OBSERVATIONS ON THE FORAGING BEHAVIOR AND AVIAN PREY OF THE NEOTROPICAL CARNIVOROUS BAT, *VAMPYRUM SPECTRUM*

SANDRA L. VEHRENCAMP, F. GARY STILES, AND JACK W. BRADBURY

ABSTRACT.—The foraging behavior of *Vampyrum spectrum* was studied in the field by radio-tracking, evening roost observations, and systematic collection of the prey parts found in the bottom of a roost containing five bats. Field observations, roost monitoring, and netting records all suggest that the bats hunt solitarily. One radio-tracked bat hunted over an area of 3.2 hectares, and spent most of its time in deciduous woodland, secondary growth, and forest edge, rather than in the riparian forest where the roost was located. The avian prey species were identified from the feathers collected in the roost over a one-year period. Of the 18 species (about 86 individuals) identified, most were common residents of the tropical dry deciduous forest. Non-passerines were significantly preferred over passerines. *Vampyrum* appear to select birds which weigh between 20 and 150 grams (g), sleep in foliage rather than in holes or burrows, and either roost communally or have a strong body odor. It appears that the bats locate their avian prey by scent rather than by vision or echolocation.

Although at various times considered a vampire or a frugivore (Husson, 1962; Villa, 1966), *Vampyrum spectrum* is now widely recognized as the largest carnivorous microchiropteran in the New World (weight, 180 g; wingspan, 900 millimeters, mm). In captivity, these bats are known to devour a wide variety of birds, rodents, and other bats (Greenhall, 1968). Feathers, bat wings, and rodent tails have been found in the bottom of *Vampyrum* roosts (Wehekind, 1956; Goodwin and Greenhall, 1961; Ditmars, 1936), and the remains of bats, passerine birds, and arboreal rodents have been identified in stomach contents (Casebeer et al., 1963; Peterson and Kirmse, 1969).

On a recent trip to Costa Rica, a roost of *Vampyrum* was located and systematic collections were made of the prey remnants dropped in the tree for over a year. The identity and frequency of each prey species consumed in the roost were recorded. A comparison of the nocturnal habits of preferred prey species and species not taken by *Vampyrum* suggested some likely techniques used by the bats to detect and capture prey. A knowledge of the bats' energetic requirements and the energy content of the prey was used to evaluate the contribution of prey brought back to the roost to the total diet. In addition, *Vampyrum* were radio-tracked to determine their foraging habits.

MATERIALS AND METHODS

In August 1973, a *Vampyrum* roost was located in a hollow tree a few meters (m) from the Corobici River on the property of Hacienda La Pacifica, Cañas, Costa Rica. The tree contained four adult-sized and one very young *Vampyrum spectrum*, as well as a small colony of *Saccopteryx bilineata* and a porcupine (*Coendou mexicanus*). The roost was visited weekly from 23 August 1973 to 16 November 1973 and at intervals of four to six weeks from December 1973 through August 1974. At each visit, all of the animal remains in the bottom of the roost were

469

collected. These usually consisted of feathers, but one avian gizzard and the humerus of a small bat (H. Camacho, personal communication) were also noted.

The feathers collected from the roost were identified to species by comparison with specimens at the Universidad de Costa Rica by Stiles. Where flight feathers were involved (as was usually the case), the feather tract and usually the exact feather in question were identified. Two or more different feathers in about the same stage of wear or preservation (feathers were destroyed or damaged by ants within a few days of being dropped by the bats) were assumed to be from the same bird. Thus, the number of birds represented by feathers given below are minimum estimates.

At sunset on 11 November 1973, Vehrencamp and Bradbury placed a mist net near the roost opening, and captured all but one of the adults. The three captured bats were sexed and measured, and miniature radio transmitters set at different frequencies were glued to their backs. Unfortunately, two of the transmitters ceased to function by the end of the first day, although they remained attached to the bats' backs for several weeks. The third radio continued to function for several weeks, and this bat (an adult male) was radio-tracked on three occasions. The foraging routes of the bat were monitored by triangulation from two fixed receiver stations 200 to 300 m apart. Each station utilized either an AVM Instrument Company receiver or a Drake SPR 4 receiver with a SC 2 high frequency converter. The direction of the signal was determined with a 7-element Yagi Cushcraft antenna and a compass. Walkie-talkies were used to synchronize the direction reading at the two stations. The transmitters utilized the 148 MHz frequency band (crystal controlled) and were constructed following a custom design.

