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Foraging of vampire bats (Desmodus rotundus) in Atlantic wet lowland Costa Rica

by

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With the exception of two recent studies (CRESPO *et al.*, 2; WIMSATT, 15), attempts at analyzing in depth the temporal patterns of foraging and general nocturnal activity of the vampire bat ("el vampiro"), *Desmodus rotundus* (Geoffrey) have been meagre. In light of the potential role of vampires as serious vectors of various mammalian diseases, including rabies (GOODWIN and GREENHALL, 6; GREENHALL and PARADISO, 8), studies of the above sorts on the behavior and general ecology of these animals are indeed warranted. Furthermore, ecological studies of vampires may elucidate how foraging is affected by various factors such as character of the local terrain, population densities, availability of favored roosting sites, accessibility of potential prey animals, and seasonal climatic changes.

This paper presents and discusses some new data on the temporal foraging patterns of vampires at one locality in Costa Rica. Most studies on vampires have been concerned with only very short periods of observing foraging activities (BROWN, 1; DALQUEST, 3; VILLA, 13), and even the more elaborate study of WIMSATT (15) concerned data obtained from only five nights of observation. The present study differs from all of these previous ones in that temporal foraging patterns of vampires were studied over eleven successive months, with extensive observations on vampire activity at two roosts in conjunction with another series of observations on vampires attacking cattle. Of prime interest in this study were these parameters of foraging activity: temporal persistence of roost (population) fidelity; length of nightly foraging periods; length of nightly feeding periods (considered here as a part of the foraging period); and nightly exodus and return schedules of foraging indi-

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viduals to roosts. Unlike previous studies, the present study takes into account seasonal climatic changes (wet and dry seasons) as affecting foraging activity of vampires.

There has been steadily growing a sizable body of information indicating that the Central American dry season affects the behavior of various plants and animals. JANZEN and SCHOENER (10) present data showing that the dry season in various regions of Costa Rica leads to an appreciable lowering of species diversity and numbers of individuals per species among insect populations inhabiting secondary growth herbaceous vegetation. YOUNG and JANZEN (19) studied the temporal changes in the trophic structure and species composition (and other characteristics) in an insect community for 21 successive months in Costa Rica, and discuss the effects of the dry season upon various descriptive parameters of this assemblage. YOUNG (18) found that foraging in the hermit hummingbird, *Phaethornis superciliosus,* is greatly influenced by the Costa Rican dry season in terms of the type of food eaten. With regard to other vertebrate populations, JANZEN (9) hypothesized that various species of nectivorous and frugivorous neotropical bats alter their foraging behavior in accordance with dry season effects on the flowering and fruiting patterns of preferred host plants. Such studies suggest that not only do dry season-induced changes in the accessibility of preferred food sources influence the activities of those animals that must search for them, but that also the nutritional requirements of the foragers themselves may be affected by the dry season—a period of pronounced "environmental hardship" (stress) for certain groups of terrestrial organisms inhabiting specific climatic regions. Data obtained in the present study on the foraging behavior of vampire bats are discussed within the context of dry season effects.

STUDY PROCEDURES

The general locality of this study was Finca La Selva (hereafter referred to as "La Selva") (10° 26' N; 89 m elev.), Heredia Province, Costa Rica, in the Atlantic wet lowland climatic region. This region usually experiences high rainfall throughout the year (an average total of 4200 mm annually) with slight peaks occurring in June-July and November-December. In addition, there is a short but pronounced dry season throughout January, February, and the first half of March; the remaining months comprise a long wet season. La Selva is located within the large continous strip of broadleaf evergreen forest that extends down along the Caribbean Coast of Central America from Veracruz-Tabasco, Mexico south to the Darién, Panamá. More specifically, it is an area of chiefly primary growth rain forest (wet tropical forest) flanked on three sides by large expanses of open pasture lands. The savanna-like pastures are dotted with small-sized, but numerous clumps of large forest trees that survived land-clearing efforts several years before. On much of the immediate surrounding pasture lands, many head of cattle (chiefly Brahma hybrid stock) graze all year round.

