

# FORAGING AND DAY-ROOSTING DYNAMICS OF CANOPY FRUIT BATS IN PANAMA

DOUGLAS W. MORRISON

**ABSTRACT.**—Radio-tracking was used to monitor day-to-day changes in feeding areas, day-roosting sites, and roost group composition of two species of foliage-roosting fruit bats, *Artibeus lituratus* and *Vampyrodes caraccioli*. The bats changed roost sites almost daily but did not move to sites closer to current feeding areas. Relatively stable groups of one male and two or three females with young used and reused several foliage sites in areas of 0.5 to 2.5 ha and commuted to feeding areas up to 2.5 km away. Sit-and-wait predators like owls seem to be attracted to fruiting trees. The bats suspended or greatly reduced feeding passes to fruiting trees during periods of bright moonlight, but searching and commuting flights occurred even in the brightest moonlight. Predation pressure is implicated in the evolution of both foraging and roosting behaviors.

Recent studies of the Jamaican fruit bat, *Artibeus jamaicensis*, indicate that the relative permanence of day-roosting sites may influence both foraging and social behaviors. Female *A. jamaicensis* that roosted in tree hollows commuted almost twice as far to food trees as males using more transient day roosts in foliage (Morrison, 1978a). Because foliage roosts (e.g., palm fronds and subcanopy trees) appear to be much more abundant than suitable tree hollows in a tropical forest, it may be easier for foliage-roosting bats to find suitable sites closer to the fruiting trees than in use. Female *A. jamaicensis* probably return to tree hollows to reduce predation on themselves and the young they leave behind while foraging. A harem mating system appears to have evolved around male defense of hole roosts used by postpartum estrus females, with foliage roosts occupied by subadults and solitary males (Morrison, 1979).

Unlike *A. jamaicensis*, most species of canopy fruit bats are reported to roost in foliage (Goodwin and Greenhall, 1961). The present study was undertaken to determine whether the behaviors described for *A. jamaicensis* are typical of canopy frugivores in general or are in some ways unique due to the hole-roosting habits of the females. In this report I describe the foraging behavior and roosting dynamics of two canopy fruit bats, *Artibeus lituratus* and *Vampyrodes caraccioli*, both sexes of which roost in foliage. Using radio-tracking I was able to monitor night-to-night changes in feeding areas and daily changes in roosting sites and composition of roosting groups. Both species showed affinities for roosting sites and roosting groups that did not require returning to a single, permanent roost site.

*Artibeus jamaicensis* interrupt their foraging activities to return to their day roosts during periods of bright moonlight (Morrison, 1978b). Close monitoring of foraging movements revealed that the inhibitory effects of moonlight on *A. lituratus* and *V. caraccioli* are less clearly defined. In spite of interspecific differences, these observations support the hypothesis that lunar phobia has evolved to reduce vulnerability to visually orienting predators.

## MATERIALS AND METHODS

Barro Colorado Island in the Panama Canal Zone is a 15-km<sup>2</sup> island covered by semi-evergreen, moist tropical forest. Rainfall averages 2,800 mm per year, with less than 10% of this falling during the 4-month dry season, January through April. This study was conducted during 6 months of the rainy season, May through August and November through December 1978.

Several species of bat on Barro Colorado show a preference for figs (*Ficus* spp.) and other