RESULTS AND DISCUSSION

Roost Composition

Between August and November 1973, there were always four large bats and one suckling pup in the roost. Usually they all hung together in a tight clump, but on two occasions, there were two clumps of two bats. On 11 November, the group consisted of a large, reproductively active male (190 g, forearm = 108 mm, testes large), a juvenile male approximately six months old (132 g, forearm = 107 mm, testes small), a young, non-parous female (162 g, forearm = 108 mm, teats unused, not pregnant), and a reproductive female (not captured, but presumed to be the fourth adult in the group because of the presence of a suckling pup). The juvenile male and perhaps also the young female were probably the young of the reproductive pair.

Foraging Behavior

The time of departure and return to the roost of bats during the early evening was monitored on five occasions. On 12 September, all but one of the adults had left the roost by 1830. A bat was seen or heard returning to the roost at 1900, 1915, and 1940. A roost check at 2000 confirmed that all four adults were present, and there were no new feathers in the bottom of the roost. Minimum estimates of first foraging bouts ranged from 30 to 70 minutes (min) on this particular evening. On 11 November, the night of mist netting, the adult male escaped the net as he left the roost at approximately 1830, but was captured as he returned from foraging at 1930. He had obviously hunted successfully during this hour, as his abdomen was full and distended; he was not carrying prey. On 12 November, the adult male was radio-tracked from the time he left the roost at 1835 until 2300. The first bout of foraging lasted 130 min. He remained at or near the roost for 40 min, and then foraged again for a 55-min bout. On two subsequent nights of radio-tracking (17 November and 1 December), the male did not leave the roost at all between 1830 and 2200. On 17 November, a roost check at 2100 revealed that the male was alone in the roost with the youngster, but on 1 December all four bats were present in the roost at 1930 (with no new feathers). Because no all-night roost monitoring or radio-tracking was conducted, the total number of feeding bouts per night is not known. It is clear that the time spent foraging varies greatly from
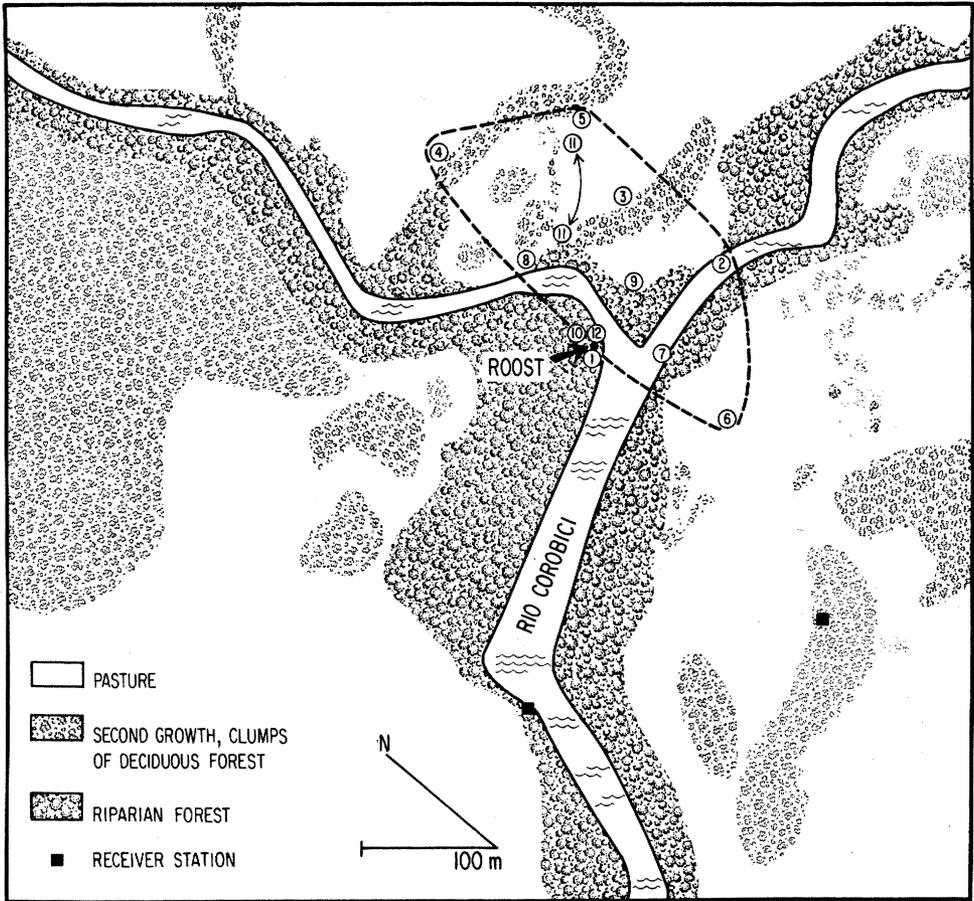
FIG. 1.—Movements of a radio-tracked adult male *Vampyrum* during a single evening, based on triangulation from two receiver stations. The triangulation points are numbered in chronological order as follows: (1) 1830 h; (2) 1835 h; (3) 1946 h; (4) 2004 h; (5) 2009 h; (6) 2019 h; (7) 2024 h; (8) 2044 h; (9) 2046 h; (10) 2049 to 2125 h; (11) 2130 to 2220 h; (12) 2223 h.

