
Reciprocal Altruism in Bats and Other Mammals

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In this paper five conditions are specified which must be met before reciprocal altruism, rather than kin selection, should be invoked. Four purported mammalian examples—social grooming in coati, cluster position in roosting pallid bats, information exchange among greater spear-nosed bats, and blood regurgitation among vampire bats—are examined to determine if reciprocal altruism is necessary to plausibly explain each situation. Results from a computer simulation which apportions the relative selective advantage of vampire bat food sharing to kin selection and reciprocal altruism are then presented. The results demonstrate that the increase in individual survivorship due to reciprocal food sharing events in this species provides a greater increase in inclusive fitness than can be attributed to aiding relatives. This analysis suggests that reciprocal altruism can be selectively more important than kin selection when altruistic behaviors in a relatively large social group occur frequently and provide a major fitness benefit to the recipient even when that recipient is related to the donor.

KEY WORDS: Association; Bats; Coati; Food Sharing; Grooming; Inclusive Fitness; Kin Selection.

CONDITIONS FAVORING RECIPROCAL ALTRUISM

Trivers (1971) proposed reciprocal altruism (RA) primarily to account for apparent altruism expressed between distant relatives or different species. Although he acknowledged that RA might also operate among relatives, he pointed out that obtaining evidence for RA independent of kin selection (Hamilton 1984) in such a situation would be problematic. Not surprisingly, the majority of subsequent purported examples of RA have made unrelatedness a prerequisite (e.g. Packer 1977; Connor and Norris 1982; Seyfarth and Cheney 1984). Before specifying the conditions necessary for a stable RA system, I want to emphasize that individuals can receive fitness benefits through RA independent of their relatedness. Furthermore, since (1) several theoretical treatments (Boorman

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and Levitt 1980; Axelrod and Hamilton, 1981; Brown et al. 1982; Eshel and Cavalli-Sforza 1982) suggest that the initial increase in frequency of reciprocity requires that reciprocal altruists interact preferentially as they would in kin groups, (2) many social animals form groups containing kin, and (3) expectation of future association is a condition of RA (see below), one should expect RA to occur more often among relatives than among nonrelatives. For this reason, I believe that RA may be more widespread than is currently acknowledged.

For a behavior to qualify as RA, five conditions must be fulfilled: (1) the behavior must reduce a donor's fitness relative to the selfish alternative, (2) the fitness of the recipient must be elevated relative to a nonrecipient, (3) performance of the behavior must not depend on receipt of an immediate benefit, (4) a mechanism for detecting individuals who receive benefits but never pay altruistic costs has to exist, and (5) a large but indefinite number of opportunities to exchange aid must exist within each individual's lifetime. These requirements require some elaboration and justification. In essence, conditions 1 and 2 specify that the behavior is altruistic. Note that the payoff situation for the two-person prisoner's dilemma game (cf. Axelrod and Hamilton 1981) meets these conditions. If both parties cooperate in that game, they receive a payoff less than the payoff to a selfish individual who defects, provided that the partner attempts to cooperate. Thus, as Boyd (1987) discusses at greater length, cooperation in this game can be viewed as altruism, since the partner must refrain from taking the cheater's payoff. Exchange of selectively neutral behaviors, therefore, would not fall within this definition of RA.

Condition 3 separates some cases of mutualism from RA. This condition is meant to exclude situations in which the donor acts altruistically only if the recipient simultaneously provides a return benefit. In most situations, this kind of dependency between behaviors is removed once some delay between altruism and return benefit is introduced. Although no absolute time interval can be specified, the delay must be sufficient to provide an opportunity for individuals to cheat by not returning the altruistic act at a later time. For this reason, stable RA systems must meet condition 4 by having methods for detecting cheaters.

The fifth requirement is based on the 1981 analysis by Axelrod and Hamilton of the iterated prisoners' dilemma game. If the number of opportunities for altruism is finite and the last opportunity can be predicted with certainty, a lifetime strategy of repeated altruism prior to a final selfish act will have a higher payoff than will continuous altruism. Of course, once the "cheat on the last move" strategy is established, then "cheat on the penultimate and ultimate moves" becomes superior. Cheating will continue to invade until all individuals are completely selfish. This last condition means, then, that RA should occur among individuals who can expect to have sufficient altruistic opportunities that any pair is unlikely to know when their

last altruistic opportunity will occur. Thus, expectation of future association is necessary.

