

Food Sharing in Vampire Bats

Two nights without a blood meal and a vampire bat starves to death—unless it can solicit food from a roostmate. A buddy system ensures that food distribution among the bats is equitable

by Gerald S. Wilkinson

At night—long after most visual predators have stopped prowling—vampire bats emerge from their roosts and take to the wing, flying low across the landscape in search of warm-blooded prey. Within an hour or two, having found appropriate victims and fed on their blood, the bats return to the roost to sleep, feed their young and interact with nestmates.

Until recently little was known about either the behavior or the life history of the common vampire bat, *Desmodus rotundus*. For many years biologists were more interested in the animal's physiology than in its social organization, which was thought to be relatively simple. A number of recent studies, however, reveal that vampire bats are remarkably social: females cluster together during the day but at night reassort themselves, creating a fluid social organization that is maintained for many years. Moreover, it is now known that long-term associations among females enable bats to regurgitate blood to one another on a regular basis and so significantly increase their chances of survival.

The reason for regurgitation behavior was revealed in studies carried out more than 15 years ago by Brian K. McNab of the University of Florida, who showed that a vampire bat will die if it fails to feed for two nights in a row. After 60 hours without food it

loses as much as 25 percent of its weight and can no longer maintain a critical body temperature. To fuel the body's metabolic engine and avoid death, individuals must consume 50—sometimes even 100—percent of their body weight in blood every night.

Yet feeding is not always easy, especially for young bats, who must learn to bite quickly and to do so without inflicting pain on their victims. I have seen horses toss their heads, swish their tails and rub against obstacles to rid themselves of hungry bats. Although the bats counter such defensive strategies by returning to the same animal (a known target) several nights in succession or by feeding sequentially from fresh wounds, from 7 to 30 percent of the bats in a cluster fail to obtain a blood meal on any given night. By soliciting food from a roostmate, a bat can fend off starvation—at least for one more night—and so have another chance to find a meal.

In 1978 Uwe Schmidt, a zoologist at the University of Bonn, presented the first evidence that females regurgitate blood to their pups. At that time Schmidt had kept bats for more than 10 years in a turret at Poppelsdorfer Schloss, an old castle that is now the main research building of the university's Zoological Institute, and had spent much of his career observing their behavior. Schmidt discovered, for example, that shortly after birth, the pups are given regurgitated blood—in addition to milk—by their mothers; he also found that on some occasions a pup will take blood from an adult other than its mother. In one case he even observed an orphaned pup who was being suckled by an adoptive parent. Food sharing of this sort, in which individuals provision other members of a group, is extremely rare in mammals; in addition to bats, only a few species—such as wild dogs, hyenas, chimpanzees and human beings—are known to display such behavior.

Food sharing appears to be altruistic: a donor bat gives up food—which might otherwise be used to ensure either its own survival or the survival of its offspring—to a recipient bat, whose chances of survival are thereby increased at no apparent cost to itself. Yet true altruism has never been documented in nonhuman animals, presumably because such a one-way system is not evolutionarily stable. The reason is that donors, who lose resources, are eventually outcompeted by recipients, who have more resources and so survive longer, produce more offspring and pass more of their genes on to the next generation. Careful studies of altruistic behavior by a number of investigators reveal that many acts of apparent altruism actually take place either between relatives (and so are a form of kin selection) or between individuals who exchange resources on a more or less equal basis, in which case they can be considered to be acts of reciprocal altruism, or reciprocity.

Having heard of Schmidt's work, I wanted to study vampire bats in their natural habitat to see whether blood regurgitation is an act of kin selection or reciprocity (or both). I set off for Costa Rica, and there, with the help of my assistants Robin Weiss, Michael L. Jones and Terri Lamp, I studied a population of *Desmodus rotundus* for 26 months between 1978 and 1983.

I hoped by observing their regurgitation behavior to see if the bats were feeding only their relatives, and

COMMON VAMPIRE BAT, *Desmodus rotundus*, is found from Mexico south to Argentina and Chile, particularly in areas where the land has been converted to pasture. Females, such as those shown here, gather together in caves and hollow trees during the day, emerging only at night to search for warm-blooded prey.