night to night, and some individuals may not forage at all on certain nights. The success of foraging bouts cannot be ascertained, because not all prey are brought back to the roost.

On 12 November, the adult male was radio-tracked for 4.5 hours (h) as he foraged. The locations of his position are shown in Fig. 1. This bat remained within radio contact during the entire period, never venturing more than 200 m from the roost. The total area enclosed by the triangulated points was 3.2 hectares. He spent most of his time foraging due north of the roost in an area consisting of deciduous woodland, secondary growth, and pasture. Most of the tracking points lie on the edges of forests and tree clumps in the pasture. He spent almost no time in the riparian forest along the river. Two fixes, taken while he was flying, were located in the river itself, suggesting that rivers may be used as flyways to reach major foraging areas beyond the riparian habitat.

We have no evidence that *Vampyrum* forages in groups. The fact that roost-mates always leave and return to the roost singly and at different times strongly suggests that the bats forage solitarily. In all published instances of mist-netting, only single bats

TABLE 1.—*Number of individuals of different avian prey species identified in each feather sample from the roost of* Vampyrum.

Avian species and weight (g)	23 Aug. 1973	7 Sept. 1973	22 Sept. 1973	30 Sept. 1973	7 Oct. 1973	13 Oct. 1973	20 Oct. 1973	27 Oct. 1973	7 Nov. 1973	16 Nov. 1973	21 Dec. 1973	29 Jan. 1974	13 Mar. 1974	29 Apr. 1974	19 Aug. 1974*	Total
Leptotila verreauxi (Verreaux' white-fronted dove) 150	1															1
Columbina passerina (common ground dove) 40			1	1	1			1			1		2			7
Scardafella inca (Inca dove) 60													1			1
Zenaida macroura (mourning dove) 110					1				1							2
Zenaida asiatica (white-winged dove) 125											1					1
Coccyzus minor (Mangrove cuckoo) 45											1	1–2	1	1		4–5
Piaya cayana (squirrel cuckoo) 110	1										1			1+		3+
Crotophaga sulcirostris (grove-billed ani) 70	1	1	1	2	2	1	1	2	1	1	3–4	2–3	3+	2+	1+	24–26+
Brotogeris jugularis (brown-shouldered parakeet) 70							1		1			1	2			5
Aratinga canicularis (orange-fronted parakeet) 85					1	1		2		1	1–2	1+	1	1+	1+	11–12+
Trogon melanocephalus (black-headed trogon) 90											1	1		1		3
Eumomota superciliosa (turquoise-browed motmot) 60	1	1										1		1		4
Muscivora forficata (scissor-tailed flycatcher) 39											1	1				2
Campylorhynchus rufinucha (rufous-naped wren) 36					1				1		1	1		1		5

