OBSERVATIONS ON THE NEOTROPICAL DISK-WINGED BAT, *THYROPTERA TRICOLOR* SPIX

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Abstract.—Study of 42 marked *Thyroptera tricolor* in Puntarenas Province, Costa Rica, revealed that the animals live in groups of six to seven individuals. The members of each group always roost together in a rolled leaf of a plant, usually of the genus *Heliconia.* Each roost is occupied for one day. Each group seems to occupy an exclusive roosting area that averages 3000 square meters.

The disk-winged bat, *Thyroptera tricolor* Spix, is one of two species in the Neotropical family Thyropteridae. It occurs from southern Mexico through much of tropical South America. A second species, *T. discifera,* occurs in parts of Central and South America. These small, delicately built bats (average weight about 4 grams) have forwardly directed funnel-shaped ears and very small eyes like funnel-eared bats (family Natalidae) and smoky bats (family Furipteridae). *Thyroptera* differs from bats of these other two Neotropical families, however, in having well-developed suction disks located at the wrist and on the ventral surface of the hind foot. These disks, the anatomy and functioning of which have been studied in detail by Wimsatt and Villa (1970), allow the animal to attach itself to smooth surfaces, such as leaves or glass. So far disk-winged bats are known to roost only inside the rolled new leaves of members of the banana family (Musaceae) or related plants. Within the leaves the bats arrange themselves in a vertical row in a head-up posture, attaching themselves to the leaves by means of the suction disks.

Our studies of these bats in lowland Costa Rica revealed that the number of suitable roosts in a given area on any given day is very limited. Thus it is possible to locate all the potential roosts and find the resident bats with a considerable degree of predictability. After capture the animals may be marked for future recognition, and relocated at will. Here we present the results of two weeks of study of these intriguing little bats in Puntarenas Province, Costa Rica. Our findings suggest that the bats are organized into roosting colonies, that the members of each colony remain together, rejoining even if separated, and that each colony occupies an exclusive roosting area.

Methods

The study area was on the Osa Peninsula on the Pacific coast of Puntarenas Province at approximately 8° 42′ N and 83° 3′ W. We were stationed at the Tropical Science Center Field Station, 5 kilometers west of Rincon de Osa at an elevation of 40 meters above sea level. The vegetation in the area is classified as Tropical Wet Forest in the Holdridge Life Zone system (Holdridge, 1967). The annual rainfall is approximately 4117 millimeters (mm), with a relatively dry period during January–March, when monthly rainfall is 77 to 92 mm, followed by steadily increasing precipitation from 161 mm in

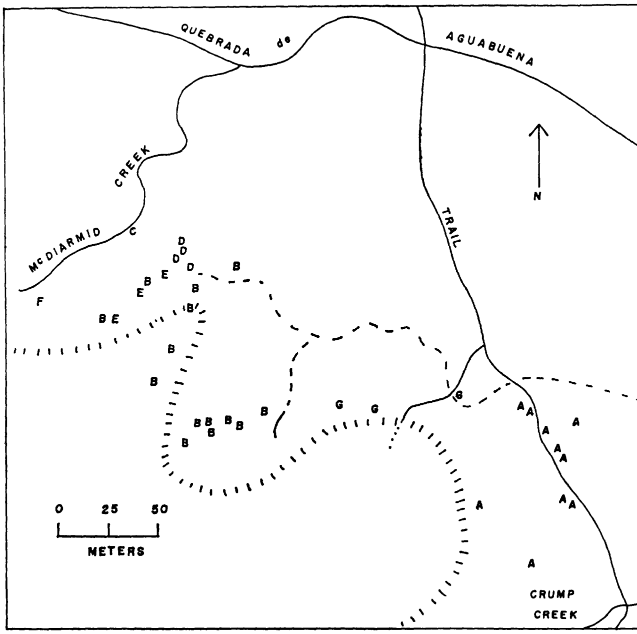

FIG. 1.—Diagram of study area. Letters refer to sites of capture of seven colonies of *Thyroptera tricolor* listed in Table 1. Entire area between Crump and McDiarmid creeks, the Aguabuena, and the hills indicated by hash marks was searched for bats.