While this study was in progress, nightly air temperatures were recorded usually at five different times (sunset, 9 PM [C.S.T.], 12 midnight, 2 AM, and 4 AM). Total daily rainfall was recorded by means of a standard rain gauge.

At La Selva, within primary growth rain forest, two colonies of vampires were located in early September, 1968; both were roosted in large trees that were about 500 yards apart in an almost north-south compass direction, and at about the same ground level. Although most likely present within the same general vicinity (indicated by data presented later), no other vampire colonies were found despite intensive searching over a 1300 acre area. Colony No. 1 roosted in the hollow of a large "Ceiba" *(Ceiba pentandra)* tree while Colony No. 2 roosted between two, large, gnarled buttresses of a giant "Escobo blanco" *(Terminalia bucidoides)* tree. The roost site containing Colony No. 1 also housed several individuals of the Greater Sac-Winged Bat, *Saccopteryx bilineata,* and there appeared to be very little interaction between this insectivorous species and the vampires over the entire study period. Similar observations of vampires roosting in mixed-colony associations with various other bat species have been made before (GOODWIN and GREENHALL, 6). Colony No. 2 was comprised solely of vampires during the study period. It was difficult to determine how long both roosting sites housed the present vampire colonies, but the presence of large quantities of guano under both indicated that these were "favored" roosts and had probably been used by vampires for several years. When this highly solidified guano was broken into, a faint odor of ammonia was noticed—a diagnostic character of vampire roosts. The utilization of crevices formed by tree buttresses for vampire roosting sites has not been previously reported.

Each colony was observed for a total of eight closely-spaced nights per month, for eleven months (September, 1968 through July, 1969). As much as possible, nights of observation were alternated between the two colonies and no observations were made on nights of persistent heavy rainfall. As seen in previous studies (WIMSATT, 14), it was observed now that nights of heavy rainfall tend to suppress the activity of vampires. On a given night, each colony was studied from 4 PM to 5 AM (13 hours per night), in addition to making other observations during daylight hours on a more or less opportunistic basis from time to time. On each night of observation at a colony, the numbers of individual vampires leaving and returning to the roost were recorded over successive two-hour intervals. Notes were also kept on the flight behavior associated with leaving and returning to the roost. All of these observations were greatly facilitated by using a large (4 ft by 8 ft) rectangular piece of white cloth (bed sheet) tacked taut on a wooden frame staked into the ground at one side of the roost entrance and about four feet from the tree. In this position, the cloth provided an excellent back-drop against which to see individual bats leaving and entering the roost throughout the night. On various nights of study, this back-drop was transferred to the opposite side of the tree as an attempt to control for effects of presence of the observer and

apparatus upon vampire activity at roosting sites.

During daylight hours, records were kept on the appearance of young bats in the colonies, along with counts of adults in order to estimate changes in colony size during the study period.

Another major part of this study had to do with the systematic observation of vampire activity at cattle in the nearby pastures. Shortly after observations of vampire activity at roosts had begun, it became apparent that the cattle population grazing in the nearby pastures was infested with vampires. Three fenced pastures abutting on the forest of La Selva were selected for detailed observation on this infestation. One pasture located due north of the forest, composed of 36 acres of grassland, supported an average of 118 head of cattle (based on monthly counts); the second pasture, 28 acres, northeast of the forest supported an average of 55 head. The latter pasture was separated from the first by a thin strip of tall trees. The third pasture was moderately removed from the other two, due east of the forest and separated from the second pasture by a large expanse of small trees and other woody secondary growth vegetation. This pasture, 52 acres of grassland, supported an average of 80 head during the study period. From month to month, there was very little change in the numbers of cattle in each of these pastures. On nights when vampire activity at roosts was not being studied, activity of vampires at cattle in these pastures was studied for the same length of time (11 hours) per night and usually for nine or ten days per month. For each night of observation, records were kept on: numbers of vampires attached per host (cow); numbers of attacked cows; and the presence of young vampires (of nursing age) at hosts (attached to the backs of their mothers). In order to assess to what extent individual vampires from the two colonies were actually foraging and feeding on these cattle, samples of adult vampires from each colony were marked (banded) by fitting a colored aluminum band on the forearm of each individual. Individuals from Colony No. 1 were marked with red bands and individuals from Colony No. 2 with blue bands. Initially, eight vampires from each colony were marked in this manner and their subsequent appearances on the cattle in these three pastures were recorded. This method of marking vampires has been used with success before (WIMSATT, 16). Nights of observation on vampires attacking cattle were rotated among the three pastures and only one pasture was visited on a given night.