Excluding primate and cetacean examples of potential cases of RA, since they are treated elsewhere in this issue, three out of the four suggested examples of RA in other mammals have been described for bats: cluster position in roosting pallid bats, *Antrozous pallidus* (Trune and Slobodchikoff, 1978), exchange of information regarding ephemeral food sources among greater spear-nosed bats, *Phyllostomus hastatus* (McCracken and Bradbury 1981), and blood regurgitation among common vampire bats, *Desmodus rotundus* (Wilkinson 1984). The one other possible case of mammalian RA which has been reported is social grooming among coati, *Nasua narica* (Russell 1983). In the next section of this paper, these four suggested cases of RA in mammals are critically examined to determine if they fulfill the criteria for RA outlined above.

Social Grooming in Coatis

Throughout much of Latin America, coatis roam the forests in search of food in bands containing three to five adult females, several nonreproductive young of the prior year, and several infants or juveniles born in the current year (Kaufmann 1962; Russell 1983). During one month in the dry season, a single male joins these bands to mate with the adult females. For the remainder of the year, males are solitary. Just prior to the beginning of the wet season, pregnant females independently leave their bands for 2 weeks to give birth in tree nests to three to five infants. After 2 weeks, the young are sufficiently mobile that the females can rejoin their band. Mortality is high enough that zero to two young per female survive 2 years. Male survivors leave the band at this age, whereas females typically remain. [Actually, Russell (1983) described several instances of second year (nulliparous) or third year (primiparous) females joining existing bands.] Thus, bands may contain one or more matriline. Although no genetic data are available, the intense defense of a band's females by a single male during the breeding season (Kaufmann 1962) suggests that young born in a band in any one year could share a common father. This would cause subsequent generations of females after an immigration to be related across, as well as within, matriline.

Although most of each day is spent in search of invertebrates, fruit, or small vertebrates, at midday and in the evening after the band has ascended sleeping trees, individuals groom themselves and each other. Juveniles receive half their allogrooming from adults other than their mothers, and adults groom other adults significantly more than they groom juveniles or subadults (Russell 1983). During the breeding season adult females groom adult males more than they groom each other (Kaufmann, 1962). Reciprocal grooming occurs since the mean percentage of total grooming bouts which are performed by the more frequent groomer is 57% (Russell, 1983). Interestingly,

the only exceptions to this pattern occurred between recent immigrants or subsequent emigrants and other band members. Recent immigrants groomed members of their band more than they were groomed, and females that subsequently left a band did not have highly reciprocal grooming relationships with other members of that band (Russell 1983). Russell argues that allogrooming is a case of RA because grooming is reciprocated after some delay, females form reciprocal grooming relationships with both related females and unrelated females and males, females within a band have fewer ectoparasites than solitary males, and symmetry of the grooming relationship appears correlated to the strength of affiliation among adults within bands.

These data appear to meet several of the conditions for RA. Insofar as ectoparasites lower the fitness of an individual by disease transmission, their removal benefits a grooming recipient, thereby satisfying condition 2. Although grooming sometimes occurs simultaneously, many episodes involve one animal lying passively while the other grooms, so a delay between grooming and being groomed often occurs, as required by condition 3. The observation that some females left a band in which grooming relationships were not symmetrical suggests that cheating may be detected and punished, which would satisfy condition 4. Moreover, since grooming occurs daily and terminates with death or immigration, neither of which should be predictable to both participants, condition 5 is met. However, the assumption that grooming reduces a donor's fitness because energy and time are spent that could otherwise be used for food acquisition can be questioned. Dunbar and Sharman (1984) have demonstrated that time spent by baboons in allogrooming is conserved, whereas time spent resting is adjusted to permit an increase in feeding time when needed. Thus, allogrooming probably has no direct fitness cost, although it may have fitness benefits. Social grooming in coatis might, however, reduce vigilance time since group living in coatis appears to increase predator detection (Russell 1983). In support of this conjecture, after females with infants rejoin their bands, grooming of the infants is confined to the evening when the coatis are in tree nests (Russell 1983). Presumably, mothers do not groom at midday because it would preempt vigilance time. Thus, the available evidence regarding coati social grooming neither fails nor strongly supports the RA criteria.

The high level of relatedness within coati bands suggests that kin selection may be an important reason for social grooming. Unfortunately, Russell (1983) did not have sufficient information between all pairs of individuals to determine if relatedness, past association, or both could predict either grooming frequency or symmetry. The observation that a few unrelated animals (including the breeding male and adult females) did groom each other symmetrically suggests that kin selection is unlikely to be a sufficient explanation for social grooming in coatis.