April to 659 mm in October. During August, when our study was conducted, rainfall averages 511 mm. A detailed description of the vegetative characteristics of the region may be found in Holdridge *et al.* (1971). Our study site had been selectively logged, and was a mixture of primary forest trees and second growth of various ages. Light gaps caused by this logging as well as tree-falls permitted the growth of a fairly lush understory of palms and plants of the families Marantaceae and Musaceae. The latter two were especially important for the bats, since in each the growing leaves form a funnel-shaped cone that provides the typical roost-site for *Thyroptera.*

Our study area (Fig. 1) was triangular, encompassed 1.92 hectares, and was bordered by the Quebrada de Aguabuena, two of its tributaries, Crump and MiDiarmid Creeks, the highlands bordering the Aguabuena drainage, and a trail leading from the Aguabuena to Crump Creek.

Every one or two days during the period 11 to 24 August 1972, we systematically traversed this area examining rolled leaves that might shelter bats. Bats captured were weighed, the forearms measured, and the flight membranes marked by a series of pin pricks for recognition before they were released. Because the bats did not return to the leaves in which they had been captured, we opened each leaf, removed the feces deposited by the animals, and looked for other kinds of occupants. We then measured the distance and compass bearing to the last point of capture of that colony, and plotted the new point of capture on a map of the study area. Early in our study we measured and marked all the young leaves of *Heliconia* and *Calathea* (two genera that provided most bat roosts) that we could find in our area, and then remeasured these leaves at intervals to determine their growth rates.

Results

Roosts

We found *Thyroptera* regularly in rolled leaves of *Heliconia* (Musaceae) or occasionally *Calathea* (Marantaceae) which were growing in the forest, in forest clearings, or occasionally along the edges of roads or trails. Hundreds of such leaves examined in Panama which were growing in unshaded situations in open areas, and dozens growing in such situations on the Osa contained no bats. However approximately every fourth suitable rolled leaf examined in our study area, where plants were sparsely distributed and shaded for part of the day, contained *Thyroptera.* Villa (1966) also noted the occurrence of these animals in shady forest. Almost all bats were found in leaves in which the diameter of the opening was between 50 and 100 mm. Observation of marked leaves indicated that they were in this favorable size range for about 24 hours. Once the leaves open at the tip, thus admitting beetles and other animals which may damage the leaf, the growth from a rolled to an open leaf is very rapid (Steve Stearns, personal communication; Fig. 2). During our study suitable leaves were not very common, and this may have contributed to our success in locating bats. One fairly thorough survey of our area revealed approximately four such leaves in each sector where a roosting aggregation of animals lived. We found the animals most commonly in leaves of *Heliconia imbricata*, with *H. rostrata* being somewhat less commonly used. *Heliconia latispatha*, which grew more commonly in open areas, was rarely used. Occasionally we found bat feces in the leaves of *Calathea* sp., but these plants seemed not to be very important as roosts.

Several kinds of beetles and their larvae were often found in the leaves with the bats, as were minute flies, perhaps *Drosophila.* A leaf without bats might shelter a large orthopteran, but we never found bats and orthopterans in the same leaf.

Colony Structure

We found 11 different groups of bats that we were able to study, and two additional groups that escaped before we could obtain data about them. Group size ranged from one to nine, with a mean size of six, and a mode of seven. On only one occasion did we find a single individual occupying a leaf under conditions where we did not suspect previous disturbance and disruption of an aggregation. In all other cases three or more bats comprised a roosting assemblage. Five such groups were recaptured from one to 16 times. In all cases the group was comprised of the same individuals each time it was recaptured, except that two individuals disappeared from the largest group, A, part way through the study and one individual disappeared from group C. Sometimes the members of a group became separated as a result of the disturbance when we captured and examined them, so that later the same day we found them in several separate roosts, or even in a roost with members of another group. However, when located on a subsequent day all the bats of