Other individuals from each colony were marked with aluminum bands in order to obtain an estimate of homing ability of vampires in the Atlantic wet lowlands of Costa Rica. This analysis of homing was a small study, conducted towards the termination of the other observations outlined above.

RESULTS AND DISCUSSION

The mean nightly air temperature (computed as the mean of five readings per night and then averaged by months) during parts of the wet season (September through December and June through July) was 19.0±1.83 C (range between 17.5 and 22.3 C) and for the one entire dry season (January

through May) it was 23.0 ± 0.95 C (range between 19.5 and 24.0 C). Rainfall averaged close to 300 mm monthly during the wet season and only 5 mm during the dry season this particular year. These data on rainfall indicate that the dry season for this year (1968-1969) was unusually severe in that this period was longer (by 2.5 months, including the latter half of March, and all of April and May) and characterized by far less rainfall (the usual dry season monthly average being close to 100 mm) than other dry seasons in this region of Costa Rica over the last ten years. These climatic data on rainfall are given in Fig. 1. Most likely, the boundaries between tropical seasons are variable from year to year, and for a given year, seasons should be defined in terms of relative (and not absolute) quantities of rainfall as recorded over successive months (JANZEN, 10).

Table 1 summarizes colony size; within each colony, numbers of individuals remained relatively the same until March and April when a few births occurred. That vampire colonies such as the ones studied here tend to be small (Table 1), ranging from anywhere between 20 to 100 individuals of both sexes per colony, has been noted previously by several investigators (2, 3, 13, 14, 15). Although based on data obtained from only two colonies, it appears that vampires do not breed continually throughout the year in this particular climatic region of Costa Rica (Table 1). This is in contrast with other observations of vampire colonies in other countries (CRESPO *et al.*, 2; GOODWIN and GREENHALL, 6; WIMSATT and TRAPIDO, 17). The few adult losses (Table 1) that took place during the study period could have been due to death away from roosts or emigration. The reason was not determined, but it is known in Panamá that certain species of hawks are predators of vampires (DUKE, 4).

TABLE 1.

Monthly numbers of individuals in two colonies (roosting sites) of vampire bats (Desmodus rotundus) *at Finca La Selva, Heredia, Costa Rica, 1968-1969. Counts were made at each colony for eight nights per month.*

	Wet Season				Dry Season					Wet Season	
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.
					Colony No. 1						
Adults	42	42	42	42	40	40	40	40	40	40	40
Young*	0	0	0	0	0	0	4	3	0	0	0
Total	42	42	42	42	40	40	44	47	47	47	47
					Colony No. 2						
Adults	57	57	57	54	54	54	54	54	53	53	53
Young*	0	0	0	0	0	0	9	5	0	0	0
Total	57	57	57	54	54	54	63	68	68	68	68

* These figures refer to numbers of births in the colonies.

