Chapter 7

SOCIAL ORGANIZATION AND BEHAVIOR

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I. INTRODUCTION

Understanding when a social behavior is performed and between which individuals requires knowledge of two factors: (1) how individuals distribute themselves in space and time and (2) the relative costs and benefits of the behavior in terms of its effect on the reproductive success and survival of the participants. Dispersion patterns are determined, in part, by the location of refuge and feeding sites. A group of bats may roost in a cave, for example, because it is the only cave in the area. However, if there are multiple roosting or feeding sites of equal value, then continued use of a site with other individuals will also depend on the costs and benefits of the interactions at the site. Those interactions which prove beneficial, in an evolutionary sense, to both participants favor continued association at the site while interactions harmful to either participant may result in avoidance.

Associations between two individuals which persist over time are significant for understanding vampire bat social behavior for two reasons. The first reason is obvious. Two individuals cannot engage in a social behavior within a roost or while foraging if they are not at the same location at the same time. The second reason is more subtle in that it requires an appreciation of how social behaviors evolve. Long-term association with the same individuals and/or association with close relatives over many consecutive generations permit the evolution of behaviors which decrease the reproductive success or survival of donors while increasing the reproductive success or survival of recipients. The mechanisms responsible for this behavioral evolution have been termed reciprocity[1,3,45] and kin selection,[16] respectively. These mechanisms provide a method for not only understanding the evolution but also for predicting the current distribution of behaviors which appear to cost a donor while benefiting a recipient. For example, kin selection makes the prediction that food should be shared only with close relatives while reciprocity generates the expectation that food will be shared between bats which roost together frequently, irrespective of their degree of relatedness.

In this chapter, I attempt to show how the distribution and kind of social behavior displayed in the wild by common vampire bats, *Desmodus rotundus*, can be understood as a consequence of their specialized diet and their social organization. Unfortunately, the social organization and behavior of the other two vampire bat species, *Diphylla ecaudata* and *Diaemus youngi*, have not been described sufficiently to allow comparison. *Diphylla* and *Diaemus* differ from *Desmodus* in that they apparently prefer avian to mammalian blood.[12] Future studies may reveal whether the description of the social organization and behavior presented here for *Desmodus* is representative of all vampire bats, or if prey type preference exerts sufficient selective pressure, either ecologically or phylogenetically, to alter these aspects of vampire bat biology.

II. SOCIAL ORGANIZATION

A. Spatial and Temporal Dispersion Patterns within Roosts

1. Adult Females and Young

Roosting groups of common vampire bats range from solitary individuals in hollow trees[50] to aggregations in caves with over 2,000 bats. Most colonies, though, contain 20 to 100 bats.[4,7,23,24,47,54,56] Roosting sites which contain over 50 individuals typically contain identifiable groups of 10 to 20 adult females with recent young.[39,51] At the La Pacifica site in

Consequently, 1 to 18 adult females were observed per roost with a median of 5.7 bats during 1,355 visits to a roost tree.[50] These observations are consistent with other researchers,[4,8,39,46,54] who have reported that females utilize multiple roosts.

Although the identity of individuals within any given roost tree varied, the composition of female roosting groups was stable. For example, two adult females banded near the same location at the La Pacifica site in 1970 consistently shared roosts between 1978 and 1981.[49] Furthermore, five adult females banded in one roost at La Pacifica in 1978 still roosted together in 1983.[50] In fact, at this site each female roosted with a median of 5.7 other adult females more often than would be expected by chance.[50] The limit to these associations is unknown, but *Desmodus rotundus* have lived 19.5 years[55] in captivity and growth rings in dental cementum indicate that they can survive 18 years in the wild.[24] At La Pacifica adult mortality was 24%.[49]

Female dispersal generated a low average degree of genetic relatedness within a group despite all marked female young which attained a year of age remaining in their natal groups. On average, one unrelated female successfully joined each group every two years.[49,51] These immigrants were either nulliparous young of the year or adult females with recent young. By inferring common ancestry from matched mother-offspring pairs and from genotypic information obtained from seven variable blood enzymes, path analysis estimated the average group relatedness among adult females to be 0.11 ± 0.17.[49] Genotypic correlation estimated $r = 0.02 \pm 0.01$,[51] while a demographic model using observed variables gave $r = 0.08$ to 0.10.[52] Since the genotypic correlation for samples from three groups of adult females captured in solution depressions in a cave at another site in Costa Rica gave a similar estimate for average relatedness,[51] the pattern of female dispersal and recruitment observed at La Pacifica may be representative of other populations.