TABLE 1.—*Continued.*

Avian species and weight (g)	23 Aug. 1973	7 Sept. 1973	22 Sept. 1973	30 Sept. 1973	7 Oct. 1973	13 Oct. 1973	20 Oct. 1973	27 Oct. 1973	7 Nov. 1973	16 Nov. 1973	21 Dec. 1973	29 Jan. 1974	13 Mar. 1974	29 Apr. 1974	19 Aug. 1974*	Total
Thryothorus pleurostictus (banded wren) 20													1			1
Icterus pustulatus (streak-backed oriole) 45		1			1											2
Icterus galbula (Baltimore oriole) 40									1							1
Arremonops rufivirgatus (olive finch) 23				1												1
Unidentified				1+					1+		1		1+	1		5+
Total	3	4	2	5+	7	2	2	5	7+	2	12–14	9–11+	12+	9+	2+	83–87+

* On 3 June 1974 and 30 June 1974, the roost was visited, but no bats were present, and no feathers found.

were captured (Peterson and Kirmse, 1969). Greenhall (1968) observed a single *Vampyrum* pursuing a small bat in flight. We also observed a solitary *Vampyrum* on a moonlit night flying low and slowly over deciduous and secondary growth vegetation. This observation also supports evidence from our radio-tracking study that *Vampyrum* forages in broken woodland, secondary growth, and forest edge situations.

Transport of Prey to the Roost

The fact that some prey are returned to the roost suggests that certain colony members may be provisioning others. Observations of a breeding pair plus pup in captivity revealed that the male frequently brought food to the roost which was taken by the female (Bradbury, personal observation). Our own observations at the roost suggest that at least one adult always stays behind with the youngster to guard it while the others leave for their early evening foraging bout. It is possible that prey brought back to the roost are eaten by this individual. However, we never saw feathers deposited in the roost in the early evening, and the male caught returning from foraging was not carrying prey. It is also possible that the guarding adult forages much later in the night, after the others have returned, and that this individual brings its prey back to the roost. Because it takes a *Vampyrum* about 30 min to consume a small bird or mouse, prey which are caught towards morning may be carried to the roost to avoid daylight exposure. A third explanation for the transport of prey to the roost is the provisioning of juveniles. While the suckling, non-volant pup probably receives a large portion of nourishment from its mother, it may eat some meat. The juvenile male and perhaps also the young female were probably inexperienced hunters and may receive food from adults.

Avian Prey Species

The feather samples collected from the roost are summarized in Table 1. The preferred prey species at all times of year is the groove-billed ani. Other prey taken regularly include two species of parakeets, a motmot, a small dove, two cuckoos, and a wren. No seasonal change in prey choice is evident, with the exception that the mangrove cuckoo and the black-headed trogon are only taken during the dry season. All of the feathers collected are from adult birds, and there is no evidence that nestlings are taken by the bats. The prey species range in weight from 20 to 150 g (see Table 1). The size of several of the species eaten is remarkable; the Verreaux' white-fronted dove, a large, strong-flying species, weighs practically as much as does the bat itself.

The majority of the species chosen by *Vampyrum* are characteristic of the tropical dry forest, and a few are found most frequently in riparian situations (for example, motmot, mangrove cuckoo). The sleeping habits of most species have received little study, but so far as is known, none of them regularly roost in holes. A few do use holes or burrows for nesting (for example, parakeets, trogons, motmots). However, only the females of these species roost in the nest burrow, and then only during the nesting season (Nottebohm, 1969; Skutch, 1956 and 1958). After the breeding season, both adults and young apparently roost in vegetation, as is the case with most other species taken by *Vampyrum*. No feathers were collected from any of the hole-roosting woodpeckers, which are common in this area and fall into the weight range of other prey species.

Vampyrum appears to prefer non-passerines over passerines; 86 percent of the individuals and 67 percent of the species identified in the roost samples were non-passerines. This is not simply due to a prevalence of non-passerine species in this area. Of the approximately 120 land birds resident at La Pacifica (Stiles, unpublished data), about 75 are within the 20 to 150-g weight range of known *Vampyrum* prey; 34 species, including the hummingbirds and 27 small passerine species, are under 20

g; and 25 species, all but one of which are non-passerines, are above 150 g. Of the species in the 20- to 150-g range, only the woodpeckers are probably immune from attack because they roost in holes too small for *Vampyrum* to enter. This leaves 64 potential prey species, 22 non-passerines and 42 passerines. Of the eligible non-passerines, 12 (55 percent) are taken by *Vampyrum*, and of the passerines, 6 (14 percent) are taken. This preference for non-passerines is highly significant ($P < .001$, Chi-square test).