One outstanding character of these two colonies is that they appear to remain relatively the same size and that each constitutes a more or less autonomous group of individuals which occupy the same favored roost continuously. Vampires leave and return to these roosts every evening when foraging (Table 2) and there appears to be a high degree of roost fidelity. There is no evidence of a considerable turnover among the individuals present in these two roosts from one day to the next. Not only did vampires return to these roosts nightly throughout the eleven-month study period (as seen for 8 days each month), but always "red-banded" individuals remained in Colony No. 1 and "blue-banded" individuals remained in Colony No. 2. Nor did the numbers of unmarked individuals in each colony vary greatly from day to day. Such apparently well developed roost fidelity is in dispute with the findings of WIMSATT (15). He found a high degree of turnover in individuals at two vampire roosting sites in Mexico (Teapa and Tlacotalpan localities) during a five-day study and interprets this as these particular vampire colonies being "temporarily associated members of a larger, mobile population". Wimsatt goes on to hypothesize that such a population of vampires utilize multiple roosts "among which individual bats shift on a daily and perhaps wholly opportunistic basis". No doubt Wimsatt is correct for the colonies he observed, but the situation undoubtedly changes for different vampire colonies — depending primarily upon the proximity and accessibility of suitable quantities of prey animals to favored roosting sites. Roost fidelity, non-existent in Wimsatt's study and well developed in the present study, must be, at least in part, a function of the location of prey animals. If a large, easily-accesible population of prey animals is always in close proximity to one or many favored vampire roosting sites, *a priori,* there would appear to be little reason for these foraging vampires to seek out multiple roosts—since the utilization of multiple roosts implies a shifting or dwindling of suitable prey animals per unit time. In the present study, there would appear to be little need for multiple roosts since cattle are both abundant and in close proximity to vampire roosts. Data (to be presented later) on the occurrence of marked individuals from the roosts studied show that at least a portion of these colonies is utilizing this particular cattle population as a prey source—and doing so for at least eleven successive months. WIMSATT (15) does not mention anything about the type of prey being used by vampires in his study, nor anything about the proximity of potential prey animals to the roosts he observed. However, he points out that roost fidelity may be affected by accessibility of prey. Perhaps in Wimsatt's study, prey animals were not continually available at one general location on successive nights. This appears to be true when comparing the high degree of roost fidelity seen under the conditions existing in the present study with the almost complete lack of it in the vampire colonies studied by Wimsatt in Mexico. Certainly more extensive studies are needed concerning the relationship between vampire roosting sites and prey sources—with analysis of vampire density at prey and proportions of these individuals returning to specific roosts nightly.

TABLE 2.

*Numbers of vampires present in the two roosting sites over successive two-hour intervals nightly during the study period**

Period	Wet Season Sept.	Oct.	Nov.	Dec.	Dry Season Jan.	Feb.	Mar.	Apr.	May	Wet Jun.	Jul.
					Colony No. 1						
4 PM-Sunset	42	42	42	42	40	40	44	47	47	47	47
Sunset-7 PM	29	31	30	23	13	10	13	15	14	35	33
7-9	29	27	27	18	7	6	8	7	8	31	30
9-11	12	12	10	8	0	0	0	0	0	14	16
11-1 AM	24	26	29	28	8	11	10	9	10	29	24
1-3	35	37	40	37	10	13	15	16	15	38	38
3-5	42	42	42	42	40	40	44	47	47	47	47
					Colony No. 2						
4 PM-Sunset	57	57	57	54	54	54	63	68	68	68	68
Sunset-7 PM	40	40	44	39	9	8	9	11	10	48	45
7-9	38	36	32	27	2	0	1	3	5	41	37
9-11	17	17	16	17	0	0	0	0	0	23	26
11-1 AM	32	30	28	32	16	9	13	10	12	44	40
1-3	40	42	44	47	20	14	18	21	19	57	51
3-5	57	57	57	54	54	54	63	68	68	68	68

* These figures were obtained by initially counting each night the vampires in each roost (just prior to sunset) and then tabulating the numbers of individuals leaving over two-hour intervals.

Nightly patterns of foraging over successive months are summarized in Table 2. The time schedule of individuals leaving and returning to the roosts was very similar for both colonies. None left before sunset nor did any return after 5 AM. Vampires were active for eleven hours per night (although not for all individuals in a colony) and this varied with season: while individuals were active for eleven hours irrespective of season, during the dry season a greater number of individuals from each colony foraged nightly and did so for longer periods of time (Table 2). Mist net data from another source agree well with these findings. During July, 1967, a total of 33 vampires were captured on one evening in six mist nets in the vicinity of Río Tenorito, Guanacaste Province, Costa Rica (ANDREW STARRETT, personal communication). This area possesses a tropical dry climate (tropical dry forest region) and during July, it is in the "veranillo" or short dry season phase (there is a second, longer dry season). About 70% of these bats were caught between sunset and 1 AM, followed by a lag; the remainder being captured after 3 AM. While this lag in captures is perhaps somewhat puzzling, there is general agreement between the present findings and those of Starrett's brief study that vampires forage throughout the evening and well into the next morning.