Cluster Position in Pallid Bats

Pallid bats glean vegetation or the desert floor for such invertebrates as scorpions throughout the southwestern United States and northern Mexico

(Bell 1982). During early summer, up to 60 females gather in rock crevices or buildings to give birth, usually to 2 young (O'Shea and Vaughan 1977). The bats spend 75% of each night in one of several roosts away from their day roost. These nocturnal roosts are characterized by constant, warm temperatures that vary from 24° to 29° C during the summer months (O'Shea and Vaughan 1977). Just before dawn, females return to a day roost but do not enter at once. Instead, they fly 50 m back and forth in front of the dayroost for up to 15 minutes while making loud, low-frequency "directive" calls (Vaughan and O'Shea 1976). Then, a single adult female apparently enters the day roost followed immediately by the group. Vaughan and O'Shea (1976) suggest that this predawn circling and calling attracts any late foragers to that day's roost, thereby increasing group size as much as possible. In Arizona after the young are weaned, the group leaves the nursery colony area over 2 nights in August to spend the winter elsewhere (O'Shea and Vaughan 1977).

Trune and Slobodchikoff (1978) suggest that large roosting groups of pallid bats are important because they increase the potential insulation for juvenile bats. Bats in a cluster, either in the center or on the periphery, average body temperatures 8° C higher than single bats held at 15° C (Trune and Slobodchikoff 1976). Solitary bats also have higher O₂ consumption and more weight loss than bats in a cluster maintained at 15, 20, 25, 30 and 35° C; lowest O₂ consumption occurs at 30° C (Trune and Slobodchikoff 1976). At ambient temperatures below 30° C, body temperatures of pallid bats within a cluster are higher than those on the periphery (Trune and Slobodchikoff 1978) although the difference is a few degrees at most (Trune and Slobodchikoff 1976). In the lab, adult females and adult males allow juvenile bats to preferentially roost in the center of clusters (Trune and Slobodchikoff 1978). In that article (1978) these authors suggest that this is a case of RA because by granting another bat's young the most desirable position within a cluster, an adult female is behaving altruistically, while both the young and its mother are benefiting, since the mother is relieved of providing her young with insulation. Single females wrap their offspring in their wing membranes during the first 2 weeks after birth (Orr 1954). They suggest that both the mother and young can reciprocate. The mother can allow other juveniles into the center and the young can allow next year's young into a similar cluster.

Although this is an intriguing behavior that may be widespread in bats—clustering decreases weight loss and increases body temperature relative to solitary animals in the neotropical nectivorous bat, *Glossophaga soricina* (Howell 1976), and the temperate insectivore, *Myotis thysanodes* (Studier et al. 1970)—it is unlikely to represent a case of RA. By allowing another bat into a cluster, a bat gains insulation by increasing cluster size, thereby violating condition 1. Although condition 4 may be met, since Brown (1976) has found that these bats have unique vocal signatures that might facilitate recognition of cheaters refusing to roost on the periphery of a group, con-

dition 5 is not fulfilled if juveniles do not reciprocate until the following year. This would require the return benefit to be passed to offspring of the initial altruist. As others have noted (cf. Koenig 1988), such parental sacrifice is improbable because an alternative strategy in which adult females reciprocally exchanged places and benefits would produce a greater payoff. Because the temperature in the center of a cluster probably differs from the edge by about one degree during the summer months, an energetic cost to peripheral roosting by an adult female also needs demonstration. Newborns, however, may benefit by growing faster when kept within clusters while ectothermic.

Unfortunately, no information on site fidelity or natal philopatry is available, and degree of relatedness among adult females within a cluster is unknown. The synchronous parturition and departure suggest that female group composition could be stable over years, but, since adult males are never found in nursery roosts, juvenile males that are allowed into a roosting cluster would never participate in the same cluster the following year.

Information Exchange in Greater Spear-Nosed Bats

In Trinidad, greater spear-nosed bats form stable clusters containing 18 (SD = 5) adult females of similar age (McCracken and Bradbury 1981). A single male defends each group for up to 3 years and fathers most, if not all, young synchronously born each year in late April (McCracken and Bradbury 1977, 1981). Before the following March, female young from several different roosting clusters disperse to form new groups, while young males join existing bachelor groups. Electrophoretic analysis of five blood enzymes provides a genotypic correlation estimate (Pamilo 1984; Wilkinson and McCracken 1985) of the average degree of relatedness between all pairs of adult females within a cluster equal to 0.04 (McCracken 1987). The most plausible explanation for this nonrandom structure is that female half-sibs occasionally disperse together to form a new group (Wilkinson 1987). Estimates of average relatedness using demographic data and a modified version of Wright's island model (Murray 1985) indicate that to be compatible with the genetic correlation estimate of relatedness, adult female *P. hastatus* groups should contain several subgroups of two or more half-sisters (Wilkinson 1987).