2. Adult Males

Some field studies have indicated that males in large roosting areas, such as caves or mine tunnels, were dispersed.[4] Other workers[24] have reported finding groups of up to 27 males in a roost as well as groups of 20 to 30 bats with 5 to 10 males inside hollow tree roosts.[46,56] Although these observations appear to lack consistency, they are compatible with data collected on the La Pacifica population. There, each of the 14 hollow roost trees invariably contained at least one male. The median number of adult males per tree was 1.1. However, up to eight adult males were observed in a tree.[50] These males either formed a bachelor group in trees without females or they roosted separately on the inside of the hollow tree and defended small areas from each other. Only trees frequently housing groups of adult females had males in these positions.

This male dispersion pattern represents a clear example of a resource defense mating system for three reasons. First, resident males remained in their respective positions independently of the presence of females. Second, males from other trees entered and fought residents to remain within these trees. And third, the resident at the top of the tree had preferential mating access to females.[51]

Although the top residents accumulated 80% of the 21 observed copulations, paternity exclusion analyses using the genotypic information revealed that mean maximum paternity for top resident males was only 46% (Figure 1). Furthermore, gametic disequilibrium tests indicated that mating was effectively random with respect to genotype.[51] Consequently, although males at the top of roost trees frequented by females have higher than average

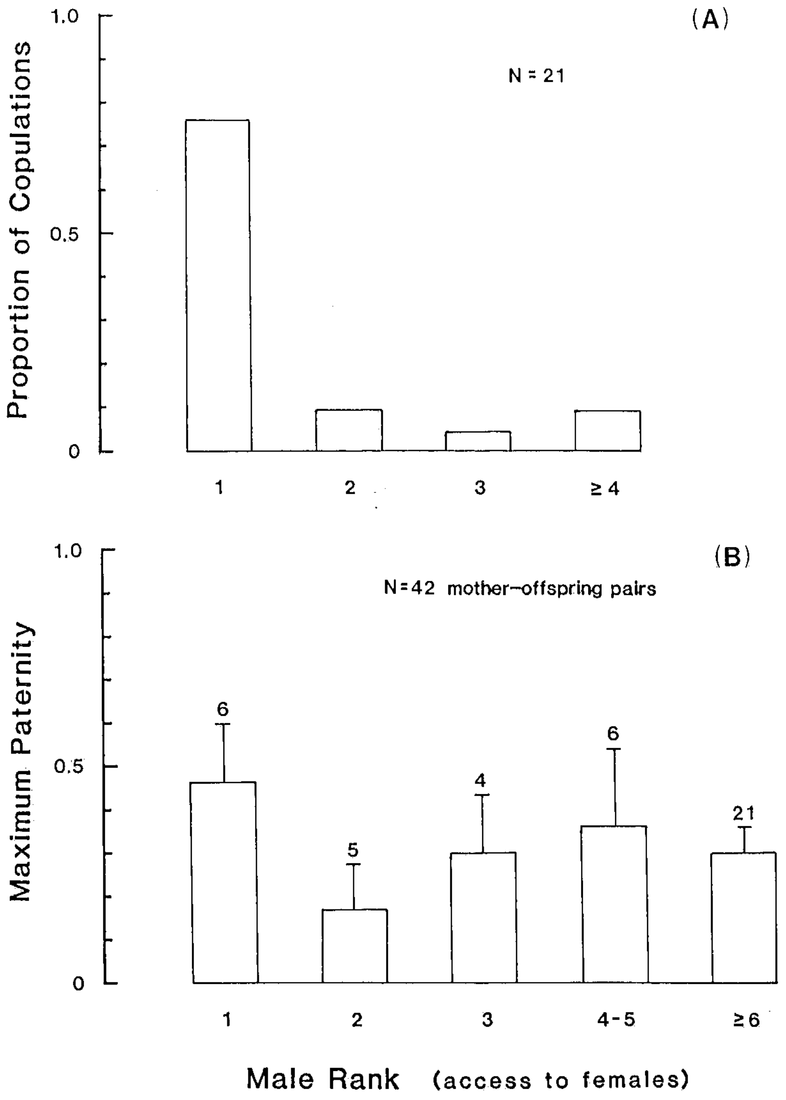

FIGURE 1. (A) Proportion of copulations observed in day roosts by adult males with access to females. Male ranks 1 to 5 refer to males arranged in descending order on the inside of the roost tree which most frequently contained females. Ranks greater than 5 indicate males which used other trees for roosts. (B) Proportion of offspring born during the study whose genotypes were consistent with adult males ranked as in (A). Error bars indicate confidence limits obtained by jackknifing the arcsin transformation of the proportions. Numbers of males per year is indicated over the error bars.