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therefore engaged in kin selection, or if they were reciprocally exchanging food (with either related or nonrelated individuals), and thus engaged in reciprocity. In order to prove reciprocity I needed to demonstrate that five criteria were being met: that females associate for long periods, so that each one has a large but unpredictable number of opportunities to engage in blood sharing; that the likelihood of an individual regurgitating to a roostmate can be predicted on the basis of their past association; that the roles of donor and recipient frequently reverse; that the short-term benefits to the recipient are greater than the costs to the donor; and that donors are able to recognize and expel cheaters from the system.

Vampire bats, which are common in tropical America wherever land has been converted to pasture and livestock are present, are ideal subjects for a study of this nature. For my research site I selected a cattle ranch in northwestern Costa Rica called Hacienda La Pacifica (which

has since been turned into an ecological research station and is now called Centro Ecologica La Pacifica).

There I found that vampire bats, in the absence of caves, spend the day in hollow trees, where temperatures are constant, the humidity is high and it is dark even during the day. Most of the trees at La Pacifica had a single opening at their base: by lying inside the opening and peering upward with the aid of binoculars and a diffuse light source, we could observe the bats for several hours at a time. By gradually increasing the amount of light (over a period of several months), we could habituate the bats to our presence and observe their interactions with one another. The single entrance at the base of the tree offered another advantage: we could stretch a fine-mesh net in front of it and catch the bats when they emerged at night to hunt. In this way we were able to tag them and subsequently quantify individual patterns of behavior.

We found that the bats emerge in search of prey every night at a time that varies with the phase of the

moon: if it is too bright outside, the bats wait until the moon goes down. Unlike the other two species of blood-drinking bats (the white-winged vampire bat, *Diaemus youngi*, and the hairy-legged vampire bat, *Diphylla ecaudata*), which feed mostly on the blood of birds, *Desmodus rotundus* feeds primarily on mammalian blood. The bat seems to prefer horses to cows, and it locates them by a combination of smell, sound and echolocation.

Having identified a victim, the bat usually lands on the animal's tail or mane and hangs from it while searching for an appropriate spot to bite. Specialized heat-sensitive cells in the nose help the bat find a place where the victim's blood vessels are near the surface. When such a spot is found, the bat quickly excises a small patch of skin with its razor-sharp upper incisors and begins feeding. An anticoagulant in the bat's saliva keeps the blood flowing during the 20 to 30 minutes needed to consume a meal. Then the bat, its stomach visibly swollen, returns to the roost, where it remains



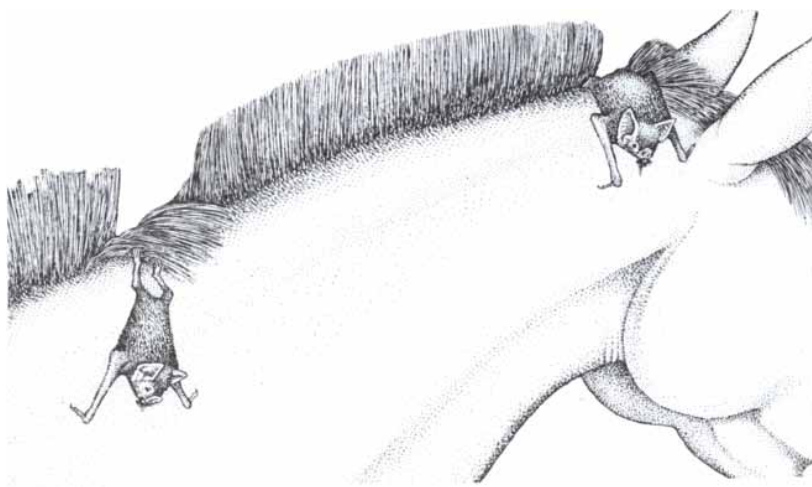


FACIAL FEATURES of the vampire bat reflect its blood-based diet. The enlarged ears help the animal search for prey and navigate by echolocation: the bat emits high-pitched sounds that reflect off objects in its path, and the echoes are picked up by the ears. Smell and heat receptors in the broad, fleshy nose enable the bat to home in on a suitable victim. After finding an appropriate spot to bite, the bat excises a small patch of flesh with its razor-sharp incisors. With the aid of an anticoagulant in its saliva, the bat then laps up the blood that flows from the victim's wound.