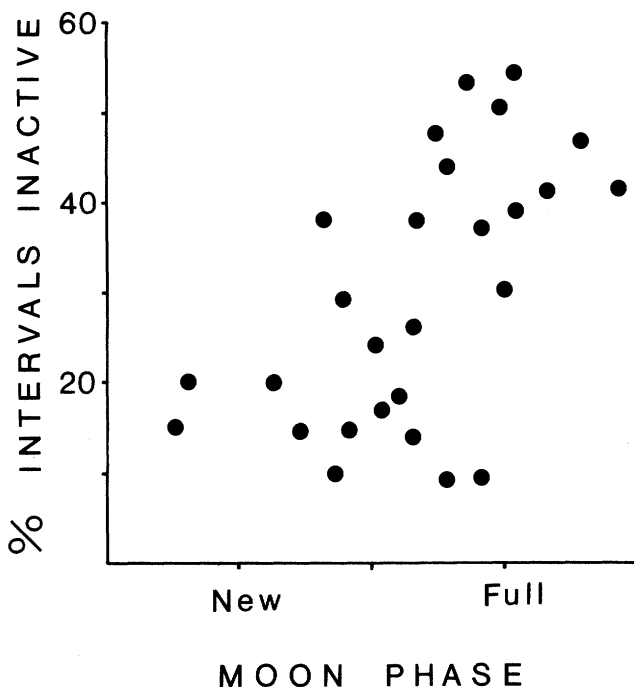


FIG. 2.—Percentage of 15-min intervals in 27 nights of foraging during which a radio-tagged *Artibeus lituratus* did not fly, shown relative to the phase of the moon.

of these nights, radio contact was maintained from the time the bat left its day roost until it returned at dawn. Observations on two female and one male *V. caraccioli* totalled 85 h over 16 nights, with 4 complete nights recorded. The other seven radio-tagged bats had early transmitter failure, roosted out of range, or foraged in areas too far from the trails to be accessible at night.

## RESULTS

### *Feeding Behavior*

The foraging behaviors of *Artibeus lituratus* and *Vampyroides caraccioli* were similar. Both left their day-roosting areas about 45 min after sunset, although departure times varied within individuals (range of SD, 5–18 min) and among individuals (e.g., two *A. lituratus* females consistently departed before dark,  $20 \pm 11$  min after sunset,  $n = 17$ ). From the roost area the bats usually flew directly to a fruiting tree, 150 to 2,300 m away ( $\bar{X} = 750$  m,  $n = 19$ , for *A. lituratus*;  $\bar{X} = 850$  m,  $n = 7$ , for *V. caraccioli*).

In the course of a night of foraging, the bats visited and revisited two or three (once four) different fruiting trees. During 63% of the 27 all-night tracking observations on *A. lituratus*, the radio-tagged bat took fruit from two trees 200 to 800 m apart ( $\bar{X} = 500$  m) and changed between these two trees two to five times. On 33% of the nights, the *A. lituratus* used three trees 150 to 550 m apart ( $\bar{X} = 350$  m) and changed trees from four to seven times. More limited tracking observations on *V. caraccioli* indicate a similar pattern.

When feeding, the bats did not hang on the fruiting tree but carried away one fruit at a time to a feeding roost less than 100 m away. Most flights (feeding passes) from the feeding roost to the fruit tree and back required 3 to 5 min of flying time, with most of this time spent in the hovering or circling involved in selecting a fruit. Because the bats changed fruiting trees several times a night, I was able to make a complete