from their natal group between 12 to 18 months of age.[51] As long as three months before dispersal, males had scrotal testes and were physically indistinguishable from resident males. In some cases, these subadult males were forcibly expelled by resident males. Top resident males in favored female roosts stayed in the same tree for an average of 17 consecutive

B. Nocturnal Movement Patterns

1. Adult Females and Young

Turner[46] suggested that resident vampire bats at La Pacifica moved between roosts to minimize the distance between the roost and preferred prey. Calculation of distances moved between successive radio-tracking fixes on 36 radio-tagged females do not support that proposition. The mean distance flown per night (3.44, SD = 1.82 km) was about twice the mean distance from the initial roost to the foraging center and back (1.89, SD = 1.03 km). Furthermore, only on 46 of the 116 bat nights did an individual roost in the nearest possible tree to the previous night's foraging center even though adult females visited a mean of 2.2 roosts per night.[50] Adult females apparently choose diurnal roost trees depending on which other females also roost there. This conclusion is based on statistically significant associations between adult females at the day roost even after individual preferences for trees have been removed.[50] Females may fly extra distances at night to roost with specific other females to facilitate food sharing behavior as discussed below.

Both males and females reduce their foraging activity when the moon is up;[6,46] however, females spent, on average, significantly more time (121 min) out of a roost tree at night than males (90 min) even after controlling for time available when the moon was down.[51] Although some workers[46] have suggested that vampire bats avoid moonlight because their prey are more vulnerable during the dark part of the night, the ubiquity of lunar phobia in medium-sized tropical bats points more convincingly to a visually orienting predator avoidance explanation.[29] After capturing 209 bats 2 hr before dawn, Turner[46] suggested that females were more successful than males at obtaining a blood meal, and that reproductively active females were more successful than reproductively inactive females. Analysis of feeding success for 598 bats captured 1 hr before dawn revealed, in contrast, that sex, population, reproductive condition, and moon phase had no effect on the ability to acquire a blood meal.[49] Age, however, was highly significant. Bats less than 2 years of age failed, on average, 30% of the time, while the probability of a bat 2 or more years of age not acquiring a blood meal was only 0.08.

Calculation of nocturnal activity centers for 36 radio-tagged bats at the La Pacifica site indicated that most females from the same roosting group hunted for prey in adjacent areas (Figure 2). Consequently, there was no spatial overlap in foraging activity between females from different groups. Within a group at night, pairs of adult females spent proportionally more time at the same location at night than pairs of adult males.[50] However, no correlation existed between the proportion of censuses in which two bats were observed in the same day roost and the overlap of nocturnal foraging range utilization.[50] Adult females and their recent female offspring shared 29.2% of utilized foraging ranges, while yearling female overlap with other bats from the same group averaged only 4.3%.[50]

2. Adult Males

Adult male nocturnal activity differs dramatically from that of adult females in several ways. None of the adult males which were tracked for two or more nights showed any overlap in foraging range utilization.[50] Top resident males in trees which contained females always flew to the nearest pastures to feed and then returned directly to their day roost. In contrast, males which roosted in trees rarely used by females often flew several kilometers along the river in the direction of other roosts. Invariably, these males would fly out of radio contact. Consequently, the estimates of mean foraging time mentioned above for adult