until the next night. As the bats returned to their roosting trees just before dawn, we netted them to determine which individuals had successfully obtained a blood meal.

Our first goal on arriving at La Pacifica was to tag all the bats in our

study area with lightweight bands of different colors; females were banded around the left wrist and males around the right. Each band also had a piece of reflective tape affixed to it, which enabled us to spot roosting individuals even when light levels in the



COMMON VAMPIRE BATS feed on a variety of mammalian prey but seem to prefer horses and mules to other species. They usually land on the animal's tail or mane, which gives them something to hang onto during the 20 to 30 minutes it takes to drink their fill. The animal is not always cooperative; it may shake its head and swish its tail in an attempt to dislodge the bats. A bat who fails to feed for two nights in a row will die from starvation unless it can solicit regurgitated blood from a roostmate.

tree were very low. Once the banding process was completed, we could pick a bat at random and record its behavior every 10 seconds, 100 times in succession. By working in pairs, we tagged 600 bats and accumulated more than 400 hours of such behavioral observations. Once a week we did a census of the animals in each tree to document patterns of association among bats occupying the same daytime roost. We also fitted a total of 37 bats with radio transmitters and so were able to determine the extent and degree of overlap of their foraging ranges.

We found that the social organization of vampire bats is dominated by groups of from eight to 12 adult females and an equal number of pups (one for each female). Pups are born throughout the year at about 10-month intervals; females stay with their mothers, whereas males leave between the ages of 12 and 18 months, when they become reproductively mature. In contrast to some other tropical bat species, in which males defend "harems," vampire bat males defend territories. They form dominance hierarchies within hollow trees, fighting among themselves for the alpha position near the top of the tree's hollow cavity (where females frequently cluster) and defend their territories vigorously—sometimes to the death—against intruders. The intruders are males who normally roost alone or in small groups during the day in trees that are rarely visited by females.

As we tracked the bats and monitored their associations, we were surprised to find that their social organization is stable and yet fluid. The bat population in our study area could be subdivided into three groups of about 12 adult females, each of which often subdivided into smaller clusters. Although the three groups were isolated from one another, the composition of the individual clusters that made up each group varied continually. Each group had exclusive rights to a range of about six trees, and once or twice a week the females would shift roosts (sometimes carrying their pups with them to another tree), reasserting themselves in the process.

Because female pups stay with their mothers past reproductive maturity, several generations are typically found clustered together in one tree. Yet my biochemical analyses of blood samples suggest that only about 50 percent of the offspring in a cluster share the same father. Presumably

this is because females show no loyalty to a particular tree (whereas males do) and so are periodically exposed to new males, with whom they sometimes mate. In addition, for reasons that are not well understood, females switch groups from time to time (possibly because prey have become difficult to locate); on the average a new female joins a group every two years. As a result, each group consists of several matrilineal lines, within which relatedness is high but between which it is low.

Analysis of roosting associations reveals that adult females exhibit a preference for certain other females, which cannot be explained simply on the basis of some physical feature of the roosting site. Moreover, it seems that their preference is not always for relatives but may be for nonrelatives, a finding consistent with reciprocity theory. Having determined that the bats have an affinity for one another, we needed to answer the following question: Do the bats remain together for long periods and thus have the opportunity to develop and maintain a mutual support system?