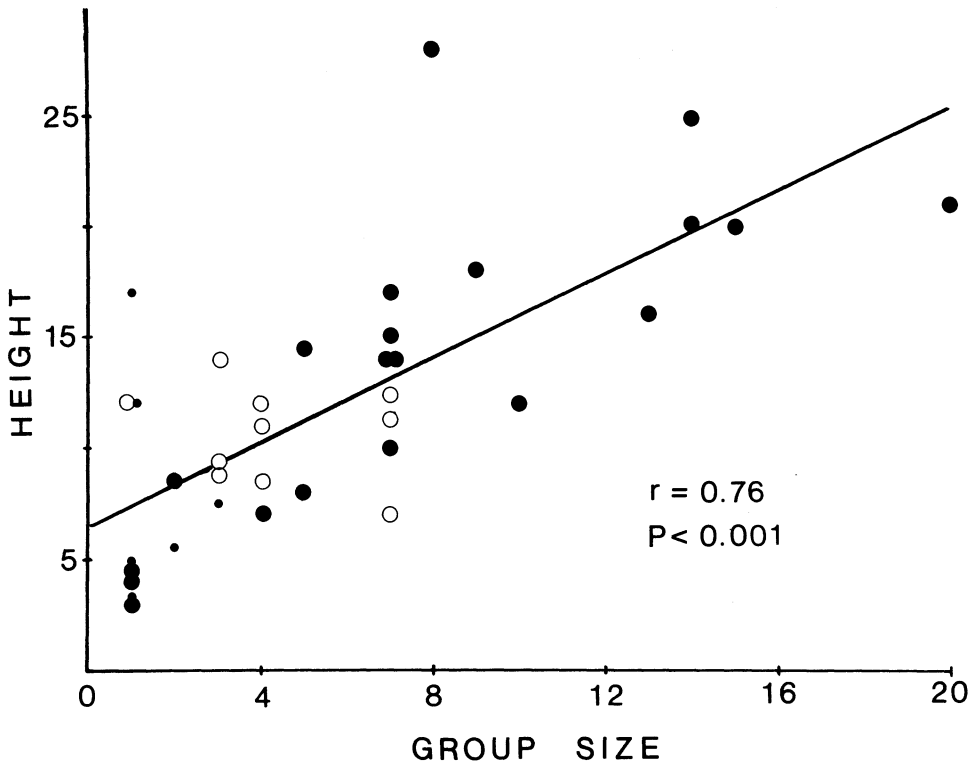


FIG. 3.—Height of day-roosting sites (in m above ground level) used by radio-tagged *Vampyroides caraccioli* females (open circles), *Artibeus lituratus* females (large dots), and *A. lituratus* males (small dots) plotted against the largest group size observed at that site.

count of feeding passes on only 4 nights. During the week following the full moon in mid-November, a 73-g, post-lactating *A. lituratus* fed for 5 consecutive nights from two fig trees (*Ficus insipida* and *F. yoponensis*). Feeding passes were directed primarily to the *F. insipida* (with 9-g figs) but over the course of the week shifted to favor the *F. yoponensis* (with 5-g figs) as the *F. insipida* fruit crop was depleted. Based on four all-night counts, this female carried away  $134 \pm 6$  g of figs per night.

#### Searching Behavior

On 12 occasions, the radio-tagged bats engaged in unusually prolonged bouts of flying lasting 10 to 33 min ( $\bar{X} = 15 \pm 8$  min). All such bouts occurred before 0100 h and most (58%) were initiated between 2000 and 2200 h. The flights were clearly not routine feeding passes or changes between fruit trees and may have been made in search of new fruit trees. The timing of these flights did not appear to be influenced by moonlight. Six of the flights, including the two longest (32 min by a female *A. lituratus* and 33 min by a female *V. caraccioli*), occurred during bright moonlight, three occurred when the moon was less than 30 degrees above the horizon, and three when there was no moon.

#### Influence of Moonlight on Foraging Activity

Overall, foraging activity was correlated with the phase of the moon. On nights 1 week before and after new moon, the radio-tagged *A. lituratus* were active throughout

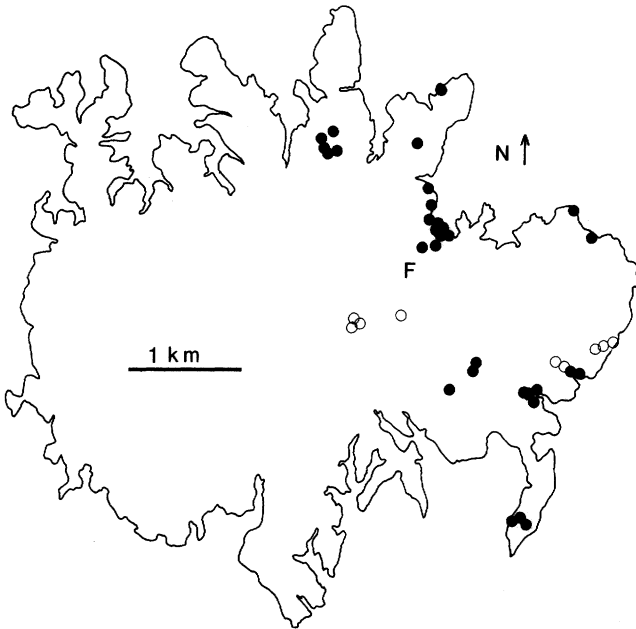


FIG. 4.—Day-roosting sites used by *Vampyroides caraccioli* (open circles) and *Artibeus lituratus* (dots) on Barro Colorado Island, relative to the feeding area (F) in which 80% of the bats were initially radio-tagged.

