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The social organization of the common vampire bat

I. Pattern and cause of association

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Summary. At a site in Costa Rica, three groups of 8–12 adult female vampire bats, *Desmodus rotundus*, utilize group-specific sets of hollow trees as day roosts. Long-term nonrandom associations between pairs of females, as measured by the proportion of time one bat spends roosting in the same tree with another bat over a 3 year period, occur even when preferences for particular trees are removed. Significant associations exist between both related and unrelated adult females. Adult male bats, however, show few associations with females or other males. By observing bats within trees and while foraging, and by monitoring feeding flights with radiotelemetry, the following potential benefits of association could be tested. Females roost together to (1) share a suitable microclimate, (2) avoid predators, (3) avoid ectoparasite infestations, (4) minimize travel to mobile prey animals, (5) respond to coercive males, (6) feed simultaneously from a bite, (7) remove ectoparasites by allogrooming, and (8) share food by regurgitating blood to other bats within roosts. The data do not indicate that any of the first five hypotheses provide significant benefits for long-term associations although predators and ectoparasite levels may cause occasional changes in roost sites. Simultaneous feeding was uncommon and apparently confined to females and their recent offspring. Allogrooming, although common, occurred independently of the presence of ectoparasites. Food sharing, however, occurred between both related and unrelated adult females with high levels of association and provides at least one selective advantage for maintaining cohesive female groups.

Introduction

Animals form nonrandom aggregations when the benefits of being in a group exceed the costs (Alexander 1974). Two types of benefits, passive and active, can be distinguished. If animals independently aggregate at a resource and that resource is patchily distributed, then groups form because of passive benefits. Active benefits, on the other hand, require interactions among individuals. Consequently, the fitness of an animal in an actively generated group should be a positive function of group size, at least initially, while the fitness of animals in a passive group should either remain constant or decrease as groups get larger. The form of the fitness function depends both on the nature of the active benefit, i.e. whether it involves selfishness (donor benefits more than recipient), cooperation (donor benefits, but less than recipient) or altruism (donor accrues some cost while recipient benefits), and which method of fitness accounting is appropriate – mutualism, nepotism (Hamilton 1964), reciprocity (Trivers 1971; Axelrod and Hamilton 1981), or some form of group selection (Wade 1978).

Defining the factors which favor the formation of active groups can illuminate the evolution of social behavior. Clearly, these groups could form at first for passive reasons which might, in turn, change the genetic and social structure of the population to favor the evolution of altruism or cooperation. Alternatively, animals might aggregate initially to engage in social behavior. Although reconstructing such a history for any species is perhaps impossible, one can identify the passive and active benefits which currently favor aggregation in a species and then compare them to those of other species to determine whether the presence of a particu-

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lar social behavior is contingent directly upon some passive factor or indirectly via a certain genetic and social structure.

In this paper I attempt to identify the factors responsible for the dispersion pattern of the common vampire bat, *Desmodus rotundus*. After documenting long-term associations among adult females, I evaluate eight hypotheses which can explain the formation of these assocations. They are (1) evading predators, (2) minimizing foraging distances, (3) choosing favorable microclimatic conditions, (4) coercing potential mates, (5) avoiding ectoparasites, (6) allogrooming to remove ectoparasites, (7) sharing a single wound site, or (8) regurgitating blood to roostmates. The major conclusion reached in this paper is that the pattern of association through time among adult female vampire bats requires active choice by individuals, primarily to ensure opportunities for sharing of blood. In the companion paper, I show how the association of females described here affects the mating system and the genetic structure within populations. The information presented in these two papers is critical for understanding the social behavior, particularly the occurrence of reciprocal food sharing behavior (Wilkinson 1984), of this animal.

Methods

Study sites and dates. Observations were made on *D. rotundus* at two sites in northwestern Costa Rica, Hacienda La Pacifica and Parque Nacional de Santa Rosa. At La Pacifica we captured and marked 205 *D. rotundus*, a few of which had been banded previously (Fleming et al. 1972; Turner 1975), and conducted observations from September to December 1978, May to December 1980, May to March 1981–1982, and December to February 1982–1983. J. Bradbury censussed this population in June and August of 1982. We visited Santa Rosa for three days once a month, on average, during the 1980–1982 study season. During these visits we banded 319 bats at a single cave and conduced nocturnal observations of feeding bats. The climate and vegetation in the region has been described by Frankie et al. (1974) and Janzen (1983).

Capture and marking techniques. We captured individuals at both sites with mist nets as they left or entered their diurnal roosts. Unattended nonvolant young were captured with a hand net within roosts at night to prevent disturbance. Each bat was uniquely marked on one forearm with two or three colored plastic bands covered with reflecting tape and on the opposite forearm with a permanent numbered metal band. We did not cut membranes to attach bands and observed neither membrane inflammation nor other evidence that marking affected survival. By June 1981, over 95% of the adult bats in the roost trees were marked at La Pacifica; this percentage exceeded 99% by January, 1982.