The answer appears to be yes. Rexford D. Lord, now at the Indiana University of Pennsylvania, determined the maximum life expectancy of vampire bats by counting the annual growth rings of their teeth and found that females can live for as long as 18 years. And from banding studies undertaken at La Pacifica by Theodore H. Fleming of the University of Miami in the 1970's, we knew that at least two of the females in our study area had roosted together for more than 12

years. In view of their longevity and the fact that each individual fails to feed periodically, we concluded that the bats meet the first criterion of reciprocity: not only do individuals have the ability to form long, stable relations with one another, but the opportunity to engage in food sharing is ever present among them.

Our next step was to determine whether blood is regurgitated randomly within a group or whether the females regurgitate only to close relatives or to prior roostmates, as predicted by kin selection and reciprocity theory, respectively. To do so, we needed to estimate the frequency of blood sharing under natural conditions.

During the course of our five-year study we witnessed a total of 110 instances of blood sharing by regurgitation. Seventy percent of the regurgitations took place between a mother and her pup and can therefore be thought of as parental care. The remaining 30 percent, however, involved adult females feeding young other than their own, adult females feeding other adult females and, on two occasions, adult males feeding offspring.

To determine whether or not bats regurgitate selectively, we compared the degree of relatedness between a recipient and a donor as well as their roost-association index (the proportion of times two individuals were seen together in the same cluster) to see if—on either account—the regurgitation values were higher than if the recipient were randomly soliciting from all potential donors in the roost. We

found as a result that both relatedness and prior association are important predictors of an individual's response to a solicitation. Our results show that vampire bats do not share blood randomly but share preferentially with individuals who are frequent roostmates and often, but not always, related, a finding that supports both reciprocity and kin-selection theories.

The next step in our study was to test reciprocity experimentally. If reciprocal altruism does occur among vampire bats, then one might predict that individuals should aid only those in imminent danger of starvation and should preferentially repay those bats who had previously fed them. To test these predictions, we captured four adult females from our main study area at La Pacifica and four from a secondary study area at Parque Nacional de Santa Rosa some 50 kilometers farther north. We knew from their tags that two of the La Pacifica bats were grandmother and granddaughter (related to one another by one fourth); the others were unrelated but had a high degree of roost association.

We initiated our experiment by habituating the bats to captivity and also to being fed nightly from plastic measuring bottles, which enabled us to record the amount of blood each bat would ingest at mealtime. Once the bats were at ease in their cages, we selected one each night at random and put it in a separate cage, where it was deprived of food. The next morning we returned the experimental bat to its original cage and observed its interactions with its cagemates. Our results indicate that blood shar-



STUDYING VAMPIRE BATS in their natural habitat requires that many hours be spent in an uncomfortable position (*left*). To observe the bats, which roost in hollow trees (as well as in caves and other dark places), the author and his assistants