the night, pausing for never more than 0.5 h at a time (Fig. 1). Dividing the night into 15-min intervals, most of the *A. lituratus* did some flying in all but 20% of the intervals (Fig. 2). In contrast, on nights around full moon, the bats suspended their flying activities for up to 55% of the 15-min intervals (Fig. 2). *Vampyroides caraccioli* showed a similar pattern, sometimes remaining inactive for periods as long as 4 h, but frequently flying even when the moon was full and near its zenith.

During short periods of inactivity, the bats stayed at the sites they were using as feeding roosts. For longer periods of inactivity (>1.5 h), the bats moved farther away (150–350 m) from the fruiting tree, but they did not go back to the day roost, even when the day-roost area was relatively close. For example, an *A. lituratus* female remained inactive 150 m from the fruit tree for 5 h before flying the 350 m to her day roost just before dawn. A second female, feeding 300 m east of her day roost, flew 350 m to a second site 200 m south of the day roost. There she remained inactive for 2.5 h before returning to the fruiting tree to resume feeding. Only once did a bat return to the day-roosting area. In this case the fruiting tree was 1.7 km from the day roost and the bat did not return to that fruit tree until the next night.

#### Day Roost Sites

Female *V. caraccioli* invariably (nine sightings) roosted during the day in groups of three or four adults, 7 to 12 m above the ground under the umbrella-like crowns of understory trees (trunks 12–20 cm in diameter at breast height). The radio-tagged male, however, roosted alone. The day-roosting behavior of *A. lituratus* was more variable. Bats were found roosting from 2.7 to 28 m above the ground in a variety of situations, such as under broken or crossed *Oeneocarpus* palm fronds, in vine-tangled crowns of subcanopy trees, and in cavelike recesses on the undersides of the crowns of canopy-height trees. Group size varied from one (usually male) to 20. The size of

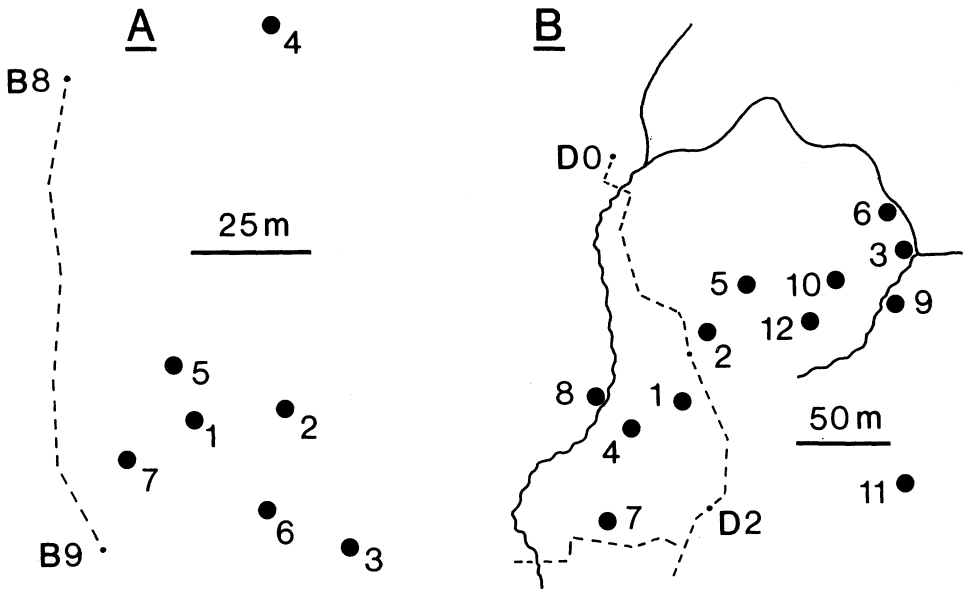


FIG. 5.—Day-roosting sites (A) used by a group of *Vampyroides caraccioli* near Balboa trail 8–9 over a period of 13 days, and (B) used by a group of *Artibeus lituratus* near Donato trail 0–2 over a period of 34 days.

