occupants. In both types of approach, the initial response of a squirrel monkey on identifying a tent was to approach closely from the side or below and to visually inspect it. A leap at the bat tent flushed the bats immediately. Only once was a squirrel monkey clearly seen to capture a juvenile bat (*Artibeus watsoni*) that had been knocked to the ground. After capture, the 4-year-old male monkey delivered seven sharp bites to the head. He

then climbed to a 2-m-high branch (most likely to avoid three curious juveniles) and proceeded to consume the entire bat in 1 minute 40 seconds. Only a few tissue fragments and drops of blood remained. Nonvolant young or weakly flying subadult bats would be especially vulnerable to both the leaping and stalking tactics of squirrel monkeys. With other small vertebrate prey items such as lizards and frogs, the entire body is usually ingested.

In three additional instances, squirrel monkeys were observed eating small brown objects on the ground after such leaps at tents. Because of the distance involved and the speed at which objects were consumed, positive identifications could not be made, but it is likely that they were bats. Despite observed attempts, there is no evidence of a squirrel monkey successfully stalking roosting adult bats. A bat tent's supporting leaf petiole very sensitively conveys warning of squirrel monkey movement or of any similar predator. Interestingly, all attempts to stalk roosting bats were made by juvenile squirrel monkeys, and only adults leapt at bat-occupied tents.

Squirrel monkey foraging behavior is not conducive to long-term tent occupancy by bats in frequently foraged areas. Tent-making bats are sensitive to disturbance and readily abandon tents. Indeed, the strong impression we received while walking through the troop ranges, which varied monthly from 1 to 2 km^2, was that the density of bat tents and the percentage occupied by bats was much greater in areas that had not been utilized by squirrel monkeys within the previous several months. Concomitantly, when squirrel monkeys first foraged in an area after a several-month lapse, they located and searched tents much more frequently than in areas where they had foraged regularly for several weeks.

In addition to bats using tents as roost sites, wasps also utilized them as sites to construct paper nests. As wasps and bats were not observed using the same tent concurrently, we believe that when wasps take over a tent, they subsequently prevent the bats from using it. This is almost surely the case with the most common wasps found in bat tents, the genus *Polybia*. *Polybia* wasps are medium-sized, construct small (4–6-cm diameter) spherical paper nests, and are noted for their aggressive behavior toward intruders. When monkeys noticed a wasp nest in a bat tent, the tent was approached from a nearby branch, tree, or from underneath. The monkey leapt at the tent, often repeatedly, attempting to knock the nest to the ground. The wasp nest was not touched directly, but rather jarred from the exterior of the tent. Once contact was made with the tent that contained wasps, the monkey hit the ground and rolled from one to several meters, thus avoiding direct attack by wasps. When a nest was successfully knocked to the ground and broken, the monkey would grab a piece of the broken nest and run some distance away where he would stop and consume the larvae. If the nest remained intact, it was broken into pieces, each piece was carried away from the main nest, and the larvae were consumed. Squirrel monkeys were observed on 11 occasions knocking wasp nests from bat tents in this manner, and then feeding upon the wasp larvae. Again, a few adult males were the most successful foragers with this technique.

Double-toothed kites *(Harpagus bidentatus)* at Corcovado consistently followed troops of squirrel monkeys and to a lesser extent white-faced capuchins *(Cebus capucinus)*. The kites perched on horizontal branches amidst foraging monkey troops. Animals disturbed by the monkeys' foraging activities, upon escaping the monkeys, became susceptible to kite predation. Prey items taken by kites in this manner at Corcovado included small arboreal lizards, grasshoppers, katydids, cicadas, and bats.