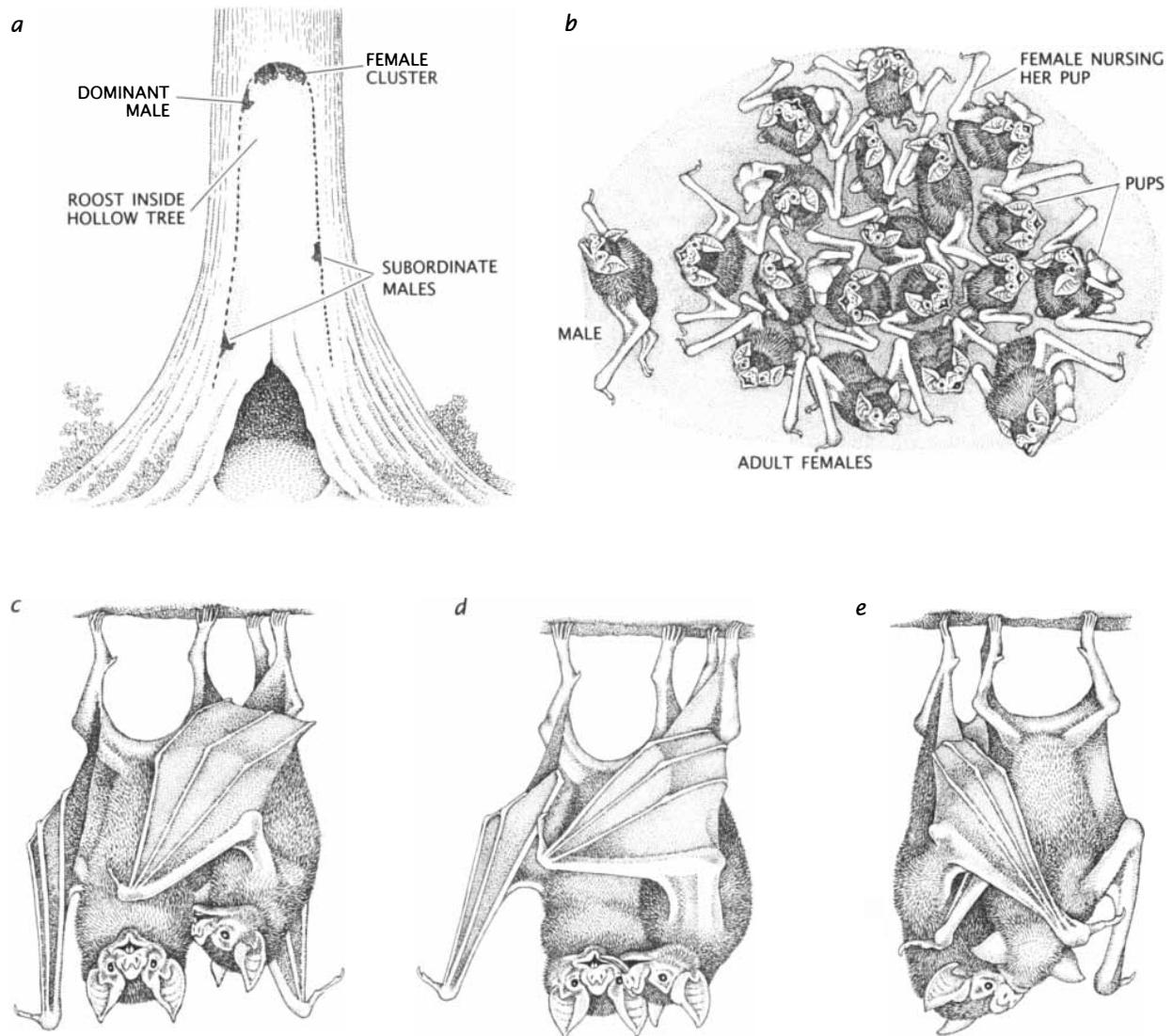
spent from two to six hours a day on their backs, peering upward with a diffuse light. Colored bands placed around the wrists of the bats (*right*) made it possible to identify individuals and follow their interactions over a five-year period.

ing nearly always took place between bats from the same population. Only once did it occur between strangers. Moreover, we found that blood sharing was not random, even among bats who had a high degree of prior association. Instead it appeared that the unrelated bats developed a buddy system, so that two individuals would regurgitate almost exclusively to each other—a strong indication that their roles reverse on a regular basis.

Another criterion of reciprocity theory is that the cost of donating blood must be small relative to the benefit

it provides to the recipient. In other words, by regurgitating blood to a roostmate, the donor should be able to save its roostmate's life without substantially risking its own. To test whether or not this was true for vampire bats, we needed to measure the costs and benefits of blood sharing in two ways: directly by determining the amount of blood and the frequency of its ingestion required to prevent starvation and indirectly by estimating the effect of blood sharing on long-term survival by means of computer simulations.