Considerable evidence suggests that these 80–100 g omnivorous bats sometimes aggregate at rich food sites. During most of the year, individual females maintain exclusive foraging areas that adjoin the foraging areas of clustermates (McCracken and Bradbury, 1981). Occasionally, however, radio-tagged females from adjacent foraging areas congregate at a single site (McCracken and Bradbury, 1981). Although this species primarily eats sequentially ripening fruit—such as *Cecropia peltata* (Fleming 1982)—swarms of alate leaf cutter ants, *Atta cephalotes*, and flowering *Hymenaea courbaril* trees provide temporary rich food sources that McCracken and Bradbury (1981) argue favor RA. Bloedel (1955) reports a group of 30 *P. hastatus*

feeding on swarming termites, and Goodwin and Greenhall (1961) describe flocks of up to 100 bats feeding on the aril of sapucaia nuts (*Lecythis zabucajo*) while making loud, audible vocalizations. McCracken and Bradbury (1981) suggest that these relatively low-frequency sounds are used reciprocally to advertise the location of rich food sources, such as emerging ant or termite swarms, within the foraging area of a single female. This RA could then explain the long-term stability of female roosting groups, since mutualism, kin selection, and group selection can be ruled out (McCracken and Bradbury 1981). Because these bats roost in close proximity and often return to roost carrying or covered by food, such as pollen, unsuccessful foragers within a cluster might detect individuals who cheat by not advertising.

Subsequent to the work conducted by McCracken and Bradbury, I discovered that these bats occasionally nurse a clustermate's young during the first 2 weeks after birth, and adult females frequently groom each other within a cluster (Wilkinson 1987). Thus, we now know that other possible benefits to stable group formation, which McCracken and Bradbury rejected, exist in this species. Nevertheless, the food information exchange idea does satisfy conditions 2 through 5, since access to a previously undetected high-protein food source must enhance reproductive performance, if not survival; a delay between advertisements occurs; a plausible mechanism for cheater detection exists; and the annual adult survivorship of 90% (McCracken and Bradbury 1981) ensures that multiple opportunities for information exchange will be available. Advertisement would represent a cost, thereby fulfilling condition 1, if the availability or quality of the ephemeral food source is diminished by having more than one bat visitor. Unfortunately, there is no direct evidence that the calls are reciprocated or, in fact, represent advertisement; they may have a defensive function. Although a flock of 30 bats may consist of a female cluster with young, a flock of 100 must contain several clusters and is unlikely to represent part of a reciprocal advertisement scheme. Until more data are available, information exchange in *P. hastatus* cannot be distinguished from selfish information transfer as has recently been described for colonial cliff swallows (Brown 1986). Whether kin selection or RA best account for communal nursing or social grooming in this species awaits further study.

Blood Sharing by Vampire Bats

The common vampire bat feeds exclusively on blood, most often that of domesticated mammals (Turner 1975). In northwestern Costa Rica, groups of 8–12 adult females with their current young utilize a common set of day roosts in either hollow trees or caves (Wilkinson 1985a) and maintain non-overlapping foraging ranges with neighboring groups (Wilkinson 1987). These groups form by restricted female dispersal; on average, one female transfers between groups every 2 years. In contrast, all juvenile males disperse 3 or more km prior to attaining reproductive maturity (Wilkinson

1985b). The mating system is resource-defense polygyny—adult males fight for access to preferred female roost sites. Observations of copulations indicate that top males perform up to 80% of all matings in a group; however, paternity exclusion analyses using enzyme polymorphisms reveal that maximum paternity of top males is less than 50% (Wilkinson 1985b). Because these top males are deposed, on average, every 1.5 years, female dispersal causes a relatively low average r (between 0.08 and 0.11) within female groups (Wilkinson 1984, 1985b, 1987).

Although communal nursing has been described for this species in captivity (Schmidt and Manske 1973; Mills 1980), all 42 pups banded in Costa Rica nursed from a single female (Wilkinson 1985b). Provisioning by blood regurgitation was observed on 110 occasions during 400 hours of behavioral sampling during this study. Of these observations, 77 involved a mother feeding her dependent offspring, whereas 33 occurred between two adults or an adult and juvenile. Regurgitations between bats other than mothers and their young did not occur at random but were distributed preferentially both to close matrilineal relatives and individuals having high past roost association (Wilkinson 1984). In conjunction with observations of reciprocal blood exchanges among captive, unrelated roostmates, these results support reciprocity, in addition to kin selection, as an explanation for this altruistic behavior (Wilkinson 1984).