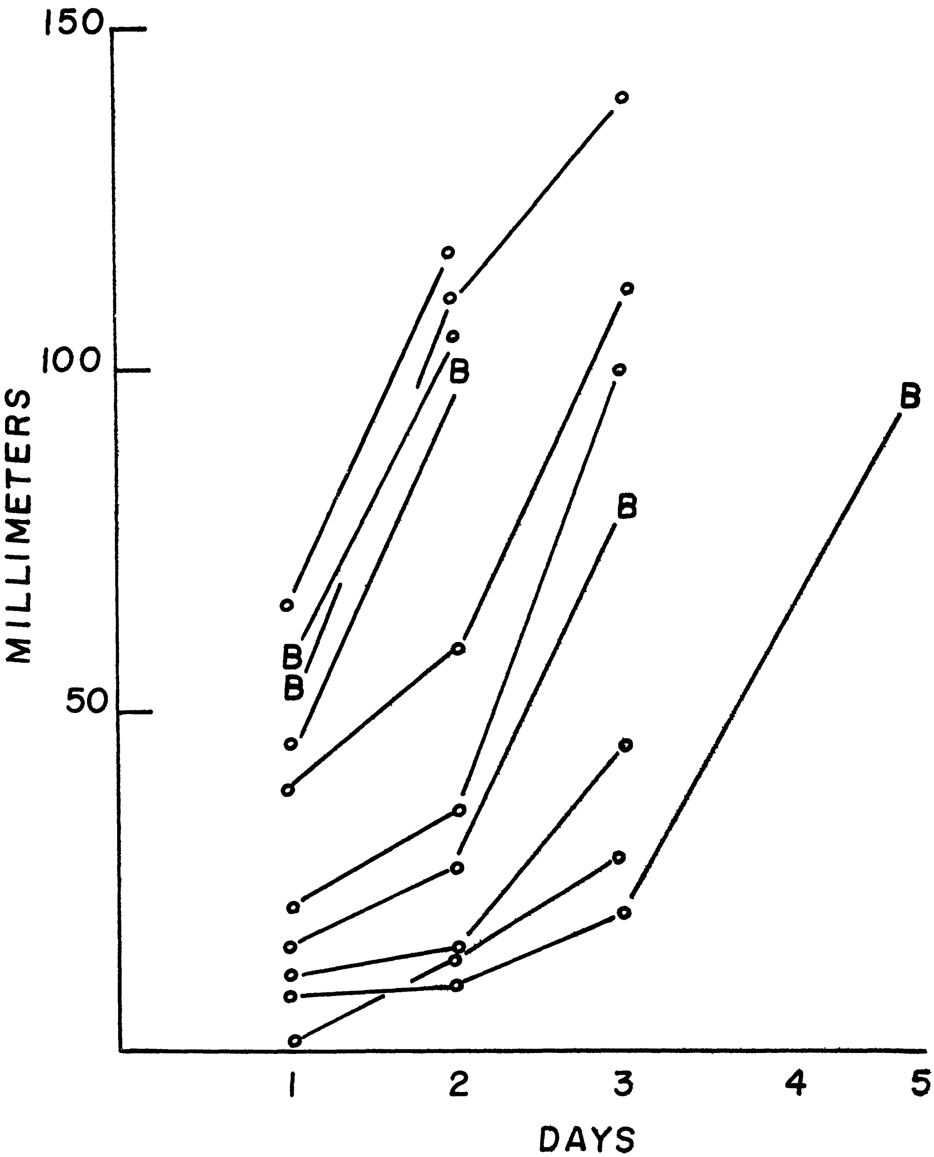

FIG. 2.—Growth of some individual *Heliconia* leaves. Each series of points connected by lines represents the increase in diameter of the opening into one rolled leaf. Points indicated by B represent occupancy of the leaves by *Thyroptera.*

the original group were back together. Each roosting aggregation thus showed a definite social cohesion and we refer to them as "colonies."