the group was significantly correlated with the site's height above the ground ( $r = 0.76$ ,  $P < 0.001$ ; Fig. 3).

Both species favored day roosts near the shoreline or on ridge tops. Of 37 different sites used by *A. lituratus*, 71% were less than 200 m from the shoreline and eight of the 11 sites in the island's interior were at the tops of hills or ridges (Fig. 4). Of 13 sites used by *V. caraccioli*, 38% were near the shoreline and 58% on ridge tops.

#### Fidelity to Day Roosts

Although the bats rarely used the same day-roosting site on more than 2 consecutive days, all but one (a lactating *A. lituratus* who had lost her young) returned to the same general roosting area for the life of their transmitters. For example, during the 12 days the transmitter stayed attached, a group of seven *V. caraccioli* (including three young) used seven different sites within an area of 0.5 ha (Fig. 5A). A month later the same group was seen again roosting at site 5.

*Artibeus lituratus* showed similar fidelity, but to larger day-roosting areas. By chance I radio-tagged a second *A. lituratus* female in a group I had been following for 15 days. This allowed me to extend my observations on this group to 34 consecutive days. During this period the group used 11 sites within a 2.5-ha area (Fig. 5B) and made 16 changes averaging  $110 \pm 65$  m per change. Most of the sites were used for only 1 ( $n = 7$ ) or 2 days ( $n = 6$ ). Three sites (numbers 1, 3, and 9) were unusual in that they were used for periods of 4 or 5 days and were reused 6 to 10 days later. These favored roosts, accounting for 56% of the 34 days, were the darkest of the 11 sites. Sites 1 and 3 were in cavellike recesses in dense, subcanopy vegetation and site 9 was at the fork of a large branch heavily covered with vines and dead leaves. All three sites were 15 to 16 m above the ground. A second group of *A. lituratus*, sighted 15 times over a period of 26 days in November, used four sites spaced about 50 m

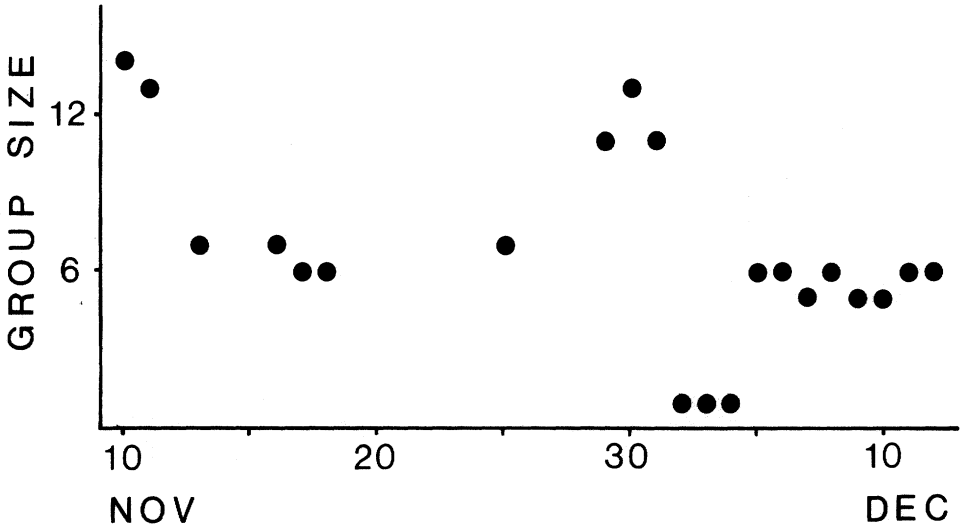


FIG. 6.—Daily changes in the number of bats in a group of *Artibeus lituratus* over a period of 34 days.

apart. Three other radio-tagged *A. lituratus* females were monitored less intensively but showed the same fidelity to day-roosting areas.