From McNab's work as well as our own, we knew that a bat must consume from 20 to 30 milliliters of blood every 60 hours to prevent starvation. In addition, we knew that a bat on the brink of starvation can gain up to 12 hours of life and another chance to find food if it is given blood by a roostmate. A cooperative roostmate, who has recently fed and therefore has an elevated metabolic rate, loses less than 12 hours by donating a blood meal and so has 36 hours and two nights of hunting left before reaching the point of starvation. According to



MALE AND FEMALE vampire bats often roost in the same tree (a). Females cluster near the top of the cavity, some 12 or more feet from the ground, where they are guarded by a single dominant male. Two or three subordinate males occupy the same tree but roost closer to the ground. As many as 12 females, each with a young pup (the pups differ in size because births occur throughout the year), may gather in one tree (b). Although the composition of the roosting groups varies from

day to day, some females associate for many years and regurgitate blood to one another, a behavior that is a form of reciprocal altruism. A hungry bat solicits regurgitated blood from a roostmate first by grooming (c), which consists of licking the potential donor under her wing, and then by licking the donor's lips (d). If the donor is receptive, she responds by regurgitating blood (e). Only bats who are close relatives or who have had a long-term association give blood to each other.

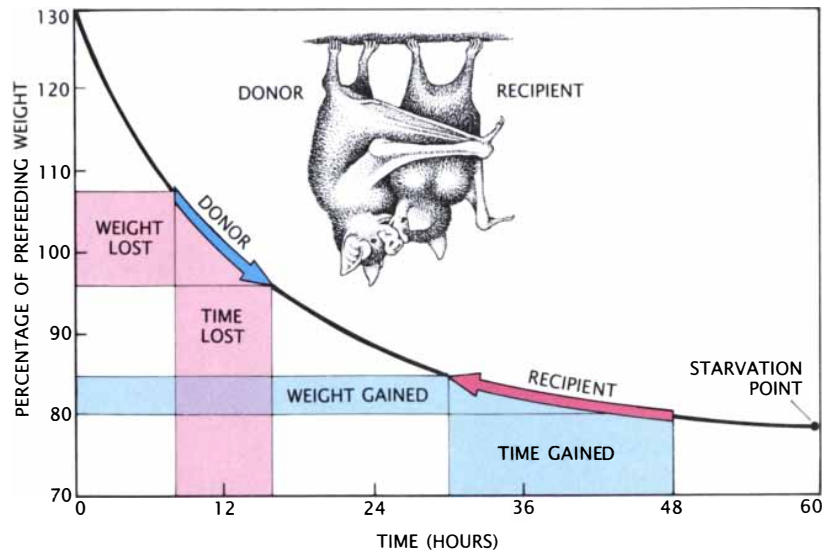
reciprocity theory, then, only bats with less than 24 hours of life remaining should be fed by their roostmates. Our experiment with captive bats, in which we withheld food for 24-hour periods, showed exactly that.

For a reciprocal-exchange system to work, it is necessary for bats to recognize one another and be able to detect and exclude cheaters. Although we have yet to prove that cheaters either exist or are excluded from the system, we have reason to believe that the bats are capable of individual recognition. To begin with, we know from our observations of captive bats that only individuals who have had a prior association will regurgitate blood to one another. It therefore seems likely that they must recognize each other in some way.

Circumstantial evidence strongly suggests that social grooming plays a role in roostmate recognition. The bats spend more than 5 percent of each day grooming and licking one another, and the behavior seems to be an important prelude to regurgitation: hungry bats frequently groom potential donors (females who have recently fed). As with blood regurgitation, grooming occurs more frequently among individuals who either are close relatives or have previously associated with one another than it does among bats who are strangers.

Additional evidence that bats recognize each other has been provided by Schmidt. By analyzing sonograms he and his students have found that the bats emit individually distinct vocalizations. Such "contact calls" often accompany grooming sessions and have the acoustic characteristics (variable frequency and low intensity) that are necessary to encode individual identity. Auditory signals (and possibly olfactory cues) of this type presumably enable individuals to recognize their long-term roostmates as well as cheaters who solicit blood but do not themselves respond to solicitation.

It seems, then, that both reciprocity and kin selection promote blood sharing among roostmates and that regurgitation is beneficial—at least in the short term—to a recipient. How might such energetically costly behavior affect overall survival rates within a population? To establish that reciprocity can persist in an evolutionary sense, one must be able to demonstrate, at least theoretically, that bats who share food with their roostmates have a higher annual survival rate than those who do not.