Within the colonies there was no definite sex or age structure (Table 1). However, when all the bats examined are considered together the sex ratio is roughly 1:1. Of 58 animals aged, 33 per cent were young. All young were

TABLE 1.—*Characteristics of colonies of* Thyroptera tricolor. *Colonies H, I, J, and K were found outside the study area and the individuals were preserved. One individual escaped before being examined from each colony marked by an asterisk.*

Colony	N	Adult male	Adult female	Juvenile male	Juvenile female	Mean weight	Mean forearm	Average (and greatest) distance between recaptures (m)	No. recaptures	Roosting area × 100 square meters
A	9	4	1	4	0	4.1	36.0	42 (73)	11	42
B	7	1	3	2	1	3.7	36.0	55 (91)	16	65
C	6	3	2	0	1	3.9	35.9	—	0	—
D	5	2	2	0	1	4.2	36.6	14 (35)	3	10
E	4	1	2	0	1	4.2	36.6	29 (33)	2	9
F	5	3	1	0	1	4.1	35.8	—	0	—
G	6	2	2	1	1	4.1	36.3	30 (58)	2	26
H*	4	0	1	2	0	—	36.3	—	—	—
I*	7	2	1	2	1	—	36.1	—	—	—
J	1	0	1	0	0	—	36.7	—	—	—
K	7	2	3	1	0	—	—	—	—	—
Mean	5.6	1.8	1.7	1.1	0.6					

full grown and betrayed their immaturity only in the possession of the somewhat darker immature pelage and, in the case of females, nipples were minute and gave no sign of previous lactation. In the older females with paler pelage the nipples were invariably enlarged from previous use. No animals were lactating.

Reproduction

Seven females from outside our study area were preserved. Of these, two showed no signs of previous reproductive activity. One, though having the enlarged nipples of a previously reproductive adult, was not pregnant. One appeared to have recently given birth but showed no signs of lactation. Three animals were pregnant with a single, small (2.5 mm) embryo each. These pregnant animals showed no external signs of their condition, and it is therefore likely that we handled a number of females in early stages of pregnancy. Extrapolating from these few data, 60 to 80 per cent of adult females were pregnant in mid-August 1973. Embryos carried in mid-August would result in births in October (the peak of the rainy season) if *Thyroptera* has a two month gestation period like the similarly sized Neotropical insectivorous bat *Myotis nigricans* (Wilson and Findley, 1970).

We were surprised, in examining preserved female *Thyroptera*, to note that they have simplex uteri, a condition so far found in bats only in the family Phyllostomatidae. An examination of females of the closely related *Natalus stramineus* revealed that they have bicornuate uteri as do most other bats.

Roosting Areas

All the places where each colony was located are shown in Fig. 1. Each colony occupied an exclusive area except that individuals of colony B sometimes moved into the D or E area when disturbed. We suspected a close "family" relationship between colonies B and D not only because of this spatial relationship, but also because B contained one, and D two, bats with a distinctive partially white pattern on the flight membranes.

Home Range Characteristics

Distances between recaptures for all the bats ranged from 5 to 91 meters with a mean of 42.5 ± 4.2, S = 25.0, coefficient of variation = 58.8 per cent. The mean distances between recaptures for the several colonies ranged from 14 to 55 meters (Table 1). If we assume that the greatest distance between roosting sites of a colony approximates the diameter of the roosting area and that the shape of the area is approximately circular, then the areas range from 855 square meters to 6501 square meters, with a mean of 3028 square meters. Using these data, the bats should occur at a density of 3.3 colonies and 19.8 bats per hectare (ha). We actually counted 3.7 colonies and 21.9 bats per hectare in our measured study area.