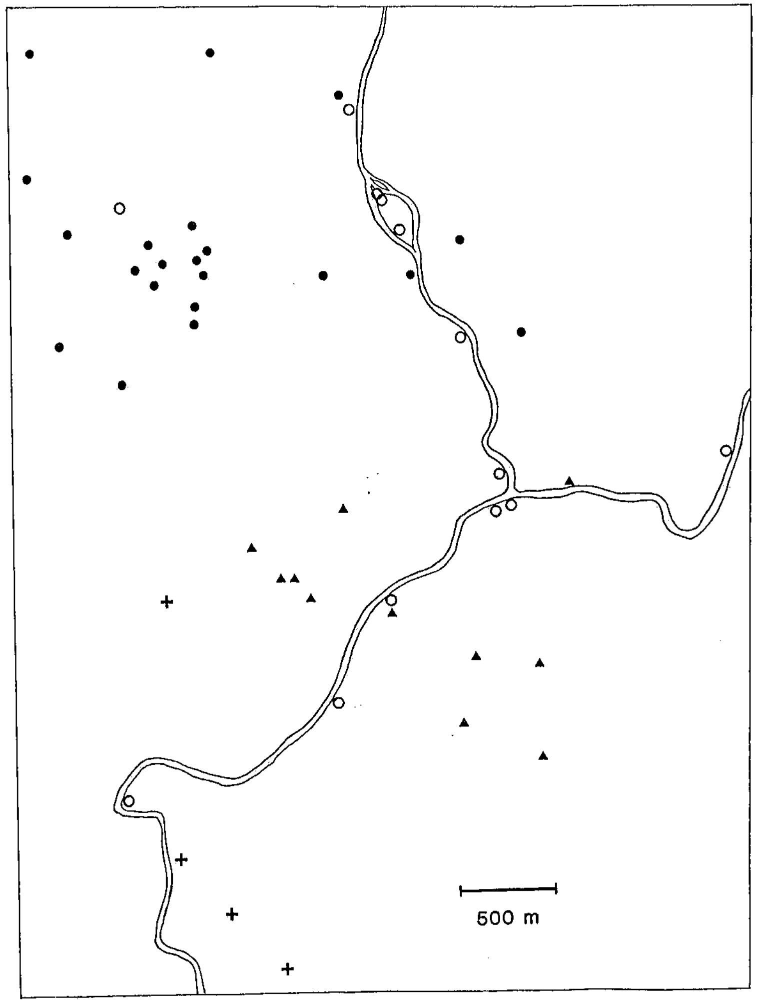

FIGURE 2. Geometric activity centers of 36 radio-tagged vampire bats at the La Pacifica study site. Each point represents a minimum of 3 nights of triangulations taken at 10 min intervals only during the time each bat was outside its roost. Day roosts are indicated by ○ and activity centers for the three adult female groups are denoted with ●, ▲, and +. (From Wilkinson, G. S., in *Recent Advances in the Study of Bats*, Fenton, M. B., Racey, P. A., and Raynor, Eds., Cambridge University Press, New York, 1987, 299. With permission.)

III. SOCIAL BEHAVIOR

A. Interactions within Day Roosts

1. *Food Sharing*

Vampire bats share food by regurgitating blood. This behavior was first described in captive groups between adult females and their own young[38] and later between adult females and foreign young and between two adults.[28,35] In the wild I have observed females feed