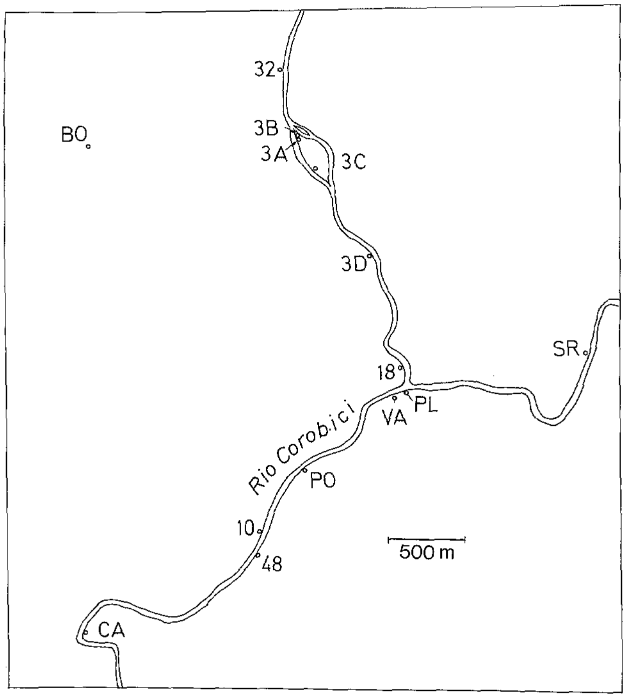

Fig. 1. The La Pacifica study site. Hollow tree roosts are indicated by circles with adjacent letter codes

In addition to banding, we routinely weighed, measured the length of forearm and tibia, and counted numbers of two species of streblid fly ectoparasites on each bat after every capture. When first captured, 0.05 to 0.1 ml of blood was taken from the propatagium by venous puncture for use in electrophoretic studies (Wilkinson 1985). We aged adult males by the presence of scortal testes larger than 5 mm in diameter (recaptures of bats with known birth dates showed that such testis size is attained at 12 to 14 months of age). Adult females were identified by the presence of used nipples or by feeling a fetus (earliest first birth was observed at 15 months of age). We estimated the age of young bats to the nearest month by comparing their relative forearm and tibia lengths to published growth rates (Schmidt 1978).

Roost association analyses. By searching the riparian forest at La Pacifica we discovered nine hollow tree day roosts in 1978. Five more roosts (Fig. 1) were located in 1981 by following radio-tagged bats. At regular intervals (mean$=8.3$, SD$=2.6$ days, $n=65$, excluding intervals greater than one month) beginning in June 1981 we recorded the identity of all marked bats within each tree on a single day by looking inside each tree with a headlamp and binoculars. All radio-tagged bats were found in these 14 trees except a few individuals which disappeared for several days from roost CA (Fig. 1). Since these bats eventually returned, at least one roost was never discovered. Nevertheless, the censuses should provide nonbiased estimates of the two roost association measures described below for most bats in the study area.

The first measure of association is the symmetrical index of Fager (1957),

$$I_{ij}=\frac{2N_{ij}}{(N_i+N_j)}$$

where N_i is the number of censuses on which bat i was observed and N_{ij} is the number of times bats i and j were observed roosting in the same tree, to estimate the proportion of time two bats roosted together. The *t*-statistic,

$$t=\frac{(N_i+N_j)\,(2N_{ij}-1)}{(2N_iN_j-1)\,(N_i+N_j-1)},$$

(Fager 1957) was used with infinite degrees of freedom to test if the association occurred by chance.

The second measure attempts to discriminate between passive and active attraction to trees by estimating the expected number of times two bats should have been seen together if they randomly visited roosts in proportion to the number of times they were seen in each tree. This statistic,

$$\chi^2=\frac{\left(N_{ij}-\sum_{k=1}^{14} P_{ik}P_{jk}T\right)^2}{\sum_{k=1}^{14} P_{ik}P_{jk}T}$$

where T is the smaller of the two N_i's and P_{ik} is the proportion of observations that bat i spent in tree k, was tested using one degree of freedom. Only associations between bats observed in more than one tree can be detected with this measure.

We calculated these statistics only during the interval in which both bats were banded and had been observed. Individuals seen on fewer than 10% of the censuses were excluded because the significance tests proved unreliable with small samples.

Roost microclimate measurements. After a census, relative humidity was measured in roosts with a sling psychrometer and temperature was recorded from dial thermometers mounted inside trees. A thermograph was set up in three trees and just outside one in the riparian forest to obtain continuous records of temperature changes during 96 h periods.

Radio tracking and nocturnal observation techniques. We followed a total of 55 radio-tagged bats at La Pacifica between 1980 and 1982. Radios were constructed (cf. Wilkinson and Bradbury, in press) to weigh less than 8% of the prefed weight of a bat and to transmit at frequencies near 148 khz. Before gluing radios to the fur with silicone silastic, we anaesthetized bats with 60 s exposure to cotton saturated with ether (Metafane, Pittman Moore, Inc., Washington Crossing, New Jersey 08560, USA). Each bat recuperated in cloth holding bags for at least 30 min before being released into a roost tree. Direct observations with a night vision device (NVD model 221, Javelin Electronics, Inc., 6357 Arizona Circle, Los Angeles, California 90045, USA) of bats with radios flying and feeding did not reveal any behavioral modification attributable to the radio. In the roosts, bats with radios as well as other roostmates sometimes licked and scratched the radios; this may explain, in part, why most radios did not remain attached more than seven days.

During the 1981–82 season we combined radio-tracking with direct observations to document interactions among bats while feeding. Bats were located with an AVM receiver (model LA-12) attached to a 4 or 7 element Yagi antenna. The antenna was mounted on a 4 m pole which rested in the middle of a table with compass bearings painted on its surface. Two people located on hills or on platforms in trees took simultaneous bearings on each radio every ten minutes and dictated the bearings over walkie-talkies to a third who determined the bat's coordinates by triangulation using a programmable calculator. The third person then drove to the appropriate pasture and attempted to locate the feeding bat. Once found, the bat was observed with the NVD using infra-red (IR) illumination supplied by a headlamp covered by a Kodak no. 87 Wratten gelatin filter. Because the colored bands reflected IR light, we could identify bats to sex at distances up to 50 m with a 200 mm zoom lens attached to the NVD. However, we could only confirm individual identity for radio-tagged bats because colors could not be readily distinguished in the NVD. We also used the NVD to observe bats on horses in corrals at Santa Rosa.