As seen here, WIMSATT (15) found that vampires forage only after dark, but other aspects of his findings on foraging of vampires in Mexico differ from patterns seen in the present study. He found that near Tabasco, Mexico, vampires were active only during approximately two hours in the early evening. This observation was made on only one evening and it may be atypical of vampire foraging behavior. However, other short-duration studies in Mexico also indicate a similar restriction of maximum foraging activity to the early evening hours (2, 3). Perhaps of crucial importance on this discrepancy again concerns the general accessibility and type of prey. In these previous studies, no observations were made on vampire activity at their prey. Observations on vampire activity in the present study indicate that vampires forage and feed throughout the evening and early morning hours at La Selva, agreeing well with observations of activities at roosts over the same months. As pointed out by WIMSATT (15), an assessment of the generality of vampire foraging behavior neccesitates studying the phenomenon at several different localities—clearly, diffferences among specific local factors may be relevant in eliciting various types of locality-specific types of behavior. The difference in length of foraging period between the present study and that of WIMSATT (15) suggests this to be the case.

Another finding of this study which is not presented in Tables 2, was that individuals foraged only once per night—once an individual vampire returned to the roost, it did not leave it again on that same night. This was best observed at the roosting site of Colony No. 2, where individuals, upon alighting in the tree crevice, could easily be seen and observed for further movements. Foraging only once nightly by individual vampires was also reported by WIMSATT (15).

The amount of sunlight may be the critical factor accounting for differences in the emergence schedules of vampires from their roosts between wet and dry seasons (Table 2). During the dry season, there is a much greater amount of total solar radiation since there is a greater amount of unobstructed sunlight available per day than during the wet season. GOULD (7) found that total solar radiation did not affect the emergence time of the temperate zone bat, *Tadarida femorasacca*. JONES (11) discussed the possibility that temperature rather than light is the critical factor in determining emergence times of temperate zone bats from their roosts. For tropical bats, it seems more plausible that light is the more important factor, as differences in diurnal air temperatures are in general far less than in temperate regions.

The data given in Table 2 suggest that vampires tend to remain away from their roosts for longer periods during the dry season than during the wet season. During the dry season, the actual return flight behavior to roosts was also different: usually individuals would land some distance from the roost and walk over to it and then enter it. These individuals always appeared to be very heavily "engorged" with blood and had some difficulty walking. GOODWIN and GREENHALL (6) believe that such awkward walking may be diagnostic of recent heavy feeding (ingestion of blood). During the wet season, individual

vampires returning to the roosts appeared less engorged and invariably they flew directly into the roost. Unfortunately, data were not obtained on the amount of blood ingested by individual vampires during nightly forages. Data of this sort, expressed in body weight differences before and after foraging (weighing marked bats just before leaving the roost and again just after returning to it) on a given night, would be one way to demonstrate that vampires ingest more blood during the dry season than during the wet season. While it is true that returning individuals appeared more engorged with blood during the dry months, quantitative data on this is lacking. WIMSATT and GUERRIERE (16) demonstrated that captive vampires ingest large quantities of blood per diem (sometimes greater than 50% of their fasting body weight) and that such engorgement is obligatory—it provides sufficient solids from the solely liquid diet to meet nutritional requirements. Local seasonal climatic changes may affect the degree of feeding, since during an extended dry period more nutrients, in addition to more water, are necessary to maintain subsistence. Data to be discussed below show that vampires spend greater lengths of time attached to their prey during the dry season—suggestive but not conclusive evidence that in fact vampires feed longer (ingest more blood) during this time. The alternative explanation that vampires spend more time at temporary (digesting) roosts during the dry season and do not increase their feeding, seems unlikely.