The preference for non-passerines probably indicates that these birds are more easily located by *Vampyrum*. Species such as the doves and cuckoos (44 percent of the species identified, 56 percent of the individuals) roost in dense, often thorny shrubs or trees adjoining rivers, pastures, and clearings. This may facilitate a clear flight line for rapid escape from the roost when necessary, making the birds less vulnerable to attack by ambulatory mammals and nocturnal snakes. However, it may make them more readily detectable by bats hunting along foliage edges. In addition, the members of certain non-passerine families such as the cuckoos, trogons, and motmots are noted for their strong body odor (Wetmore, 1968). This trait occurs in 29 percent of the species and 49 percent of the individuals taken by *Vampyrum*. Olfaction is thus implicated as a prey detection technique.

Several of the prey species, notably parrots, anis, scissor-tailed flycatchers, white-winged doves, and Baltimore orioles, roost in large groups at fixed traditional sites; other species such as wrens and many doves often roost in pairs or small family groups (Dickey and van Rossem, 1938; Slud, 1964; Wetmore, 1968; Skutch, 1959; Stiles and Vehrencamp, personal observation). Group roosting occurs in 61 percent of the species and 76 percent of the individuals identified as *Vampyrum* prey. Most passerines, and most of the species not taken by *Vampyrum*, roost solitarily. Communal roosts are apparently more easily located than are single birds. Roosts containing many birds, and traditional sites used by a few birds night after night, may be more easily detected by olfaction because of the concentration of excrement. Groove-billed ani roosts, for example, can be detected olfactorily by a human at a distance of several meters. In addition to being easier to locate, such roosts might be visited repeatedly, if the bats could catch one bird without disturbing the others.

It is not clear how *Vampyrum* actually does catch birds in a communal roost. For species roosting in non-thorny, somewhat open vegetation, the bat may be able to land near the outside member of a roosting clump and grab it without disturbing the others. For species roosting in thorny and impenetrable foliage, however, the bat would somehow have to scare the birds out into the clearing. Because diurnal birds have extremely poor vision at night, they probably could not hide themselves quickly from a *Vampyrum*. This behavior would certainly disturb all of the birds in a roost, and would probably cause survivors to abandon the site. Wrens are the only birds taken by *Vampyrum* that regularly build roosting or "dormitory" nests, as well as breeding nests. The former are usually, but not invariably, in thorny vegetation (Skutch, 1961). One occasionally finds wren nests of both types with neat round holes chewed into the nest chamber; Skutch (1960) believes this to be the work of bats, and this may be one way *Vampyrum* catches wrens.

Although no single characteristic is shared by all of the species taken by *Vampyrum*, 83 percent of the species and 95 percent of the individuals were found to have either group roosts or strong body odors. Groove-billed anis are the only species with both characteristics, which may explain why they are taken so frequently. For both types of species, olfaction is a more likely method of detection than vision or echolocation. This conclusion is further substantiated by the lack of feathers from birds which roost in exposed, conspicuous sites. These include several passerine species which roost on narrow, unfoliated branches overhanging rivers, and orioles and flycatchers which build conspicuous, pendant nests (the three samples of orioles were taken during the

non-breeding season). Wrens, which also build conspicuous nests, are sometimes taken by *Vampyrum*. However, they roost in groups in these nests rather than singly like orioles and flycatchers. This attests again to the importance of group roosting and olfactory conspicuousness as cues to *Vampyrum*.

Several aspects of avian sleeping habits remain poorly known. This is especially true of birds which roost solitarily or in pairs, because the roost sites are often difficult to find. For most solitary roosters, we do not know whether the same roost is used on subsequent nights. According to the argument presented above, a solitary bird roosting in the same site each night could be more easily detected than a solitary bird which changes its roost frequently. Passerines may vary their roosting sites more frequently than do non-passerines. The paucity of data on birds' sleeping habits prevented the use of multivariate statistical techniques, which would have sorted and ranked the relevant characteristics of *Vampyrum* prey on the basis of their relative importance.