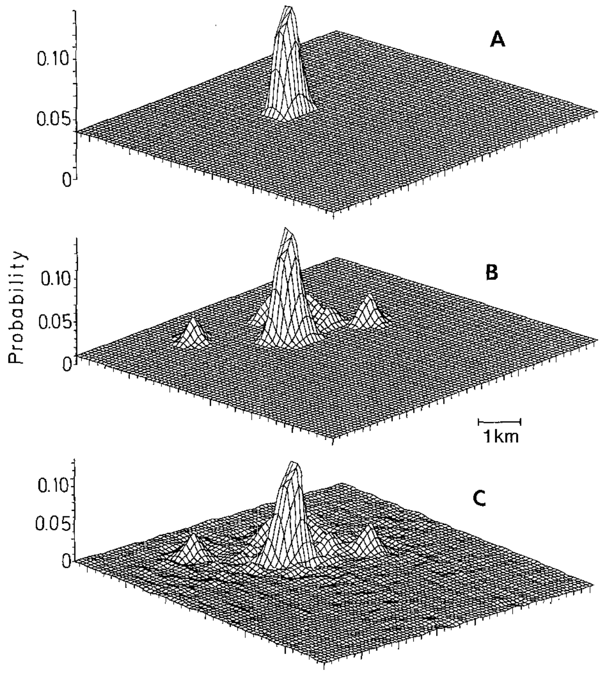

Fig. 2 A–C. Utilization distributions calculated using the nonparametric technique of Anderson (1982) for female YW based on 8 consecutive nights of radiotracking from September 15–23, 1981. The height of the surface represents the probability of locating the bat at x, y coordinates; the sum of all heights in **C** equals one. The surface in **B** corresponds to the MAP(0.95) UD. It was constructed by setting to zero those *z*-coordinates which after being ranked had a cumulative sum less than 0.05. In **A**, *z*-values which had a cumulative sum less than 0.5 (MAP(0.5)) were set to zero. The shallow irregularities in surface **C** represent residual effects of the Fourier smoothing algorithm

Radio tracking data analyses. I used data from 36 bats for which we obtained coordinates during every ten minute period out of the roost to calculate centers of activity (Hayne 1949), distance traveled, and a nonparametric estimate (Anderson 1982) of each bat's utilization distribution (UD). The value of the UD at an x, y coordinate represents the probability of observing that individual at that location. Consequently, the probability of finding two animals in the same area can be calculated by finding the overlap in volume of their two UDs. The minimum area which encloses all UD values with a cumulative sum of X is depicated in Fig. 2 for three values of X and is noted as MAP(X) following Ford and Krumme (1979) and Anderson (1982).

Since the variation in the MAP(0.5) estimates was less than that for MAP(0.95) areas based on cumulative data from successive nights within and between years (Fig. 3), I used MAP(0.5) UDs to calculate overlap. I excluded individuals for which I only had one night of data from these computations because the UDs produced by a single night did not produce estimates as consistent as those for UDs obtained from two or more nights (Fig. 3). When comparing foraging overlap to

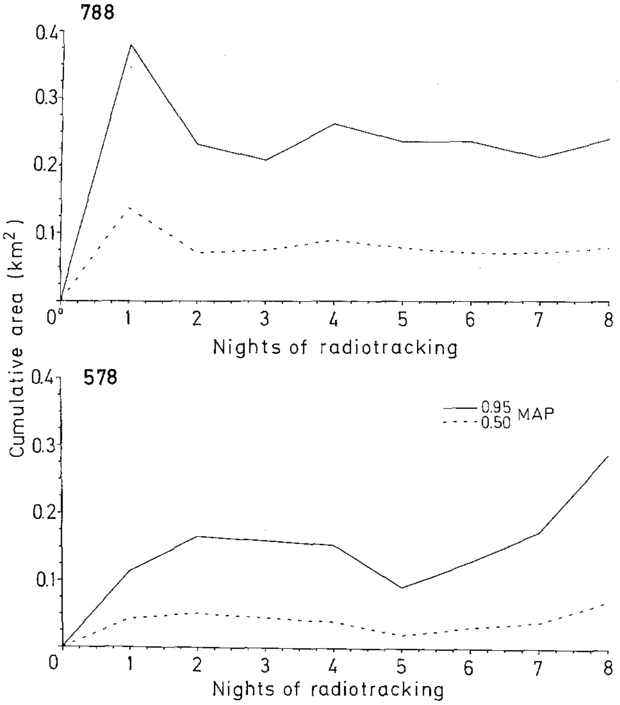

Fig. 3. Home range estimates calculated using MAP(0.95) and MAP(0.5) based on cumulative data collected over 8 nights. Female 578 (YW) was radiotracked from September 15–23, 1981. The data for female 788 (YGG) come from tracking done between December 18–22, 1981 and January 3–6, 1983

roost association, I only used the 1981–1982 data for 9 of the 11 adult females in one, UP, of the three groups (see Results) to prevent biasing the analysis by including animals from less successfully radio-tracked groups.