Measurements

Average weights and forearm measurements for these bats are included in Table 1. Weights were not taken individually. Forearms of females averaged slightly greater than those of males (36.80 as opposed to 35.57), a tendency seen in almost all of the insectivorous bats of the family Vespertilionidae (Williams, 1972). The average weight of 42 bats was 4.02 grams (g), providing a biomass estimate of 88 g/ha.

Locomotion

When the bats moved on a substratum neither the pollex nor any of the toes of the hind foot touched the surface. Instead the only functional contact was with the suction disk. On the wooden floor of a cage approximately 3 × 7 centimeters the animals did not crawl, but attempted by strong downward thrusts of their wings to become airborne. They were unable to attach to the wooden sides or screen top of the cage, but readily crawled up the glass front, hanging on by attaching the suction disks to the glass. In handling *Thyroptera*, they often attached their disks to our fingers. In the cage we observed the bats licking the concave surfaces of their disks, as recorded by Wimsatt and Villa (1970) and Carvalho (1939).

In flight in the forest the bats were agile and maneuverable, readily describing small circles when investigating the mouth of a rolled *Heliconia* leaf that might serve as a roost. We did not observe them flying much higher than 3 to 5 meters above the forest floor. One which landed upon, but did not become entangled in, a bat net, was approximately a meter above the ground.

Group Behavior

When we released the nine bats of colony A after their first capture, the first bat liberated flew in small circles around the bag containing the rest of its companions, alighting several times. Eventually this first bat flew approximately 5 meters away where it began to circle the entrance of a rolled *Heliconia* leaf. After alighting several times, this animal entered the leaf and disappeared. The next three bats to be released headed immediately for the leaf which the first one had entered, circled a few times and entered also. The next bat headed in a different direction, found another leaf about 8 meters from the point of release, and entered. Three subsequent bats headed directly for the second roost and entered. The last bat went to the first leaf, which he could hardly enter because the leaf was a small one, already stuffed with his companions, but forced himself in and stayed, though he remained partly visible. Our impression was strong that the released bats were receiving communications from the previous ones to be liberated. While we did not again observe the bats flocking into a roost in this manner, the animals commonly left the release point in the same direction as earlier ones. When we released the members of a colony together they frequently flew off as a group.

Fecal Collections

Data from analysis of the fecal collections will be presented in another paper. Each collection represented the deposit of one colony after a night's foraging. Since our collections were often made in the morning, the pellet accumulation may not have represented all that the colony would have deposited if left undisturbed for the whole day, and collections made later in the day may have contained more pellets on this account. The dry weights of 21 pellet collections ranged from 0.10 to 0.54 g, with a mean of 0.21 g. Each bat produced as much as 0.08 grams of feces per day. We studied captive *Eptesicus fuscus* fed mealworms which produced feces weighing 9 to 10 per cent of the weight of food consumed. Thus each *Thyroptera* may have been consuming up to 0.8 g of insects per night.

Discussion

Abundance of this species appears to be limited by the availability of suitable roosts. The extreme morphological specialization of these animals makes it difficult or perhaps impossible for them to cling to rough surfaces, such as bark, the inside of hollow trees, or rock surfaces such as the walls or ceilings of caves. The unusual head-up roosting posture is useful for an animal emerging from a vertically oriented conical shelter, but would not be appropriate for dropping from a roost on an open surface. *Thyroptera* seems never to roost head downward, despite the comments of Jimenez de la Espada (1870) which Carvalho (1939) felt stemmed from misidentifications or inaccurate observation.

Crevice-roosting bats, such as many members of the family Vespertilionidae, have markedly flattened crania compared to those species that do not wedge themselves into narrow quarters. *Thyroptera* has the typical high-domed skull of a noncrevice-roosting species. *Thyroptera* may roost on other types of foliage than musaceous leaves, but none has ever been found in such situations. Those colonies whose roosting areas lay centrally in our study area (A and B) were found every time we made a thorough search for them. If they were occasionally roosting in other kinds of situations we should have sometimes failed to find them. All evidence suggests that this species is dependent upon a very specialized kind of roost site strictly limited in its availability.