The nightly foraging activity of vampires can conceivably be broken down into some or all of these components: searching and detection of suitable prey; feeding; and return to roosts. There is, in addition, a period of digestion at temporary roosts, although no direct evidence of this is available. These activities are accomplished within an eleven-hour period (Table 2) and one way of obtaining estimates of the amount of time spent at each one is to study vampires at their prey (Table 3). It was found that four to six marked individuals (out of eight marked in all) from Colony No. 1 and six to eight marked vampires (out of eight marked in all) from Colony No. 2 appeared regularly (every month) on cattle in the three pastures under observation. Many unmarked vampires were also feeding on these cattle throughout the study period and some of these might have been unmarked individuals from the two colonies. During the wet season there was usually one vampire per cow (with only six instances of two vampires per cow seen) and the average time spent by vampires attached to these hosts was 9 ± 1.5 minutes. During the dry season, however, there was an average density of seven vampires per cow, with an average time of 17 ± 2.6 min spent attached to hosts nightly. The actual range of vampire densities during the dry season was five to nine individuals and usually several of these were present on a host for at least part of the same time as there were differences in the arrival and departure times among individuals. It was also observed in marked vampires that once an individual had departed from a host, it did not return to that same animal on the same night. There were no major differences between pastures for these data and all three seemed to be exploited by vampires. Although several

cattle were heavily infested by vampires during the dry season, none of these died during the study period. It was difficult to determine if the same cows were repeatedly attacked on different nights since prey animals were not marked. However, there were a few instances of two or three cows having easily-remembered patterns of wounds and these individuals were not always re-attacked on different nights. Actual feeding by vampires on the cattle was not studied due to various technical difficulties but the behavior associated with the lapping of blood after incision has been described in detail elsewhere (VILLA, 12).

TABLE 3.

Increase of vampire density and of time of attachment per prey animal during the dry season (January through May).

Month	No. days studied	No. cattle	Mean nos. attacked	Mean nos. bats/cow	Mean time bats attached
Nov.	9	55	28	1	8.5 min
Dec.	6	55	26	1	9.5
Jan.	10	55	11	7	16.5
Feb.	10	57	13	7	17.0
Mar.	9	55	15	7	15.5
April.	10	56	12	6	17.0
May	10	56	11	7	18.0
June	10	56	25	1	9.0
July	10	55	24	1	9.5

Individuals from the two colonies studied did not segregate themselves at prey: not only were both "red-banded" and "blue-banded" vampires seen in the same pastures, they were also seen together on the same hosts on several different occasions.

The increased foraging (and probably feeding time) of vampires during the dry season is in part related to an increased demand for sufficient levels of nutrients. Based on the exit schedules of individuals from roosts and from records kept for times (clocking) of appearances of vampires at cattle, it was computed that searching and detection of prey usually required 1.0 hours during the wet season and 2.4 hours during the dry season. The period of attachment (and presumably feeding) to prey, as already stated, was 9 minutes for the wet season and 17 minutes for the dry season. It was not possible to determine the numbers of different hosts visited on a given night by individual vampires and whether or not this was affected by season climatic change. For this reason it can only be speculated that other parts of the foraging activity such as "digestion at temporary roosts" (if it exists at all) and return to roosts were probably shorter during the dry season owing to an increased amount of time spent at prey. The increase in amount of time spent away from roosts during the dry season on a nightly basis (an increase of about 1.4 hours) not only involved extended feeding periods (from 9 to 17 min per host), but

possibly additional visitations to other hosts. However, data are not available on this suspected additional foraging at the present time. All that we know is that vampires take longer to return to their roosts during the dry season, and that part of this additional time involved longer feeding periods at the hosts under observation.

YOUNG (18) suggested that the hermit hummingbird *Phaethornis superciliosus* alternates between different types of food between wet and dry seasons at La Selva, being primarily a nectar forager during the wet season and an insect forager during the dry season. Similarly, it is possible that vampires seek out additional food sources during the dry season. However, the consistent appearance of marked individuals at cattle throughout the study period indicates that vampires probably do not exploit other suitable prey animals for blood in either wet or dry seasons. This is not to say that vampires do not have other potential food sources at this locality, but rather that under the conditions prevailing in this study, cattle are presumably the most exploited prey at all times.