Diurnal observation methods. We conducted over 400 h of continuous scan behavioral sampling (Altmann 1974) within roost trees. During diurnal observation periods of 1 to 6 h we recorded all animals in view every 10 min and any cases of fighting, allogrooming, nursing, or blood regurgitation. From these data I calculated rates of behaviors for individuals. The females remained sufficiently clustered at the top of the trees to permit complete records of all interactions. We conducted observations with diffuse light and binoculars after habituating the bats to light for several months. Observations using IR light and the NVD verified that after habituation the bats' behavior was not affected by the diffuse light. Relatedness between bats was determined by matching marked offspring to mothers (cf. Wilkinson 1985).

Statistical procedures. Because many comparisons of interest involve measures between all pairs of individuals which necessarily lack independence, I devised Monte Carlo randomization tests (e.g. Huey et al. 1983). These tests hold some variable constant, such as the number of animals of each sex, while randomizing the type (e.g. sex) of each individual with respect to some pairwise measure, such as roost association or foraging overlap. Since the potential number of pairwise combinations in each case was too large to enumerate, I used a computer to randomly assign types a large number of times to compute the distribution for each statistic. To test for independence between sex or age and foraging overlap, the statistic I calculated was the ratio of the mean overlap between two bats of the same age or sex class to the mean overlap between two bats from different age or sex classes. To test for independence between overlap and the two association measures, I randomized one factor while holding the others constant and compared the mean absolute difference between each measure for the observed and randomized data sets. For this test I normalized the χ^2 association measure by the largest calculated value.

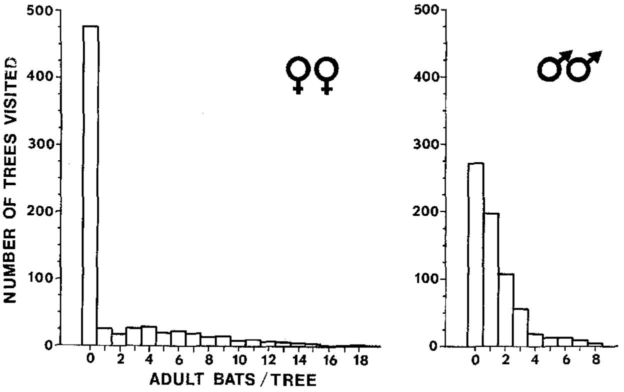

Fig. 4. Frequency of marked adult (>1 year of age) bats of each sex observed in hollow trees during all 70 censuses

All probability levels for evaluating significance are based on one-tailed comparisons unless stated otherwise. Explanations of the parametric tests used can be found in Sokal and Rohlf (1981); Hollander and Wolfe (1973) discuss the nonparametric tests.

Results

Roosting patterns within and between sexes

The distributions of adult males and adult females in roost trees (Fig. 4) deviated significantly from Poisson expectation; the variance to mean ratio for males was 2.02 and for females, 6.28, indicating that both sexes were aggregated with females forming larger groups. The median number of adult females found roosting together was 5.7; for adult males this number was 1.1. On any census, males occupied more trees than females. Over all censuses, 60.4% of the 1355 trees checked contained at least one male while only 31.4% contained females.

The differences between male and female dispersion patterns persisted through time as well as space. Adult males moved among fewer roost trees than females ($P<0.001$, Mann Whitney U-test). The median number of trees used by adult males was 1 (range = 1–4, $n=54$) while the median for females was 2 (range = 1–6, $n=61$). Furthermore, roost association was not independent of sex. There were fewer significant male-male associations (36 I_{ij}, $P=0.011$; 8 χ^2, $P<0.001$) and fewer significant male-female associations (105 I_{ij}, $P<0.001$; 35 χ^2, $P<0.001$) than expected if significant

Table 1. Mean number of significant associations per individual adult bat among all pairwise comparisons within and between sexes

Sex	Index	Mean	No. dyads	No. bats
Females-females	I_{ij}	7.4	861	42
	χ^2	3.4	861	42
Males-males	I_{ij}	2.6	465	31
	χ^2	0.6	465	31
Males-females	I_{ij}	3.4	1302	73
	χ^2	1.1	1302	73

associations were distributed randomly with respect to sex. Consequently, the 148 I_{ij} and 118 χ^2 associations occurring between adult females exceeded random expectation ($P<0.001$, 500 randomizations). The mean number of significant associations per individual between and within sexes (Table 1) reflect these differences.

Three groups of adult females could be distinguished at La Pacifica. One set of females, DN, was only seen in tree CA. Members of the second group, MD, were seen in trees 18, SR, PO, 10, 48 and CA. The third group, UP, moved between BO, 32, 3A, 3B, 3C, and 18. Each year, between 8 and 12 adult females could be assigned to one of these three groups on the basis of their roosting sites. During the 1981–1982 study season, though, 3 adult females (YY, WG and WW, cf. Table 2) and their young left the UP group and roosted independently in tree 3D. In 1983 two of these females again roosted with the other UP females. No significant associations formed between members of UP and MD; however, some individuals in MD did roost in CA sufficiently often to create significant associations with members of the DN group.

Within female groups obvious clusters of significant associations did not occur with the exception of the UP subgroup just mentioned. But in each group a few females formed large numbers of associations. For example, bat GG, the oldest female in group UP, formed 8 significant χ^2 associations with other adult females (Table 2). Some associations between adult females persist even longer than the five years spanned during this study. Two females in the MD group were banded in 1970 by T. Fleming (personal communication). These bats not only remained in the same area for 12 years but also formed highly significant I_{ij} and χ^2 associations during this study.