COST-BENEFIT ANALYSIS of blood sharing among vampire bats indicates that recipients benefit more than donors lose. The author weighed adult females returning to the roost after feeding and then weighed them every hour for the next 24 hours. An individual who had fed might return at 130 percent of its prefeeding weight (half the weight of a blood meal is lost through urination within the first hour after feeding), whereas a bat who failed to feed on two successive nights might return at 80 percent of its earlier weight. By regurgitating five milliliters of condensed blood to a hungry roostmate, the donor bat might drop from 110 to 95 percent of its prefeeding weight but lose only six hours of the time it has remaining until starvation. The recipient bat, however, gains 18 hours and so benefits more than the donor loses.

We knew from our netting studies that on the average about 30 percent of the immature bats (those younger than two years) fail to obtain a blood meal on a given night, whereas only 7 percent of reproductively mature males and females fail to feed. We also knew from field observations that the failure to feed appears to be random: all individuals within an age group are affected equally. With that information and the help of a computer, we determined that annual mortality for adults in the absence of food sharing (given that 7 percent of the adults fail to feed on a given night and that failure to feed two nights in a row will lead to death) should be about 82 percent. Because actual mortality among adult vampire bats is only 24 percent per year, we concluded that food sharing must be favored by natural selection.

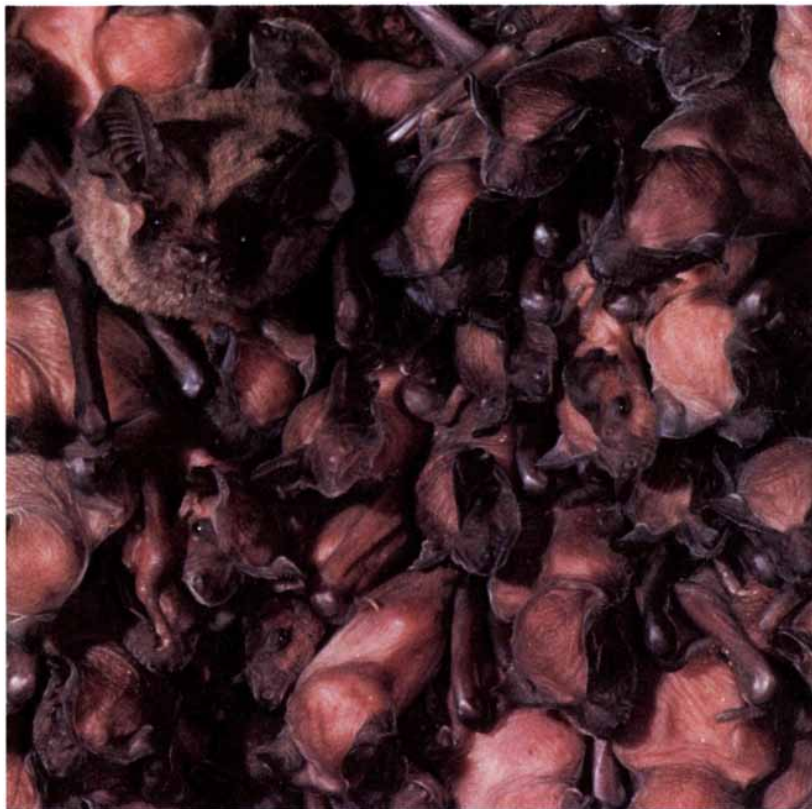
Vampire bats have evolved a system of food exchange whereby they share blood with roostmates in need. Although the behavior puts the donor at risk, the recipient is more likely to survive another night. Moreover, our studies have shown that individuals who exchange blood with their roostmates gain an immediate advantage in terms of increasing their own survival and sometimes the survival of their relatives. Hence, both reciprocity and

kin selection appear to be operative in this system.

Is food sharing a behavior unique to vampire bats? Not exactly. Females of several insectivorous bat species, including the bent-winged bat, *Minioterus schreibersi*, the Mexican free-tailed bat, *Tadarida mexicana*, and the evening bat, *Nycticeius humeralis*, nurse young other than their own.