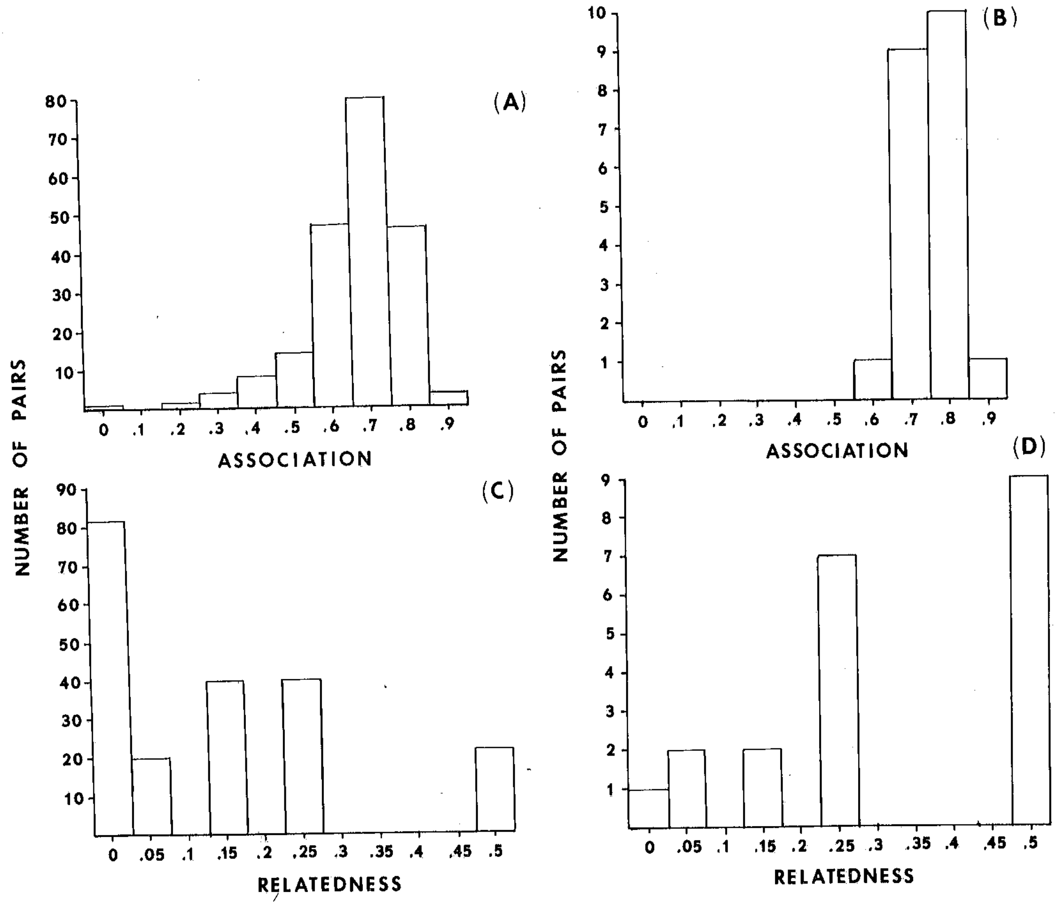

FIGURE 3. The number of pairs of individuals observed reciving blood is plotted as a function of the recipient's level of association and degree of genetic relatedness to the donor in (A) and (C). (B) and (D) show the association and relatedness between the recipient and all potential donors in the roost at the time of the regurgitation. Mothers feeding nursing young are excluded. The level of association is the proportion of times the two bats were observed in the same day roost. (From Wilkinson, G. S., *Behav. Ecol. Sociobiol.*, 17, 111, 1985. Copyright 1985 Macmillan Journals Ltd. With permission.)

only in chimpanzees,[44] Asian elephants,[10] dwarf mongoose,[31] naked mole rats,[19] and a few other carnivores.[25,26] In many of these species, reproduction is limited to a single female and the helping behavior of group members has been interpreted as an example of kin selection in which a nonreproducing individual's best option for enhancing gene transmission is by aiding relatives.[47] In contrast, all female *Desmodus* reproduce. During over 400 hr of observations in day roosts at La Pacifica, 110 cases of regurgitation, but no instances of communal nursing, were observed.[49] Seventy-five percent of these regurgitations occurred between an adult female and her dependent offspring under 12 months of age. The remaining 33 cases of food sharing occurred between unrelated and related bats.[49]

Several pieces of evidence suggest that food sharing among vampire bats which are not mother-offspring is advantageous both to donating and receiving individuals. First, food sharing between nonmother-offspring was predicted significantly and independently by an receive blood during its lifetime, as required for reciprocity to be a viable explanation. The third and most convincing evidence for reciprocity comes from an experiment on unrelated, but frequent roostmates from two populations.[49] When each bat was randomly starved for a night and then reintroduced to the cage in the morning, a cagemate from the same population invariably fed it. Furthermore, the sequence of sharing events was significantly nonrandom in that a recently starved bat preferentially fed the bat that donated blood to it when that donor was starved. In other words, vampire bats reciprocate. These results imply that these bats recognize past donors. Reciprocity theory[1] requires, in addition, that individuals should be able to detect and refuse those bats which might attempt to "cheat" on the system by rarely sharing food. Social grooming, which is discussed below, may provide this information.

The amount of blood exchanged during a food sharing session appears related to the needs of the recipient rather than any relationship, such as relatedness, roost association, sex, or age, between the participants.[49] By estimating the rate at which weight is lost prior to starvation, it was estimated that some regurgitations can provide as much as 12 additional hours before starvation to a hungry recipient.[49] In the wild, this additional time could permit a bat to find prey without risking starvation. Although adult males occasionally shared blood with adult females and young, they never shared with other adult males and were never fed even when starved experimentally.[49] These results further supported both the reciprocity and kin selection explanations since adult males did not share roosts with females or each other for long periods of time and were unrelated both to females and other males, although perhaps not to juveniles in the same roost. The few cases of male sharing may represent paternal behavior or bartering in which a male provides food to gain access to mating opportunities.