Numerous significant χ^2 associations among adult females suggest that their dispersion pattern cannot be explained just by mutual attraction to a common resource. Passive benefits, however, could explain why there were nearly twice as many significant I_{ij} associations among females as χ^2 associations (Table 1). In the following sections I evaluate each of the eight hypotheses presented in the Introduction to determine if associations between individuals provide both passive and active benefits.

Table 2. χ^2 (above) and I_{ij} (*below*) association measures among adult females in group UP

	YY	BY	GG	WW	YW	BB	GO	WG	YGR	YRY
YGG	0.42	6.46*	12.24*	1.46	8.87*	3.72*	1.50	2.24	4.10*	6.87*
	0.27	0.61	0.71*	0.28	0.66*	0.70*	0.66*	0.22	0.77*	0.77*
YRY	4.99	8.58*	13.89*	2.47	11.19*	9.79*	1.64	0	5.38*	
	0.30	0.58	0.69*	0.23	0.69*	0.79*	0.53	0	0.67	
YGR	0.18	4.61	7.15*	0.13	10.14*	4.27*	1.12	0.12		
	0.13	0.65	0.69*	0.14	0.78*	0.68*	0.65*	0.09		
WG	42.80*	0.54	6.56*	35.32*	0.13	0.06	1.47			
	0.82*	0.27	0.38	0.72*	0.17	0.15	0.28			
GO	3.75	1.70	6.66*	0.82*	2.97	5.15*				
	0.38	0.56	0.63*	0.33	0.57	0.71*				
BB	1.83	4.54*	15.05*	0.15	14.25*					
	0.29	0.57	0.69*	0.24	0.70*					
YW	3.14	5.83*	12.56*	0.22						
	0.32	0.59	0.62	0.26						
WW	40.56*	2.10	5.89*							
	0.81*	0.40	0.47							
GG	9.17*	15.97*								
	0.5	0.72*								
BY	3.07									
	0.37									

* $P<0.05$

Avoidance of predation

While several potential predators – e.g. owls (*Tyto alba* and *Pulsatrix perspicillata*), snakes (*Boa constrictor* and *Trimorphodon biscutatus*), opossums (*Didelphis marsupialis* and *Philander opossum*) and lizards (*Ctenosaur similis* and *Basiliscus basiliscus*) – of *D. rotundus* were common at both sites (personal observation), only two carnivorous bats, *Vampyrum spectrum* and *Chrotopterus auritus*, could readily gain access to adult bats roosting high inside hollow trees. On two occasions we observed a *V. spectrum* in frequently used *D. rotundus* roosts in the absence of any resident bats. Furthermore, in a cave 30 km west of La Pacifica we once found a single *Chrotopterus auritus* alone in a chamber that usually contained 20 to 50 *D. rotundus* in addition to other bats. In contrast, for several months we observed barn owls and both species of snakes and lizards in roosts with vampire bats without noting any responses by the bats. Since resident adult males almost always remained in roosts after females moved, it is unlikely that the females moved in response to some attempted predation. We have no indication that more bats in a roost aid in either detecting, avoiding, or hindering any predator although the potential for ultrasonic alarm calling was not thoroughly examined.

Minimizing foraging distances

Calculation of distances moved between successive radio-tracking fixes do not support the proposition that females moved to minimize their travel distance to prey as suggested by Turner (1975). The mean distance flown for all bats (3.44, SD = 1.82 km, $n = 116$ nights) was roughly twice the mean distance from the roost to the foraging center and back (mean = 1.89, SD = 1.03 km). Frequently, individuals flew several km more than required for this commute (Fig. 5). Mean distances travelled per night do not differ between the sexes ($P = 0.86$ for flight distance and $P = 0.55$ for distance to foraging center, *t*-test, $n = 31$ for males and 85 for females). Furthermore, only on 46 of the 116 bat/nights did individuals roost in the nearest possible roost to the previous night's foraging center, and only 12 of the 36 radio-tagged bats returned to the nearest roost tree more than 50% of the nights monitored. The failure of individuals to return to the nearest roost cannot be ascribed to the bats' incomplete knowledge of roost locations. Every night many bats visited more than one roost, the number of which was independent of age ($P > 0.05$, *G*-test) but not of sex ($P < 0.01$, *G*-test). Females visited more roosts per night than males (Table 3).

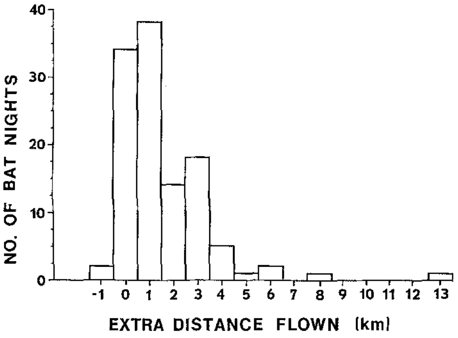

Fig. 5. Frequency of total distance traveled in a night minus the distance from the initial roost tree to the foraging center and back calculated for every night that each of the 36 bats was radiotracked

Table 3. Number of different roosts visited per night by sex and age

Sex	Age (*y*)	Number of trees visited			
		1	2	3	4
Female	≧1	19	24	7	1
	<1	22	11	1	0
Male	≧1	10	0	0	0
	<1	15	5	1	0

Choice of suitable microclimate

Individual *D. rotundus* prefer high humidity (McFarland and Wimsatt 1969) and warm temperature (McNab 1973). In the wet season at La Pacifica the relative humidity inside roosts was never below 100%. In many trees this was true even in the six month dry season presumably because of the proximity of the roosts to water (cf. Fig. 1). Although significant differences in mean temperature within roosts existed between trees ($F_{3,376} = 932$, $P < 0.001$, anova), these differences changed little during the span of time between female roost movements despite daily fluctuations in ambient temperature (Fig. 6). Two of the trees which were used most frequently by females had the highest (tree CA –28.4 °C) and lowest (tree 48 –24.5 °C) mean temperatures. Since roost movements occurred frequently within seasons, choice of microclimate cannot account for long-term female associations.