#### Roosting Group Composition

The size of *A. lituratus* roosting groups varied from day to day, but changed in ways which suggested that these groups were not random aggregations of individuals. The group monitored for 34 days fluctuated between either five and seven bats or 11 and 14 bats (Fig. 6). The drop in group size for 3 days in early December followed my accidentally moving a vine that was connected to the roosting branch at site 9. None of the bats flew away, but the site was not used again for 7 days. A second group of *A. lituratus* alternated between six and eight and 14 and 16 for 19 days, increasing to 20 for 1 day, before dropping to three or four. On two occasions when a radio-tagged female was roosting with a group of eight, there was a second group of eight at one of the other sites previously used by this bat. Two other groups of *A. lituratus* remained relatively constant at four or five and nine bats per group, and a third group alternated between five or six and ten. The two groups of *V. caraccioli* remained constant at three and four adults, respectively.

Although the sexual composition of the larger groups of *A. lituratus* could not be determined because they roosted so high above the ground, my observations on groups roosting lower down indicate that these smaller groups included only one adult male. *A. lituratus* males are large enough that when a male was roosting less than 10 m up, I was able to see his penis through the spotting scope. In three different groups of four, five, and seven *A. lituratus*, containing one, two, and three young, respectively, only one adult male was present. *V. caraccioli* were too small for me to determine their sex from the ground. However, in mid-July two groups of three and four adults gave birth to two and three young, respectively, within 2 days of each other. The adult without a young in each group may have been a male. The young of both species could be distinguished by their smaller size in July and August, but by November I could no longer make this determination with certainty.



The three radio-tagged *A. lituratus* males generally roosted alone (12 of 16 sightings) but occasionally were found with one (three sightings) or two (one sighting) other bats. One of the males roosted with a smaller, subadult male for 2 consecutive days. Another previously solitary male was joined by one, and the next day by two other bats of undetermined sex before again roosting alone. Roost site changes were similar to those of females. All three radio-tagged males changed roosts every 1 or 2 days, moving 10 to 100 m ( $\bar{X} = 40$  m) to new or previously used sites in the same general area.

#### DISCUSSION

The expectation that foliage roosting *Artibeus lituratus* and *Vampyroides caraccioli* would change their day roosts to sites nearer the fruiting trees than in use was not realized. Commuting distances from day roosts to fruiting trees were equivalent to those recorded in the same study area for *A. jamaicensis* using permanent day roosts in tree hollows (Morrison, 1978a). Although *A. lituratus* and *V. caraccioli* did change day roosting sites almost daily, individuals used and reused sites within the same 0.5 to 2.5 ha.

Both *A. lituratus* and *V. caraccioli* favored day-roosting areas near the shoreline or along ridge tops where the forest canopy is generally lower and the subcanopy trees more numerous. The combination of lower canopy and more fully developed subcanopy may increase the density of suitably cryptic roosting sites in these areas. Roost sites in branches overhanging the water ( $n = 3$ ) would be even less likely to be seen by terrestrial predators. The hypothesis that roost sites are chosen to be inconspicuous from the ground is supported by the observation that larger, potentially more conspicuous roosting groups roost higher up (Fig. 3).

A number of aspects of foraging behavior appear to have evolved to reduce vulnerability to predation. Anecdotal evidence suggests that potential predators of bats are attracted to fruiting trees. Judging by the number of vocalizations heard, there seem to be more owls around trees with ripe fruit than there are in other parts of the forest (C. O. Handley, Jr., pers. comm.). Opossums like *Didelphis marsupialis* are often seen in the branches of fig trees, and I once saw a *Philander opossum* almost capture a bat that had chanced to roost nearby.