Potential cheaters who receive a blood meal but fail to share in response to begging could be detected by social grooming that occupies, on average, 5% of adult female roosting time. Both close kin and frequent roostmates groom each other preferentially (Wilkinson 1986). Rather than act to control ectoparasites as self-grooming does (Wilkinson 1986), social grooming apparently facilitates identification of future aid-giving partners. Because it occurs frequently around a partner's highly distensible stomach, which can hold a 35 g blood meal (Wimsatt 1969), social grooming may also provide a method for assessing the recent feeding history of roostmates. In support of this proposition, social grooming occurs more often than expected before and after food-sharing episodes and correlates with regurgitation frequency (Wilkinson 1986).

This behavior fulfills the first two conditions for RA, because giving up part of a blood meal increases the probability of mortality by starvation (these bats die within 3 days if not fed) and increases the chance of survival for a bat that has recently failed to obtain a meal (Wilkinson 1984). Adults fail to feed on 10% of nights, whereas bats under 2 years of age miss every third night. Although the few cases of males sharing food with infants might represent apparent altruism contingent on subsequent mating access, the great majority of food sharing exchanges do not involve adult males and occur with a delay of 1 or more days (Wilkinson 1984). Because mortality is 50% during the first year and about 25% in subsequent years, many bats will live sufficiently long for multiple opportunities to exchange food (Wilkinson 1984). Thus, this system meets all of the criteria for RA.

As both related and unrelated females engage in food-sharing behavior, separating the selective advantage of reciprocal sharing from kin selection is necessary. Below, I describe a Monte Carlo simulation that calculates the direct effect of reciprocal sharing on an individual's subsequent probability of survival, as well the effect of its blood sharing on its own relatives' probability of survival.

Reciprocal Altruism and Kin Selection as Inclusive Fitness Components

To calculate any benefit to an altruistic act, such as food sharing, the fitness of an animal performing the selfish alternative, W_o , must be specified. An individual's inclusive fitness, W , is then the sum of baseline fitness, the component due to RA, W_{ra} , and the component due to kin selection, W_{ks} , that is,

$$W = W_o + W_{ra} + W_{ks}.$$

As Grafen (1982) has emphasized, Hamilton (1964) intended that W_{ks} include only the change in fitness to the donor's relatives due to altruistic acts by the donor. If we denote the change in individual j 's fitness due to altruist i 's acts as b_{ij} and the relatedness between i and j as r_{ij} , then

$$W_{ksi} = \sum_{j=1}^m r_{ij} b_{ij},$$

where there are $m - 1$ other individuals to which the donor acts altruistically. The m th iteration includes the effect of individual i 's behavior on its own fitness. The RA component of inclusive fitness contains the change in i 's individual fitness due to altruistic acts received from all other animals, specified by n . Thus,

$$W_{rai} = \sum_{j=1}^n b_{ji}.$$

Gathering these data from a natural population is difficult, because fitness should be measured in terms of lifetime reproductive success or a correlate, and baseline fitness must be estimated even if no animal ever performs the selfish alternative. Therefore, I used computer simulations to compute the effects of vampire bat food sharing on their probability of survival. This was accomplished by having each of the 11 adult females from the UP group (cf. Wilkinson 1984, 1985a,b) choose 1 of their 7-day roosts with a probability assigned to each tree according to its proportional use by that female. The prior night foraging success for each female was specified by a random draw in which the probability of success was 0.9 and the probability of failure was 0.1 as was observed in the wild (Wilkinson 1984). Once all females attempted to feed and had been assigned roosts for the day, those bats not

having obtained a meal randomly begged from roostmates. The roostmates refused to share unless three criteria were met: (1) the potential donor was above the median in foraging success, (2) a threshold of prior association and (3) of relatedness between the potential donor and recipient was exceeded. Actual values of relatedness and prior association within day roosts among all dyads in the group (Wilkinson 1984) were used in all runs. If these criteria were fulfilled, then the begging animal received enough blood to ensure its survival for that day and the donor subtracted 0.1 units of its prior night's foraging success. Because foraging success was accounted by drawing from a uniform distribution bounded by 0 and 1, median foraging success was 0.5 and one or more donations could drop a donor below the median and prevent further donations. If no bat in the roost met these criteria, the begging bat went hungry for that day. Roosts were then chosen and foraging success determined for the next day. Failure to feed on 2 successive days resulted in death, which precluded a bat from further food sharing.