If the bats are indeed thus limited, competition for roosts between colonies may be critical. Thorough familiarity with the roosting area would reduce the time expended in searching for a roost after the evening foraging period. The animals likely would not simply return to the shelter of the previous night. Our data on the weight of fecal material recovered from old roosts suggests that this was never more than the amount that a colony would deposit during one 24 hours period. The defense of a roosting territory, or at least a tendency for each colony to restrict its activities to a distinctive area would certainly seem to make adaptive sense. How the use of an area by one colony would exclude another is not clear. In some cases when we disturbed colony B, individuals would enter roosts occupied by the members of colony D or E. These later colonies did not prevent other bats from joining them on a short term basis.

The size of the area involved may have been related to the density of plants. If this density were too low, as it might be in completely unbroken forests, the energetic demands of searching for a roost might be such as to preclude the use of the area by *Thyroptera.* On the other hand, a forest that was so disturbed that much area was completely unshaded during the day, thus perhaps allowing the plants to become too hot for occupancy, would likewise be largely unsuitable.

If the amount of vegetative growth of the plants is at all seasonal, the season of minimal growth should be the most critical one for the bats. Then the largest territories would be needed to insure an adequate supply of roosts for the colony. In a region where the growth of the plants ceased periodically the bats probably could not occur. An especially important time should be that when the young are dispersing and forming new colonies. A sudden increase, by one third, of the size of the bat population must coincide with increased roost availability or must be quickly followed by an equivalent amount of mortality. During our two week study three of our 42 marked bats disappeared. Probably, however, the repeated disturbance the bats suffered during our study, causing them to fly in the daytime, resulted in a disappearance rate higher than normal.

Bats of one other family are known to inhabit rolled musaceous leaves. Brosset (1966) noted that in Africa *Myotis bocagei* and *Pipistrellus nanus* occupy rolled banana leaves, often to the exclusion of other roosts. Rosevear

(1965) reported *M. bocagei* occupying the flower stalks of water arum, probably *Cyrtospermum*, but he noted that these bats also occupied a variety of other kinds of roosts. So commonly does *P. nanus* use banana leaves that it has been referred to as the "banana bat." In Malaya Medway (1969) reported that *Myotis mystacinus* commonly roosts in banana leaves, that colony size ranges from one to eight, and that in scrub and secondary forest up to two out of five "suitably rolled" leaves may be occupied. Of these bats only *P. nanus* seems to have any morphological specialization for clinging to leaf surfaces. In this species thickened pads at the wrist and on the sole of the hind foot are said by Rosevear to provide the necessary adhesion. The endemic Malagasy *Myzopoda* has disks on the wings and feet, but unlike the disks of the *Thyroptera*, those of *Myzopoda* are unstalked. *Myzopoda* is reported by Randolph Peterson (personal communication) to roost in the axils of leaves of the traveler's-palm (*Ravenala*). In each of the major tropical regions of the world there are thus bats known to roost in musaceous leaves, and increasing morphological specialization for this habit are seen in bats from southeast Asia, Africa, and the Neotropics.

Summary

1. We studied *Thyroptera tricolor* during August 1973, in Puntarenas Province, Costa Rica. This species is limited to rolled leaves of musaceous plants as roosting sites. Each leaf provides a suitable roost for only 24 hours.

2. These bats occur in colonies of from one to nine, modally seven, individuals at a density of approximately four colonies, 22 bats, per hectare, and a biomass of 88 g/ha.

3. Members of a colony show social cohesion, and seek each other out as roost-mates if separated.

4. The sex ratio of the population is 1:1. Full sized, nonreproductive young made up approximately one third of the population. Within each colony there was no definite sex and age structure.

5. No females were lactating, but three of seven adult females collected contained one small embryo each. The uterus in *Thyroptera* is of the simplex type.

6. Distances between captures of colonies ranged from five to 91 meters with a mean of 42.

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