2. *Grooming*

Like some other social mammals, vampire bats spend a significant portion (mean = 5%) of their time grooming others.[5,13,53] Self, rather than social, grooming, however, appears to occur in response to ectoparasites for four reasons.[53] First, self-grooming occurred ten times as often as social grooming. Second, there was no correlation between the rate at which self and social grooming occurred. Third, adult males spent as much time self-grooming as adult females and juveniles but were never groomed by other bats. And fourth, the proportion of time spent self-grooming depended on where a bat was roosting, whereas social grooming rate depended on the sex and age of the individual. Since roost trees differed in levels of ectoparasite infestation,[50] these data suggest that while self-grooming occurs in response to ectoparasites, social grooming must have some other function.

The function of social grooming appears to be related to food sharing. Grooming rates between pairs of bats which were not mothers and offspring correlated significantly and independently with both relatedness and roost association.[53] Furthermore, donors groomed recipients and recipients groomed donors more often than expected by chance 2 minutes prior, but not after, a regurgitation. Finally, social grooming rate correlated significantly with the rate at which a bat shared blood.[53] These results suggest that social grooming may convey information both to a donor and recipient prior to but not after a blood sharing event. One possibility is that social grooming facilitates individual recognition either by olfaction[34] or audition. Social grooming could provide a method of marking and detecting scent on bats. Vampire bats emit faint low-frequently vocalizations during social grooming episodes.[32,33] Since spectral differences exist between individuals in these calls,[32,37] they may

of this suggestion, we frequently observed bats grooming each other beneath their wings near the stomach. This argument implies that when potential cheaters are detected, they will be admonished. Although we did observe chases and pushing matches between two females, frequently accomplished by audible vocalizations, we were not able to relate these incidents to the feeding histories of the participants. Further research on this potential cause of agonistic behavior between adult females, as well as on the function of the stomach extension which may have evolved to facilitate regurgitation, is warranted.

3. *Mating*

Mating apparently occurs only in day roosts[51] and is not restricted to a particular time of day. When more than one adult male used a tree which contained females as a day roost, the male at the top of the tree was observed in most of the copulations (Figure 1). But, on several occasions a male lower in the tree succeeded in copulating with a female. No aggressive actions were ever observed between males in a tree during a copulation. In contrast, in captivity males frequently contest a mating.[13] At La Pacifica, however, males were usually separated by 3 m or more on the inside of the tree and may not have been able to detect copulations. Males sometimes failed to copulate with females which lunged with exposed incisors and canines or scrambled away. Given the larger size of females, their propensity to change roosting sites, and their ability to avoid pursuing males, females appear to be able to choose their mates. Some indirect evidence suggests that females mate with particular males to avoid inbreeding.[51]

B. Interactions at Night

1. *Foraging*

Cooperation between roostmates may occur on prey at night in addition to within roosts during the day. Greenhall et al.[14] used infra-red light and image-intensifying scopes to observe vampire bats at high-density feeding on penned livestock in Oaxaca, Mexico. They described both sequential and simultaneous feeding from a single wound. As many as seven bats fed consecutively from a single bite. Since preparation of the bite area and making the incision can take 20 min,[36] by sharing a wound two or more bats could reduce their feeding time and decrease their exposure to predators. Nocturnal observations on color-marked bats feeding on free-ranging livestock at both La Pacifica and Santa Rosa in Costa Rica have indicated that simultaneous feeding from a single wound occurs infrequently and predominantly between an adult female and her recent young.[50] Sequential feeding at these low-density sites never involved more than two bats and occurred rarely.