This process was iterated for 365 days to determine which bats would die within a year under the specified association and relatedness thresholds. The expected annual mortality of each bat was obtained by iterating the yearly cycle 100 times. From these individual expected annual mortalities, I estimated W_{ra} as the decrease in average probability of annual mortality from that expected when no bats ever share food (estimated to be 0.37). To determine W_{ks} for bat i , I recorded the number of donations made by bat i to every other bat in the group and then estimated the effect of i 's donations on each recipient's mortality to obtain an estimate of b_{ij} . Thus, b_{ij} , the decrease in mortality of recipient j , was calculated as the fraction of all donations made by i and received by j in a year, multiplied by j 's W_{ra} . In other words, W_{ksi} measures the change in annual mortality due to acts made by individual i to its relatives, whereas W_{rai} contains the effect on annual mortality occurring as a consequence of acts received by individual i . The average number of food sharing events made within the group during the year, as well as the percent of these donations that were reciprocated, were also collated for each set of threshold conditions.

In Figure 1, W_{ra} is plotted against the association threshold (A) for each of the four relatedness thresholds (r) used. When all bats within the group share freely (i.e., $r = 0$ and $A = 0$), mortality decreases by 0.37 or, in other words, no bat ever dies. In fact, when $r = 0$, all bats survive if $A < 0.8$. The component of inclusive fitness due to kin selection, W_{ks} , can be extracted from Figure 1 as the difference between the two lines for any combination of thresholds. The most striking result of these simulations is that for all threshold conditions, $W_{ra} > W_{ks}$. Furthermore, W reaches a maximum value of 0.47 at three sets of thresholds: when $r = 0.5$ and $A = 0$, when $r = 0.5$ and $A = 0.4$, and when $r = 0.25$ and $A = 0.6$. Note that the cases in which $r = 0.5$ have roughly twice the standard deviation as the case where $r = 0.25$ and $A = 0.6$. If these bats attempt to minimize their mortality risk (e.g., Rubenstein 1982), this latter combination of thresholds would be the

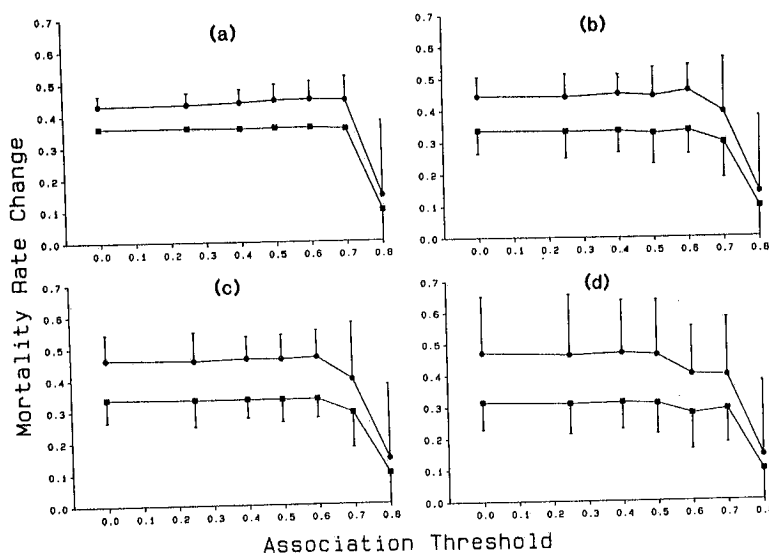


FIGURE 1. Monte Carlo computer simulation results. Closed boxes show decrease in individual mortality as a consequence of receipt of a blood meal, and closed circles indicate the inclusive fitness of individuals. The difference between the two lines represents the kin selection component of inclusive fitness. Sharing is restricted to those bat pairs that have at least the specified association index and (a) relatedness (r) equal to 0, (b) $r > 0.125$, (c) $r > 0.25$, or (d) $r > 0.5$.

best strategy to adopt. Interestingly, no food-sharing events ever occurred in the wild between bats with association indices less than 0.6 (Wilkinson 1984).

Some of the pattern in Figure 1 can be understood by examining how the number of donations made and reciprocated vary with each threshold condition. As the two thresholds were increased, the number of pairs of bats who could share decreased. Not surprisingly, the proportion of donations reciprocated increased as fewer pairs were involved in sharing episodes with the exception of $A = 0.8$ (Figure 2). So few bats met this association criterion that they rarely encountered each other, and mortality, due to the stochastic process of choosing a day roost, was sufficiently high (cf. Fig. 1) that a bat frequently died before it could reciprocate.