The increased density of vampires per host during the dry season could not have been due to an increase in colony (population) size for young bats are not yet old enough to fly on their own at this time. On several nights during April and May, it was observed that some vampires (presumably adult females) carried a single young (of nursing age) individual on their backs when attached to hosts.

The presence of marked individuals at cattle in the three pastures demonstrated that vampires can forage at least up to 1.5 miles from their roosts, as this was the approximate distance between roosts and the pastures. In a given locality containing a suitable prey animal population, probably the frequency of vampire attacks is in part dependent upon the abundance and spatial distribution of these hosts and the ability of vampires to forage over considerable distances from roosts. In order to estimate maximum foraging range of vampires, a small homing study was conducted near the end of the observations being made at roosts and cattle. Marked individuals (banded as before) were taken from each colony and released at distances of about 0.5, 2.0, 6.0, 10.0, and 18.0 miles in an almost straight-line transect between the hours of 6:30 and 9:30 PM on one evening. Individuals released at a given distance were marked (with different colored bands) differently than those released at another distance. In general, there was very little change in the terrain encompassing the distances studied as it was all open pasture lands. The initial study was replicated eight days after the first trial and the results of both trials are given in Table 4. Both trials were performed on clear, star-studded nights. The data indicate that these vampires can locate their original roost from as far away as 10, but not 18, miles. The maximum distance for successful homing performance is probably between 10 and 18 miles. The insectivorous bat *Myotis lucifugus* exhibits keen homing for 10- to 20-mile distances in rural Chester, Massachusetts as determined in a large-scale study involving releases of many individuals (GIFFORD and GRIFFIN, 5). On the

two nights when homing was studied, still other vampires in the colonies were marked differently (different colors) to serve as "controls": These individuals (not all of them) appeared at cattle in the pastures and apparently these two nights were typical for foraging vampires. Between trials, there is a striking degree of similarity in the data (Table 4) that strengthens their significance. There were no differences in homing ability between sexes.

TABLE 4.

Results of a homing study of Desmodus rotundus *using marked individuals taken from two colonies, June 1969. Figures in parantheses refer to results of a second trial eight days after the first.*

Distance transported (in miles)	No. of bats	No. of returns	Time elapsed (hours)	No. additional returns next day	Time elapsed (hours)
			Colony No. 1		
0.5 (0.5)	2 (2)	2 (2)	6.5 (6.2)	—	—
2.0 (2.0)	2 (2)	2 (2)	7.3 (7.0)	—	—
6.0 (6.0)	2 (2)	2 (2)	7.7 (7.4)	—	—
10.0 (10.0)	2 (2)	1 (1)	9.2 (9.0)	1 (0)	18.5
18.0 (18.0)	2 (2)	0 (0)	—	—	—
			Colony No. 2		
0.5 (0.5)	4 (4)	4 (4)	7.5 (7.5)	—	—
2.0 (2.0)	4 (4)	4 (4)	8.5 (8.0)	—	—
6.0 (6.0)	4 (4)	4 (4)	8.0 (8.0)	—	—
10.0 (10.0)	4 (4)	2 (2)	9.5 (9.5)	2 (2)	23.5
18.0 (18.0)	4 (4)	0 (0)	—	—	—

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SUMMARY

Extensive observations of the foraging activity of vampire bats *(Desmodus rotundus)* were conducted for eleven successive months at one locality in Atlantic wet lowland Costa Rica. This study period included parts of two wet seasons and one entire dry season. Data were obtained on nightly departures and returns of individual vampires at two roosting sites in order to estimate the amount of time spent away from roosts during the wet and dry seasons. Several individuals from these roots were marked (using different colored aluminum bands for different roosts) and nightly data were also obtained on their occurrence, along with many unmarked individuals, attaching themselves to cattle (prey) inhabiting three nearby pastures. From these two series of observations, it was found that (i) vampires exploit local cattle populations for blood; (ii) vampires invariably return to the same roosts every night after foraging; (iii) vampires spend more time attached to their prey animals during the dry season than they do during the wet season, and (iv) presumably more blood is actually ingested during the dry season. A brief study of homing ability demonstrated that vampires can return to their original roosting sites from as far away as 10 to 18 miles.