Male coercion of female movements

Several lines of evidence suggest that adult males competed for access to roost trees that frequently contained females rather than coerce females to

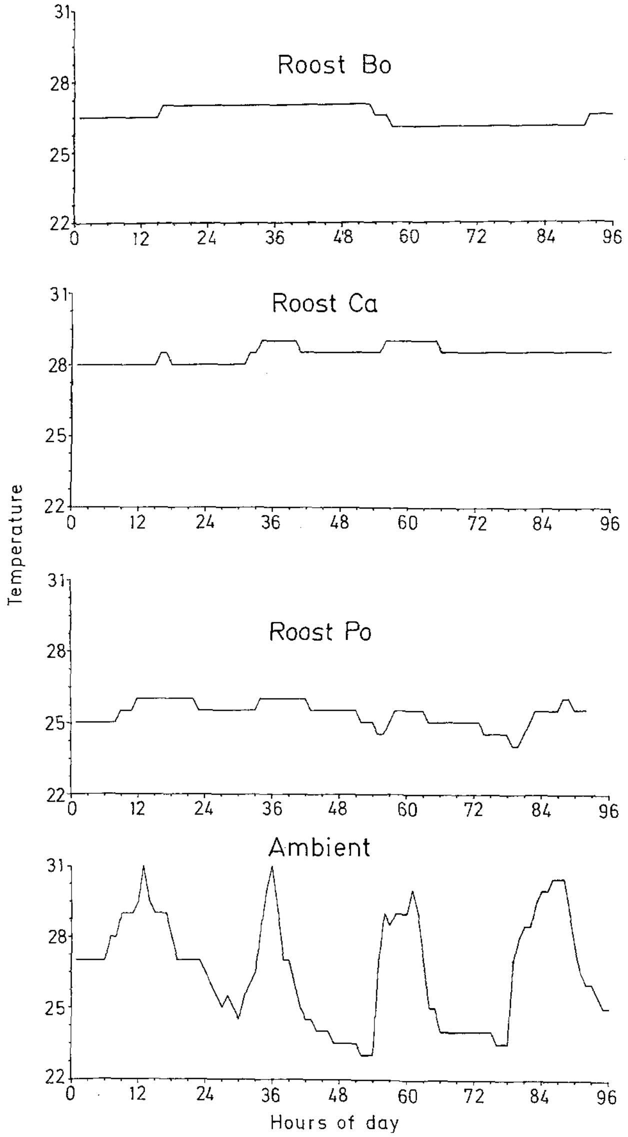

Fig. 6. Temperature changes either inside one of three hollow roost trees or next to a roost tree within the riparian forest. The dates on which these temperatures were recorded are BO: 6–9 August 1981; CA: 6–9 July 1981; PO: 1–4 September 1981; and ambient (outside of CA): 18–21 July 1981

remain in a group. As expected in either situation, there was a significant correlation between the number of adult males in a tree and the proportion of the censuses in which females were observed in that tree ($\rho=0.535$, $n=14$, $P<0.05$, Spearman Rank Correlation). When two or more adult males were seen within a female roost tree, each defended an area on the inside of the tree from other males, even when females were not present in the tree. Consequently, the few significant male-female χ^2 associations described above were not due to males moving with females. Rather, they were due to those few males which moved successfully from trees which did not contain females to those trees which did.

In addition, both netting and direct observations outside of roost trees with the NVD revealed that trees containing females often were visited at night by nonresident males. At night we observed several resident males, usually the individual at the top of the tree nearest the females, guarding the opening of a tree containing females. For example, during the first hour after sunset on 12 March 1982, on five occasions the top resident male flew after a banded male which approached the tree. Radio-tracking revealed that these chases sometimes occurred throughout the night. Furthermore, we observed a bloody fight between an intruding male and the top resident male which resulted in the deposition of the resident male to a tree which rarely contained females and the installment of the intruder as top resident for the next 11 months.

Ectoparasite avoidance and removal

As with most neotropical bats, *D. rotundus* act as hosts to several species-specific ectoparasites. Two species of streblid flies in the genera *Strebla* and *Trichobius* occurred commonly on vampire bats at both sites. These flies lay pupae on the walls of caves or trees (Wenzell et al. 1966). Emergent adults are dependent on their hosts for food and must feed every 3 to 4 h to survive (Marshall 1982). Infestations may become severe enough to be deleterious to a bat; 35 *Strebla* and 60 *Trichobius* have been recorded from single individuals (unpublished data). To determine whether bats might be moving in response to such infestations, I performed an analysis of covariance by using the number of flies of each species counted on mist-netted bats as the dependent variable and number of bats in the roost tree as a covariate with roost tree and both sex and age of the bat as independent factors. For *Strebla* flies, only sex proved to be a significant factor ($F_{1,253}=6.48$, $P=0.012$). Female bats had more of these larger flies (mean $=4.5$, SD $=5.1$, $n=152$) than males (mean $=2.4$, SD $=3.1$, $n=139$). For *Trichobius* flies, only roost tree identity and group size were significant ($F_{11,253}=3.11$, $P=0.001$ and $F_{1,253}=4.27$, $P=0.04$, respectively). Bats which were in larger groups had more *Trichobius* flies. Interaction terms were not significant in either analysis. Although these data suggest that females might benefit by moving to a different roost, the positive effect of group size on number of *Trichobius* would not favor establishing long-term associations.