The relatively small contribution of W_{ks} to W can be understood by examining Figure 3. As the number of bat pairs sharing increased due to decreasing threshold conditions, the average number of donations made per year increased more than 300 per year (Figure 3a). At this level, all bats survive, so each of the 11 bats should give blood about 30 times per year or, alternatively, make about 3 donations to each other bat. Although only 65% of these 300 sharing events are reciprocated (Figure 3b), every bat should expect to receive about 30 donations each year. Thus, the fraction of an individual's aid that can be attributed to any other bat will roughly be

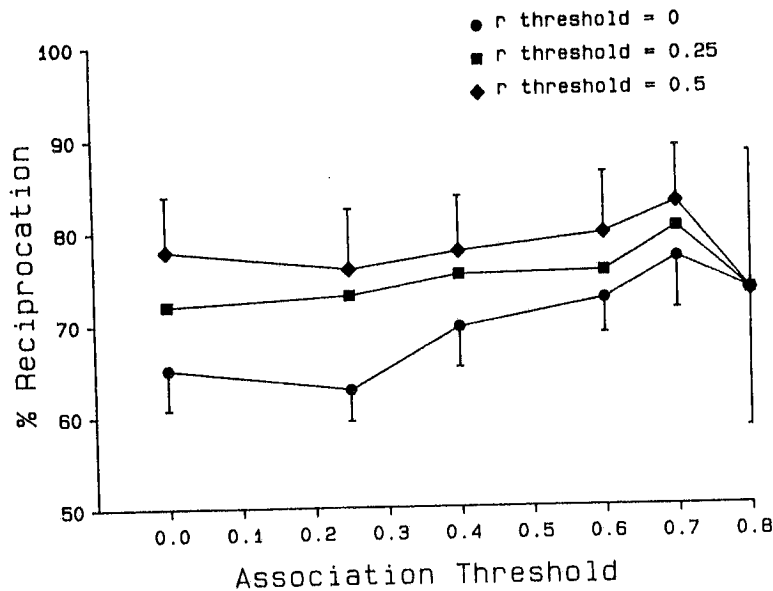


FIGURE 2. Percent of simulated food-sharing events that were reciprocated at each association and relatedness threshold specified.

$\frac{3}{30} = 0.1$. When this fraction is multiplied by W_{ra} and relatedness, which averages about 0.1 (see above), and summed over the other 10 bats in the group, the W_{ks} will be $(0.1)(0.1)(10)W_{ra} = (0.1)W_{ra}$. As Figure 1a shows, when $r = 0$ and $A = 0$, this is close to the relationship obtained by the simulation. The kin selection component increases in magnitude in Figure 1 both because the effective group size decreases (Figure 3a) and because the individuals in the sharing group are more closely related, on average.

An obvious objection to these simulations is the use of thresholds to initiate food sharing. I used this technique, rather than simulate tit-for-tat (TFT) or some other two-person strategy because I could easily specify the boundary conditions (i.e., all bats share all the time or no bats ever share) and it was computationally fast. Although this scheme assumes that individuals never cheat, relaxation of this assumption would not change the qualitative outcome of the simulation. Certainly, cheating would pay if the thresholds were set at 0. Even if bats remembered all prior food sharing events, cheaters who roosted alone would not be detected. Cheater detection is simplified if sharing is restricted to bats seen almost every day, that is, those with high prior association. This is consistent with observed cases of food sharing (Wilkinson 1984) and supplies some justification to the threshold approach. I suspect that introduction of a cheater option would produce more unimodal curves for Figure 1 in which there would be little fitness benefit to sharing with animals of low prior association.