Rather than eating in a fruiting tree, an *A. lituratus* will carry away as much as twice its body weight in figs each night to feeding roosts nearby. This is comparable to 1.5 times body weight reported for *A. jamaicensis* feeding on figs (Morrison, 1978a). Considering energetic efficiency alone, one would expect a bat to roost as close to the fruiting tree as possible. On the other hand, the farther a feeding roost is from the fruit tree, the safer it will be from predators attracted to the tree, because the area the predators must search increases as the square of the distance from the tree (Howe, in press). While actively feeding, both *A. lituratus* and *V. caraccioli* roosted within 100 m of the fruiting tree. For periods of inactivity longer than 1.5 h, the bats used sites 150 to 350 m away. Day-roosting sites were even more distant. If diurnal predators also are attracted to fruiting trees, this would help explain why the bats do not move their day roosts closer to current feeding areas.

The influence of predation is also suggested in the responses of the bats to moonlight. In *A. jamaicensis* the inhibitory effects of moonlight on foraging are clear, as in bright moonlight the bats return to their day roosts (Morrison, 1978b). In *A. lituratus* and *V. caraccioli*, feeding passes were suspended or greatly reduced in frequency, but flights between feeding areas and prolonged "search" flights occurred even in the brightest moonlight. These observations support the hypothesis that the risk of predation is greatest near trees with ripe fruit. Bright moonlight would make a bat hov-



ering around the crown of a fruit tree more conspicuous to visually orienting, sit-and-wait predators like owls. During other flying activities, the bats probably do not rise above the canopy and are moving more quickly through areas where predators are less concentrated.

Given the good visual acuity of phyllostomid bats (Chase and Suthers, 1969), flying in moonlight may facilitate a bat's finding trees with fruit. If so, it is not clear why *A. jamaicensis* suspend even search flying in bright moonlight. The lunar phobia of *A. jamaicensis* may be linked to the use of hollow trees as day roosts. A bat that returns each day to the same roost would be more likely to have evolved behaviors that maintain the crypticity of the roost, such as leaving and returning to the site in the least possible light.

*Artibeus lituratus* and *V. caraccioli* maintain the crypticity of favored day-roosting sites by changing roosts almost daily. Increasing the distance between consecutively used sites decreases the risk from predators attracted to the earlier site. On the other hand, the dark recesses these bats prefer are probably limited in number and may be almost as difficult to find as tree hollows. If so, this would help account for the observed fidelity to a familiar ridge or shore area.

The membership of roosting groups appeared to be relatively constant. The two groups of *V. caraccioli* remained stable at two and three females with young and one other adult, possibly a male. The sizes of the *A. lituratus* groups were more variable, and there may be some turnover of individuals among groups. The pattern of day-to-day fluctuations in group size (see Fig. 6) suggests that *A. lituratus* either form relatively stable groups of four to eight individuals that occasionally share a roost site with other such groups, or they form groups of eight to 20 which frequently divide into subgroups of four to eight. The few data available on the sexual composition of the smaller roosting groups suggest that *A. lituratus* and *V. caraccioli*, like *A. jamaicensis*, have harem mating systems.

The adaptive significance of the apparent fidelity of individuals to their day-roosting group is not clear. Given the patchy nature of canopy fruits, group defense of a feeding territory is not energetically feasible. Many bats from different areas converge on the same fruit tree. Females may choose to roost with a certain male and regroup around that male each morning. Alternatively, independent of the male, the females may benefit from regularly roosting with other females, such as by reciprocal sharing of information about the location of new fruiting trees (Ward and Zahavi, 1973). Males likely would compete for exclusive access to such female groups (Emlen and Oring, 1977). The reasons for group fidelity in the absence of a fixed day-roosting site warrant further study.

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*Department of Zoology and Physiology, Rutgers University, Newark, NJ 07102. Submitted 10 May 1979. Accepted 30 September 1979.*