Energetic Considerations

In order to determine the percentage of the bats' total diet represented by the roost samples, we calculated the energy requirements of all the bats in the roost and compared this to the energy content of the birds. The daily energy expenditure of the bats was determined by calculating the metabolic costs in kilocalories (kcal)/h of the bats' various activities. The daily time budget was assumed to average 12 h of sleeping during the day, 10 h of roosting awake, eating, and grooming, and 2 h of level flight. Because the roost temperature probably remained within the bats' thermal neutral zone, and the bats were clustered and very quiet during the day, sleeping costs were judged to be at or very near basal metabolic rates. Basal metabolism was calculated from the allometric equation of Brody (1964) for mammals, using the known weights of the bats (the adult male was presumed to weigh only 180 g, because he had just taken a large meal when captured; the adult female and pup were estimated to weigh 170 and 100 g, respectively). Basal metabolism ranged from 0.54 (pup) to 0.83 (adult male) kcal/h. The costs of roosting awake were estimated as 1.5 times basal metabolic rates (Wolf and Hainsworth, 1971; R. Carpenter, personal communication), and ranged from 0.81 to 1.25 kcal/h. Flight costs, estimated from the allometric equation of Thomas (1975), ranged from 10.1 (juvenile male) to 13.0 (adult male) kcal/h (the pup was assumed to be non-volant and roosting awake for 12 h/day). Thus, daily energy expenditure was between 16.3 and 48.3 kcal/day/bat, and totalled 193.8 kcal/day and 1,356.7 kcal/week for all the bats in the roost.

The energy content of a bird was estimated as 2.0 kcal/gram live weight (Odum et al., 1962). Using a conservative estimate of 75 percent assimilation efficiency for carnivores (Kleiber, 1950), the actual amount of energy available to a bat is 1.5 kcal/g of bird. During the period of weekly censusing, an average of 225.5 bird-g per week were sampled in the roost (only 96 bird-g were collected per week during the period of monthly censusing; the difference was due to the fact that many of the feathers were removed or destroyed by ants between censuses). Using only the data from the weekly census period, a minimum of 340 kcal of birds were brought back to the roost per week. This represents at least one-fourth of the bats' total weekly requirements.

Similar calculations were used to estimate the number of birds a bat needs to capture per night. An average bird weighing 70 g is worth 105 kcal. The average daily energy expenditure for the volant bats in the roost ranged from 38 to 48 kcal/day. Thus, a bat might only need to consume one bird every two to three nights. One large dove would suffice to feed all of the bats in the roost for one night, whereas a small bird would only satisfy the needs of one bat for one night. These energetic considerations are consistent with our impression that some bats did not forage on certain nights.

Such energetic calculations may also be used to select among the alternative expla-

nations presented earlier for the bat's transport of prey to the roost. The birds brought back to the roost provided 340 kcal of assimilatable energy/week, while individual requirements ranged from 267 to 338 kcal/week (volant bats only). Birds consumed in the roost probably constitute more than one average bat's requirements and are not simply the prey caught by the guarding adult. There is certainly much more energy in transported prey than is needed by the female to provide all of the pup's needs in the form of milk. The amount of energy brought back to the roost would satisfy at least 50 percent of the needs of the pup, the juvenile male and the young female. The most reasonable explanation is that prey transport is related to the presence of dependent young in the roost. Learning to capture prey is likely to be a long process in *Vampyrum*, particularly if the juveniles cannot learn by hunting with adults. Thus, juveniles may require a year or more to become fully efficient predators, which would explain the long retention of young in the parental roost.

CONCLUSIONS

If the roost samples reflect the total diet, then birds represent the major prey item of *Vampyrum* in Guanacaste. Rodents and bats, which have been frequently noted in roost samples in other locations, did not appear to be regularly taken by the bats in our study roost. These bats are specializing in stationary, hidden prey, as opposed to active and exposed prey. The capture of active prey probably requires a "sit-and-wait" strategy or a "hawking" (fast pursuit) strategy. The capture of hidden, inactive prey probably requires detection by olfaction and capture either by startling the prey out of cover or stalking. Prey preferences may differ in response to the relative efficiency of hunting by olfaction versus echolocation in sites with different rainfall, seasonality, and vegetation structure.