The other major assumptions are that (1) the behavior has no direct

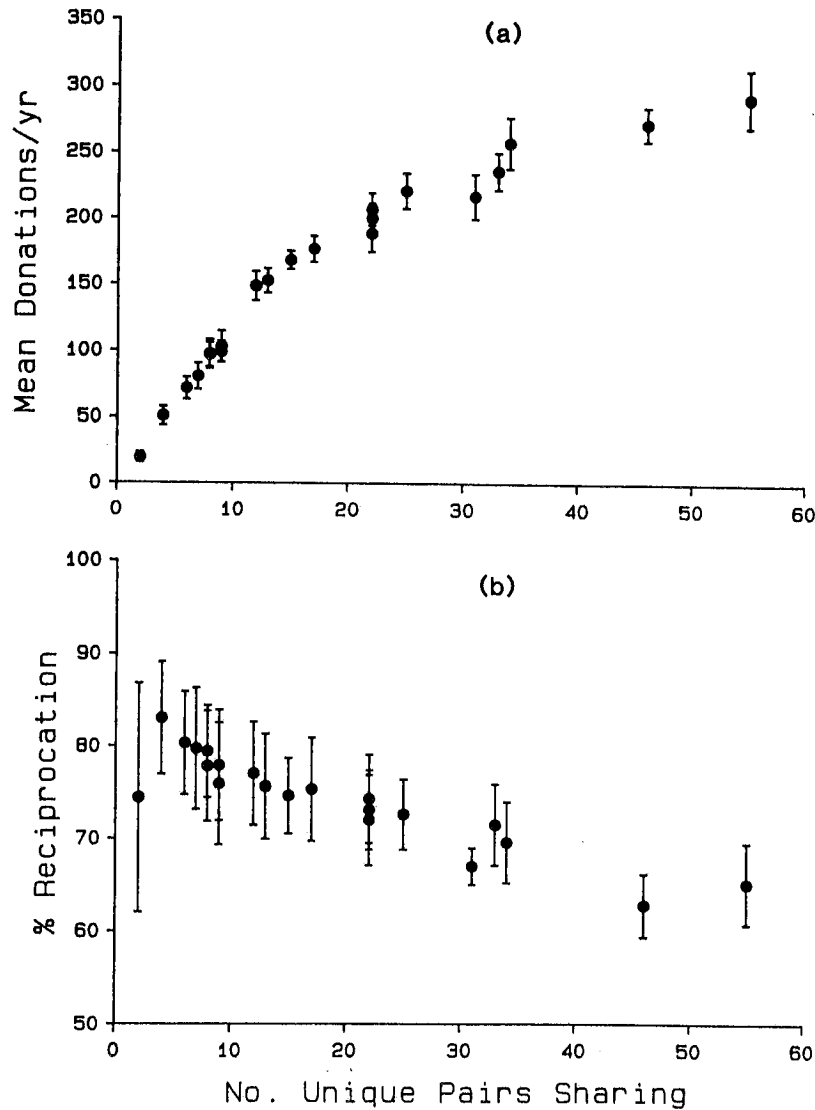


FIGURE 3. Monte Carlo simulation results as a function of the number of bat pairs that met the association and relatedness thresholds shown in Figure 2. (a) Mean number of donations made within the group of 11 bats during a year. (b) Proportion of food-sharing events that were reciprocated within the group.

cost, (2) lifetime reproductive success is adequately described by annual probability of survival, (3) the probability of successful foraging can be described by a uniform probability distribution, and (4) individual foraging success is independent both of prior success and success of group members. These assumptions are appropriate for the following reasons. Although there is a measurable loss in available time to starvation as a consequence of food sharing (Wilkinson 1984), captive bats invariably do not share blood if they

do not have sufficient reserves to survive at least 24 hours (Wilkinson 1984). Thus, assumption 1 appears valid. Females can have at most one baby every 10 months. In Costa Rica, average per capita reproduction was one infant per year (Wilkinson 1985b). Consequently, annual mortality should be highly correlated with lifetime reproductive success, which supports assumption 2. Foraging success is clearly not uniform and more closely approximates a normal distribution. However, the decisions based on foraging success probabilities are independent of distribution shape as long as the distribution is symmetrical, which means that assumption 3 has no effect on the simulation outcome. There is evidence that foraging success is independent of prior success (Wilkinson 1984), but also evidence that these bats sometimes forage in groups and may exchange information about feeding sites (Wilkinson 1985a). Violating assumption 4 in this way would increase foraging success for bats with access to such information which might decrease W_{ra} but should not affect the relationship between W_{ra} and W_{ks} .

Implications for Other Systems

Although the model just described was developed specifically to account for food sharing in vampire bats, it does, I believe, have relevance for other potential RA systems. The most important result is that reciprocal aid giving—which could be food sharing, communal nursing, coalition formation in primates, support behavior in cetaceans, or any other dyadic altruistic act—can generate a substantial selective force independent of kin selection even when performed among related animals. This result depends on whether the altruistic act has a major fitness benefit to the recipient. The magnitude of the direct benefit to reciprocation will be proportional both to this potential change in fitness and to the average number of altruistic acts received by each individual. In the vampire bat food-sharing case, this number was directly related to the number of animals that engaged in food-sharing behavior. This relationship exhibited diminishing returns (Figure 3a), with an increase in group number. The frequency of altruism should increase with group size whenever the potential cost to the donor has a random component, such as prior night's foraging success, because the number of animals capable of being altruistic will be the product of the probability of acquiring sufficient resources to share and group size. These considerations suggest that repeated altruistic exchanges among animals in relatively large groups—such as lions (Bertram 1976), elephants (Lee 1987), dwarf mongoose (Rood 1978), brown hyenas (Owens and Owens 1984), or tribal human cultures, among others—are likely to have an RA component of inclusive fitness that exceeds the component due to kin selection. Further study of such systems should provide further evidence of the importance of RA in the evolution of social behavior.

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