The bent-winged bat has not yet been studied in great detail. Gary F. McCracken and his students at the University of Tennessee at Knoxville have been studying the nurseries of free-tailed bats for the past nine years. Several million free-tails congregate in caves in the southwestern U.S. every summer to give birth synchronously to their pups. The young are kept in creches, where the density of individuals is as high as 40 pups per 16 square inches. The females roost elsewhere and visit their pups only twice a day to nurse them. As the females approach, the hungry pups swarm toward them; as many as four pups have been observed attempting to feed sequentially from one female.

To an observer, it appears as if females are feeding whichever pups reach them first. For that reason many investigators thought the females were a communal resource; after all, finding one's own pup amid



MEXICAN FREE-TAILED BATS rear their pups in communal nurseries, which may contain a million or more newborn bats. Despite the density of pups—as many as 40 within the space of 16 square inches—mothers, such as the one at the upper left, locate their own pups 83 percent of the time and so rarely nurse unrelated pups.

millions of others seemed impossible. Yet McCracken has shown, by comparing variations in blood enzymes between lactating females and suckling pups, that mothers successfully find and nurse their own young 83 percent of the time, apparently with the help of olfactory and auditory cues. Any nonparental suckling that takes place appears to be milk stealing on the part of an aggressive pup.

For species that form such enormous aggregations, such as the free-tailed bat, the benefits of creching (the pups stay warm, and the risk of predation to any one individual is reduced) outweigh the cost of occasionally nursing the wrong pup. Among free-tailed bats nonparental nursing—when it occurs—seems to be neither a form of kin selection nor reciprocal altruism but simply the result of random error.

For the past two summers my students and I have been studying nonparental nursing in evening bats in northern Missouri. These bats, like the free-tailed bats, form nursing colonies. Their colonies are relatively small, however, containing only from

30 to 200 adults, and are usually found in attics rather than in caves. Unlike the free-tailed bat, which gives birth to one pup per summer, the evening bat gives birth usually to two and sometimes to three pups at a time. Our studies indicate that a mother nurses her pups faithfully during the week following their birth but that as the pups age they tend to feed occasionally from other females. When a pup is about three weeks old, it is generally nursing from a female other than its mother about 20 percent of the time.

Is this a case of reciprocal altruism or kin selection? Because the females can be observed actively accepting or rejecting young pups who solicit milk from them, it seems they are discriminating between pups in some way. Preliminary evidence suggests that the females are selectively feeding relatives: analyses of blood-enzyme markers indicate that most often nonparental females are related—at least distantly—to the pups they nurse. In addition, data my graduate student J. Andrew Scherrer has recently collected indicate that each

pup has a unique call and that calls made by relatives resemble each other. We suspect a nonparental female may recognize related pups by comparing their calls with those of her own pup.

Research on food sharing in bats illustrates a common theme in evolutionary biology: that similar behaviors seen in different species may result from entirely different evolutionary pressures. Although kin selection is widely regarded as a powerful and pervasive evolutionary force, under certain circumstances—such as whenever animals live in small groups and the potential for frequent aid giving among them is high—reciprocity is likely to be more beneficial than kin selection—provided that cheaters can be detected and excluded from the system.

Further understanding of the forces responsible for social evolution in vertebrates requires that the mechanisms underlying individual and kin recognition be identified. Our research on aid-giving behavior in bats demonstrates that the role both kin selection and reciprocity play in a society is dependent on the recognition capabilities of the animals in that society.

Determining the extent to which individuals recognize and interact preferentially with relatives should be greatly facilitated by modern molecular techniques (such as DNA fingerprinting), which significantly enhance the ability of investigators to measure relatedness among animals in the field. Because bats possess a sophisticated auditory system that enables them to navigate and capture prey, I believe careful study of their vocalizations in social situations may yield exciting information about the mechanisms by which animals recognize their relatives and close associates. The results of such study should in turn elucidate much about vertebrate social behavior in general.

FURTHER READING

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