Squirrel monkeys were observed flushing bats on numerous occasions; in two instances an attending kite captured and consumed one of the bats. On the first occasion, a subadult squirrel monkey unsuccessfully stalked four or five roosting

Artibeus watsoni on *Carludovica palmata* by slowly climbing the frond's petiole. An attending double-toothed kite swooped in as soon as the bats flushed and captured one in flight. It then landed on a nearby branch and ate the bat. On the second occasion, squirrel monkeys flushed two *A. watsoni* from a tent in *Heliconia*. A double-toothed kite caught one bat in flight at roughly 4 m from the ground and glided to the ground with the bat in its talons. The kite readjusted its grip on the bat, flew to a branch, and ate. Bats are only susceptible to kite predation when disturbed from their roosts by foraging monkeys. Kites were commonly observed capturing insects in flight, especially large orthopterans, that had been flushed by foraging squirrel monkeys. These observations are in accord with previously published observations of the double-toothed kite behavior of capturing insects in flight that have been flushed by foraging monkeys [Greenlaw, 1967; Fontaine, 1980; Ridgely, 1976]. Our observations are the first report of double-toothed kites catching and consuming bats.

Of the four cebid monkeys in Parque Nacional Corcovado *(Alouatta palliata, Ateles geoffroyi, Cebus capucinus*, and *Saimiri oerstedi)*, squirrel monkeys are perhaps the most effective "beaters" for double-toothed kites. Typical squirrel monkey foraging behavior of manually searching and moving both living and dead foliage, combined with high activity levels (ie, frequent jumping, walking, and leaping) by large congregations of animals (35–55 individuals per troop), contribute to their effectiveness in flushing prey for kites.

Primates eat a wide variety of insects, spiders, and smaller vertebrates such as frogs, lizards, birds, and bird eggs [Butynski, 1982]; however, there are few records of predation upon mammals and only a single confirmed record of predation upon a bat. Charles-Dominique [1974:144] reported a single instance of the nocturnal potto *(Perodicticus potto)* eating a bat, stating that "we surprised a female devouring a young frugivorous bat *(Epomops franqueti)*. Capture of such prey must be relatively rare." Rosevear [1965:14] stated of West African bats, "There is a strong probability that open-woodland species which shelter in rock cavities fall victims not only to snakes but to baboons as well, which will consume any flesh they can seize upon." Sanderson [1957] mentions that sakis *(Pithecia)* eat bats.

Bats do not constitute a major component of the diet of squirrel monkeys; however, they are an additional source of protein that older, more skilled foragers exploit. The foraging behavior and resulting predation of squirrel monkeys upon bats, coupled with predation upon bats by double-toothed kites, may constitute a major source of mortality for bats.

Previously it was thought that primates had little or no effect upon bat communities. This study suggests that squirrel monkeys can have a major impact upon bat populations and reinforces the need for long-term studies of organisms within intact communities. Studies of population dynamics or predation pressure upon bats at a tropical site where squirrel monkeys are no longer present would have led to erroneous conclusions. As monkeys are removed from neotropical communities as a result of human activity, immediate and long-term repercussions affecting multiple trophic levels are to be expected.

CONCLUSIONS

1. Squirrel monkeys appear to recognize tents created by phyllostomid bats and actively search them for food, obtaining bats, wasps, and other insects.

2. Recognition of bat tents and the foraging skills needed to obtain food from them successfully seem to be an individually learned skill; adult male squirrel monkeys are most successful at exploiting tents.

3. Double-toothed kites routinely follow foraging troops of squirrel monkeys and prey upon bats and insects flushed by the monkeys.

4. Squirrel monkeys probably constitute a significant source of mortality for tent-making bats both by direct predation and indirectly by flushing bats from their diurnal roosts, thereby exposing them to predation by double-toothed kites.

RESUMEN

Los monos ardillas centroamericanos (*Saimiri oerstedi)* reconocen las hojas modificadas que murciélagos filostómidos utilizan como perchas diurnas. Los monos visual y manualmente buscan en estas carpas por murciélagos e insectos. Machos adultos son los más exitosos en la captura de murciélagos. Murciélagos jovenes incapaces de volar son más vulnerables a la predación por monos que los adultos. Murciélagos que escapan predación por monos, frecuentemente son capturados por gavilán bidente *(Harpagus bidentatus)* que siguen tropas de monos forrajeadores. La predación por monos ardillas acompañada con aquella del gavilán bidente puede ser un significativo recurso de mortalidad para murciélagos constructores de carpas.

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