Ectoparasites also could promote long-term associations if social grooming reduced the number of flies. I tested for this active benefit by computing allogrooming rates for bats observed three or fewer days before capture and then performing an analysis of covariance with the number of *Strebla* or *Trichobius* flies as the dependent variable and sex as the independent variable with grooming rate a covariate. Each of the 40 bats was observed in roost 3C between 30 and 250 min; rates varied from 0 to 0.11 instances of allogrooming received per minute. The allogrooming rate did not affect the number of *Strebla* or *Trichobius* counted on the bats when captured ($F_{1,37}=0.22$, $P=0.643$, $F_{1,37}=1.01$, $P=0.322$, respectively).

Cooperative foraging

The pairwise overlaps in MAP(0.5) UDs were independent of both roosting association measures. The probability of obtaining the same correlation or greater was 0.309 between overlap and I_{ij} associations and 0.18 between overlap and χ^2 associations (500 randomizations).

These comparisons were made with just female-female pairs because although adults and juveniles did not differ in their foraging overlap ($P=0.39$ and $P=0.12$, respectively, 200 randomizations), female pairs showed significantly greater overlap than males ($P<0.005$, 200 randomizations). These results suggest that frequent roostmates rarely, if ever, fed simultaneously from the same wound. One potential problem with interpreting these results is that most overlaps were calculated from sequential radio-tracking data. But, bats which we tracked more than once, sometimes 12 or more months later, invariably foraged in the same area (cf. Fig. 3).

Data from three independent sources – foraging overlap, simultaneously tracked bats and NVD observations – although scant, indicate that simultaneous foraging occurs primarily between females and their offspring, particularly female offspring. First, the overlap in foraging ranges of three female yearlings and their mothers were 34.65%, 26.62% and 26.17% while the mean overlap between each yearling female and all other bats in the same group (UP) was 4.25% (SD = 7.73%, $n=36$). The mean rank for overlap between female young and their mothers using all 13 bats tracked in the group was 1.3 ($P<0.001$, 200 randomizations). In contrast, the mean overlap between one yearling male and its mother was 0.23%. Second, on eight separate occasions two bats were picked up at identical bearings for 10 to 60 min. Six of these pairs consisted of adult females and yearling female offspring, one was an adult female and her yearling female grandoffspring and one was an adult female and an unrelated yearling male. Third, four out of five direct observations of bats feeding simultaneously could have occurred between a mother and her young. At Santa Rosa, 40 bats (26 females, 1 male and 13 unmarked) were seen feeding for a total of 22.5 h. We observed 3 cases, one between two females and two others between a female and an unmarked animal, of simultaneous feeding and one case of sequential feeding between two females. On three occasions we also saw a bat fly at and after another bat which landed or attempted to land on the same host animal. One occurred between two females, another between a female and an unmarked bat and the third between two unmarked bats. These agonistic interactions were accompanied by audible aggressive vocalizations (Sailler and Schmidt 1978). The rates of interactions at La Pacifica were similar to those at Santa Rosa. Twenty-five bats (10 adult females, 2 adult males, 11 yearling females and 2 yearling males) were observed feeding at La Pacifica for a total of 14.1 h. We saw two cases of simultaneous feedings, one between a mother and her yearling female offspring and the other between two adult females, and one case of a sequential feeding between two females which were not mother-offspring. One adult male displaced a yearling male from a wound site. These observations are consistent with those reported previously on unmarked *D. rotundus* (Greenhall et al. 1971).

Blood sharing within roosts

We observed 110 cases of regurgitation of blood between two bats within the roost trees. Seventy-seven of these cases occurred between a mother and her nursing offspring while 33 occurred between other related and unrelated bats in the roost (Wilkinson 1984). In 28 of these 33 cases every bat in the roost at the time of the regurgitation older than 8 months of age (the age of the youngest bat ever observed sharing blood) was banded. In 21 of the 28 cases the rank of the association index, I_{ij}, was greater than the median rank in the group ($P=0.012$, binomial probability) and 17 of the ranks of the χ^2 associations were greater than the median ($P=0.173$, binomial probability). The probability of observing a product of relative ranks between donor and recipient as small or smaller than observed for the I_{ij} was less than 0.005; for the χ^2 this probability was equal to 0.055 (200 randomizations). The probabilities for the χ^2 measures were higher than those for the I_{ij} indices because some of the bats which shared blood were observed in only one tree. As mentioned above, the χ^2 measure only reflects associations between bats which change trees. I considered all bats greater than 8 months of age potential donors because the frequency of blood donation was independent of age and sex as well as reproductive condition of females ($P > 0.05$, *G*-tests).