RESUMEN

Durante once meses consecutivos se hizo observaciones exhaustivas sobre las actividades que el murciélago vampiro *(Desmodus rotundus)* desarrolla en procura de su alimento, en una región del Atlántico húmedo de Costa Rica. El estudio abarcó dos partes de la estación lluviosa y una estación seca completa. Se recogieron datos sobre la partida y llegada nocturnas de vampiros individuales en dos nidos para establecer el lapso de tiempo que permanecen fuera de ellos. Se marcaron varios individuos con bandas de aluminio de diferente color para cada uno de los dos nidos estudiados y se recogió datos sobre sus ataques, junto con vampiros sin marcar, a ganado vacuno en tres potreros adyacentes.

De estas dos series de datos se descubrió que los vampiros (i) se alimentan de la sangre del ganado vacuno local; (ii) que regresan invariablemente a los mismos nidos después de alimentarse; (iii) que permanecen adheridos a sus presas (ganado vacuno) por más tiempo durante la estación seca que durante la lluviosa; y (iv) que presumiblemente ingieren más sangre durante la estación seca.

Un estudio breve del radio de acción demostró que éste puede ser hasta de más de 16 Km alrededor de sus nidos.

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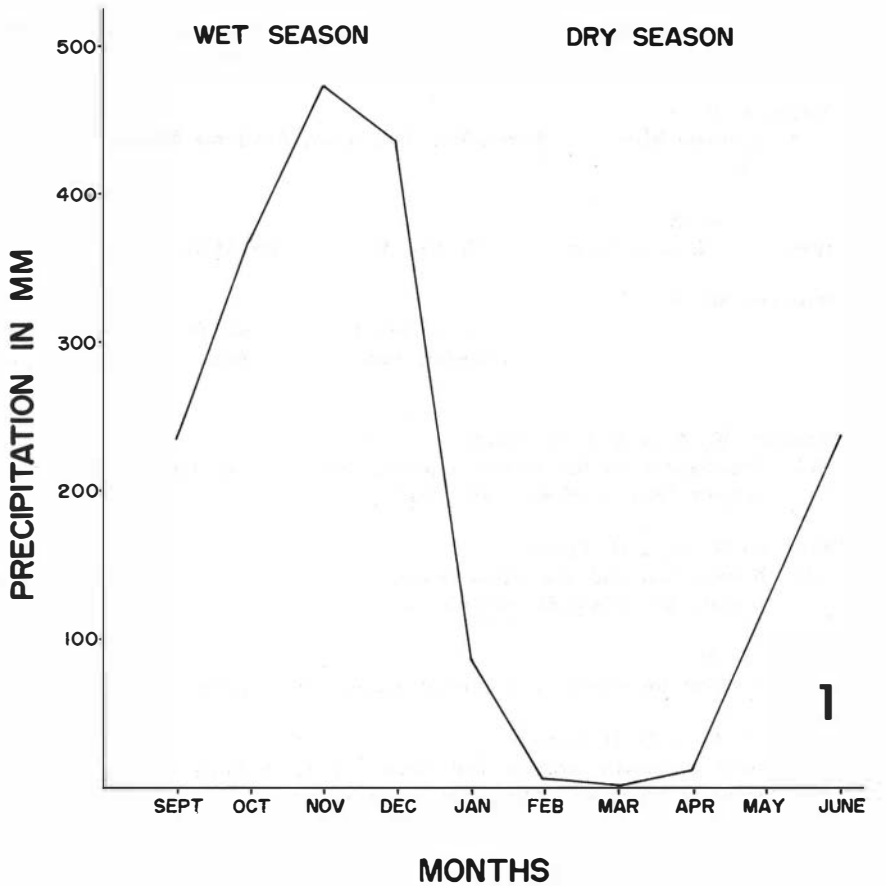
Fig. 1. The rainfall regime at Finca La Selva, near Puerto Viejo, Heredia Province, Costa Rica from September 1968 through June 1969. Although not shown here, the amount of rainfall continued to increase during July.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