Finally, the fact that *Vampyrum* specializes in prey which are odoriferous and roost in groups raises some interesting questions concerning the anti-predator strategies of the birds. Both communal roosting and offensive body odor have been suggested as mechanisms to reduce predation (Lack, 1968; Gadgil, 1972; Wetmore, 1968; Brown, 1974). At least with predators such as *Vampyrum*, this is clearly not the case. Treisman (1975) has attempted to model prey strategies as a function of the sensory modality used by the predator. In the case of olfactory predators, clumping is not advantageous when the predator always takes one or more group members. Only if grouped prey can detect and escape from predators more effectively than solitary prey, does clumping reduce predation rates. Our guess is that *Vampyrum* always gets one bird once it has located a group; even if it attempted to stalk a bird and missed, the other birds would be flushed out of the foliage and then captured by the bat. This may not be the case with other olfactory predators such as snakes or ambulatory mammals, however. While clumping may be disadvantageous against *Vampyrum*, predation by other more common predators may be reduced by clumping. One lesson from this study is that a prey species is vulnerable to many different types of predators hunting by different means. Clumping, thorny vegetation, edge sites, and thin branches over water may deter some predators while not affecting or attracting others, and the actual roosting behavior we observe is undoubtedly a compromise strategy arising from opposing selective pressures.

ACKNOWLEDGMENTS

LITERATURE CITED

BRODY, S. 1964. Bioenergetics and growth. Hafner Publishing Co., Inc., New York, 1023 pp.

BROWN, J. L. 1974. Alternate routes to sociality in jays. Amer. Zool., 14:63–80.

CASEBEER, R. S., R. B. LINSKY, AND C. NELSON. 1963. The phyllostomid bats, *Ectophylla alba* and *Vampyrum spectrum*, in Costa Rica. J. Mamm., 44:186–189.

DICKEY, D. R., AND A. J. VAN ROSSEM. 1938. The birds of El Salvador. Fieldiana: Zoology, 23: 1–609.

DITMARS, R. L. 1936. A *Vampyrum spectrum* is born. Bull. New York Zool. Soc., 39:162–163.

GADGIL, M. 1972. The function of communal roosts: relevance of mixed roosts. Ibis, 114:531–533.

GOODWIN, G. G., AND A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. Bull. Amer. Mus. Nat. Hist., 122:191–301.

GREENHALL, A. M. 1968. Notes on the behavior of the false vampire bat. J. Mamm., 49:337–340.

HUSSON, A. M. 1962. The bats of Surinam. Zool. Veshandl. Rijksmus. Nat. Hist. Leiden, 58:1–282.

KLEIBER, M. 1950. The fire of life. John Wiley and Sons, Inc., New York, 454 pp.

LACK, D. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, Ltd., London, 409 pp.

NOTTEBOHM, F., AND M. NOTTEBOHM. 1969. The parrots of Bush Bush. Animal Kingdom, 72:18–23.

ODUM, E. P., C. E. CONNELL, AND L. B. DAVENPORT. 1962. Population energy flow of three primary consumer components of old-field ecosystems. Ecology, 43:88–96.

PETERSON, R. L., AND P. KIRMSE. 1969. Notes on *Vampyrum spectrum*, the false vampire bat, in Panama. Canadian J. Zool., 47:140–145.

SKUTCH, A. F. 1956. A nesting of the collared trogon. Auk, 73:354–366.

———. 1958. The turquoise-browed motmot. Animal Kingdom, 61:6–11.

———. 1959. Life history of the groove-billed ani. Auk, 76:281–317.

———. 1960. Life histories of central American Birds, Vol. 2. Pacific Coast Avifauna, 34:1–593.

———. 1961. The nest as a dormitory. Ibis, 103:50–70.

SLUD, P. 1964. The birds of Costa Rica: distribution and ecology. Bull. Amer. Mus. Nat. Hist., 128:1–430.

THOMAS, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. J. Exp. Biol., 63:273–294.

TREISMAN, M. 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. Anim. Behav., 23:779–800.

VILLA, B. 1966. Los murcielagos de Mexico. Univ. Nac. Auto. Mexico, Inst. Biol., Mexico, 491 pp.

WEHEKIND, L. 1956. Notes on some Trinidad bats. J. Trinidad Field Nat. Club, pp. 18–21.

WETMORE, A. 1968. The birds of the Republic of Panama, part II. Smithsonian Misc. Coll. 150:1–605.

WOLF, L. L., AND F. R. HAINSWORTH. 1971. Time and energy budgets of territorial hummingbirds. Ecology, 52:980–988.

Department of Biology (C-016), University of California, San Diego, La Jolla, California 92093 and Biologia, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica, Central America. Submitted 24 June 1976. Accepted 15 October 1976.