Discussion

These results show that adult female *D. rotundus* roost with other adult females more often than expected by chance even after preference for particular trees is removed. The only nonsocial behaviours which may influence these movement patterns are avoidance of predators and ectoparasites, but neither factor suitably explains the duration of associations observed. The data indicate that a plausible explanation for such long-term associations is that bats roost together in order to share blood. Blood sharing between adult females and females and young has also been seen among captive vampire bats (Schmidt, personal communication; Mills 1980). Simultaneous feeding at a wound cannot explain the association because it occurs almost exclusively between mothers and their dependent female young. Social grooming does not appear to affect the number of ectoparasites and may, therefore, serve some other function (see below). Alternatively, allogrooming may lower the number of flies on all bats to or below some threshold which the bats can tolerate. More definite conclusions for the function of allogrooming must await further evidence. Another active benefit of association may occur through information exchange (Ward and Zahavi 1975).

Information exchange

Information exchange is possible since bats often visited a pasture, returned to a roost, and then went back to the same or a different pasture later in the same night. Females which visited several different trees in a night (Table 3) may have done so to exchange information. On one occasion, I followed a radio-tagged adult female to a roost which had not had any adult females during the day and discovered that the tagged bat and three other females, one of which was her female offspring, were in the tree. Furthermore, with the NVD we often observed two and three females leaving a tree together both early and late in a potential foraging night. But, if information exchange occurs frequently, then the bats involved should have overlapping foraging ranges as should those that share wound sites. Consequently, although mothers may escort their offspring to prey, exchange of information between adult bats appears improbable.

Individual recognition

An alternative explanation for allogrooming is that it facilitates the individual recognition necessary to maintain long-term associations. The sensory modalities used for recognition are unknown, but some evidence suggests that both auditory and olfactory cues may be important. Both types of cue should be most obvious during allogrooming. Adult females can recognize their infants from their vocalizations (Schmidt 1972) and adults frequently make a low intensity, variable frequency (5.5–14 khz) call while allogrooming (Sailler and Schmidt 1978). Although there are no data which show that these bats can recognize each other through olfactory cues, their sense of smell is very acute (Schmidt 1973) and allogrooming is frequently preceded by mutual sniffing. Furthermore, no adult female was ever observed grooming an adult male, just as no adult female was observed regurgitating blood to an adult male.

Apparent altruism and long-term associations in other species

The only other well-documented case of apparently altruistic behavior in bats is communal nursing by *Tadarida brasiliensis* (Davis et al. 1962). Recent evidence shows that nursing occurs between mothers and their offspring about 83% of the time even though a cave may contain millions of individuals. Although some young occasionally suckle from a female while she is searching for her infant, such stealing is apparently indiscriminant (McCracken 1984). Any long-term association between females has yet to be described in this species.

In several neotropical bats including *Phyllostomus hastatus* (McCracken and Bradbury 1981), *Saccopteryx bilineata* (Bradbury and Vehrencamp 1976), *Carollia perspicillata* (F. Williams, personal communication), *Artibeus jamaicensis* (D. Morrison, personal comunication), and *Glossophaga soricina* (personal observation) adult females remain together for months or years. Neither altruistic nor cooperative behavior has been reported previously for any of these species although *P. hastatus* females in the wild will occasionally nurse young which are not their own (personal observation).

In the former three species, adult males attempt to recruit females into their groups and use external scent glands to mark females or cave walls (personal observation). Male coercion, therefore, may play a role in the stability of female groups in these species, but it cannot explain long-term female group cohesion in either *P. hastatus* (McCracken and Bradbury 1981) or *G. soricina* (unpublished data). While the benefit of association has not yet been elucidated in these two species, female *A. jamaicensis* appear to move together between tree hollows in response to changes in the location of fruiting fig trees (Morrison 1978). As in *D. rotundus*, males defend the hollows rather than attempt to guard or sequester females (Morrison 1979).

Long-term associations among females which appear to behave altruistically have been reported among other mammals. For example, both food sharing and cooperative foraging occur among wild dogs, *Lycaon pictus* (Malcolm and Marten 1982), and females may den together for years (Frame et al. 1979). Wild dogs differ from vampire bats in that female, not male, wild dogs emigrate (Frame and Frame 1976) and only a single female usually gives birth (Frame et al. 1979). Furthermore, both males and females regurgitate food to young or sentinel denmates (Malcolm and Marten 1982) rather than just females. In dwarf mongoose (*Helogale parvula*), adults and juveniles help to nurse, feed and guard a dominant female's offspring, but both sexes transfer between groups (Rood 1983). Interestingly, both Rood (1978) and Malcolm and Marten (1982) mention that although most denmates are related, sex and age appear to be more important in determining which animal helps than relatedness. If association varies with sex and age as it does among vampire bats, then the patterns of aid-giving may depend on association. Unfortunately, association was not reported in either study.

Perhaps the most similar social system to the vampire bat occurs among Asian elephants, *Elephas maximus* (Eisenberg 1981). Adult females form groups of 8 to 21 and move among males which maintain smaller exclusive home ranges. Females cooperate to protect and raise young and may remain in the same group for many years. Many workers have suggested that predation pressure may have favored group formation initially in these species, but this factor alone can explain neither the duration of female associations nor communal suckling.

Although long-term association is clearly not a sufficient criterion for the evolution of cooperation or altruism, this brief survey of the literature suggests that it may be a necessary one. Recently, several workers (Bekoff 1981; Holmes and Sherman 1983) have suggested that some animals may use association (or familiarity) as a cue to detect relatedness. Such a mechanism might work well in animals with large litters and relatively short lifespans, but in the long-lived species discussed above individuals of varying degrees of relatedness can interact equally often. Caution should be exercised before inferring that kin selection (Hamilton 1964) must explain all apparently altruistic behavior since in at least one species, *D. rotundus*, association appears to be as important as relatedness in determining which bats receive food, as expected for reciprocity (Wilkinson 1984).

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