In both studies[14,50] agonistic behavior was also witnessed between two bats attempting to feed from the same wound. The hair bristling, wing beating, lunging, and audible vocalizing which accompanied these encounters on prey appeared very similar to behaviors recorded between pairs of bats fighting for access to a feeding bottle in captivity.[33,36,40] At Santa Rosa and La Pacifica these agonistic encounters involved both adult males and adult females and occurred as frequently as observations of two bats feeding either sequentially or simultaneously.[50] These data, in conjunction with the radio-tracking data summarized in Figure 2, suggest that adult females may defend individual prey animals or areas in which favorite prey can be found. The surprising constancy of adult female group size at all Costa Rica sites may indicate that group defense also occurs. Whether group size is limited by foraging distance or ability to recognize roostmates can be determined only by future studies.

some of the females had not roosted together on the previous day. Since adult females often visit more than one roost and occasionally return to the same or a different pasture later in a single night,[51] they may be leading other bats to prey. However, the direct observations of simultaneous and sequential feeding described above, as well as estimates of overlap in home range utilization,[50] suggest that most of these apparent cases of information exchange probably occurred between mothers and their recent young.

2. *Roost Defense*

When a top resident male was not out foraging, it usually hung near the entrance to its roost and chased away other males which appeared to be trying to enter.[51] These chases were often accompanied by low-frequency vocalizations[20] similar in sound to those used when a bat defended a prey animal. On several occasions, my assistants and I witnessed interactions between nonresident and top resident males inside day roosts. These encounters were always agonistic and involved the same series of behaviors as described above for prey defense. On some occasions, however, these encounters escalated to vicious fighting with the two males lunging, parrying, and biting, often for several minutes. In one instance we witnessed a top resident male get attacked and severly bitten enough times for blood to flow heavily. This male fled from the roost in daylight.[51] Fighting must be relatively common among adult males, since virtually every adult male we captured had wounds and scars which appeared to be the result of biting. The intensity of these fights, always directed to the male which has preferential access to females, implies that although the top resident male only gains about 50% paternity, this is still substantially better than males can expect at other roost sites (cf. Figure 1.)

IV. CONCLUSIONS AND IMPLICATIONS

Expression of costly social behavior, such as food sharing, in the common vampire bat clearly depends on the composition of day roosting groups. The observation that food sharing and social grooming are frequently exchanged between adult females and their young, but not among adult males, indicates that the long-term stable composition of female groups is necessary for the evolution and persistence of these behaviors. However, it is unlikely that this is a sufficient condition. The necessary transfer of food to a refuge before sharing is facilitated by a diet composed solely of blood. Furthermore, the frequency with which bats fail to feed must impose a selective pressure to favor food sharing. In contemporary populations, the hunting success rate of a vampire bat must depend on the ability of the prey to detect and subsequently disturb the bat as it attempts to feed. The high failure rate experienced by yearling bats may reflect their inability to make painless, undetectable bites[9] and must explain, in part, the 54% first year mortality.[51]

Given the apparent difficulty bats still have in acquiring a blood meal, it is intriguing to speculate on the conditions under which this behavior evolved. Biochemical, chromosomal, and immunological evidence[2,11,17,43] suggests that the Desmodontine subfamily originated from Glossophagine stock between 2 and 10 million years ago. During this period the diverse North American terrestrial mammal fauna crossed the land bridge and invaded South America.[42] This period was the peak, in terms of numbers of families, of large herding mammals in the orders Artiodactyla and Perissodactyla in South America.[42] Since Pleistocene vampire bat fossils have been found in several localities in the U.S.,[15,18] they also could have fed

time. However, when the majority of horses, elephants, and most of the other large mammal fauna disappeared from Central and South America at the end of the Pleistocene.[42] prey must have been difficult to locate. Villa-R.[48] suggests that prior to the introduction of cattle 300 years ago, vampire bats fed on peccaries, deer, tapir, seals, and agouti. I suspect that the selective advantage for food sharing was substantial during the last 40 or 50 thousand years. This ecological bottleneck may help explain the relatively recent separation of *Desmodus* from *Diaemus*,[17] given the avian diet of the latter species.

Whether reciprocity, kin selection, or a combination of these evolutionary mechanisms were initially responsible for the increase in frequency of food sharing will never be known. But, the evidence summarized above cannot be explained without invoking both reciprocity and kin selection as mechanisms acting to maintain food sharing behavior in contemporary populations. Given the expanding evidence for kin recognition in other social mammals,[41] one obvious area of future research should be elucidation of the sensory modalities used by these bats to discriminate between relatives. The ability or inability of individuals to prefer kin over unrelated individuals while manipulating past association would bring important information to bear on which of the two selective mechanisms is currently of greatest importance in maintaining food sharing behavior in this species.

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