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Reciprocal altruism between male vampire bats, *Desmodus rotundus*

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Reciprocal altruism is an example of social behaviour that has generated much interest among evolutionary theorists, but relatively few well-documented case studies. Among mammals, reciprocal altruism has been reported for the dwarf mongoose, *Helogale parvula* (Rood 1983), naked mole rats, *Heterocephalus glaber* (Jarvis 1978), impala, *Aepyceros melampus* (Hart & Hart 1992) and a few other species, but the best known and most intensively studied example is the regurgitation of blood-meals by successfully foraging adult vampire bats to unsuccessful individuals. This behaviour has apparently evolved in response to the finely balanced energy budget of vampires, which can result in starvation following as little as 48–72 h of food deprivation (McNab 1973). A foraging situation that results in an average of ~8% of adults failing to feed successfully on any given night (Wilkinson 1984), combined with the low fecundity of vampire bats, makes food sharing an essential element of survival.

The evolutionary stability of reciprocal altruism was studied by Trivers (1971), who concluded that the behaviour depends on several critical factors. Particularly important are the ability of altruists to detect and refuse cheaters, and a high probability of reciprocation in the future. Both criteria require frequent and intimate social interactions with a high degree of individual recognition. Although reciprocal altruism between adult vampires has been well studied, only female–female and occasional male–female regurgitations have been reported (Wilkinson 1988). Furthermore, reciprocal altruism between adult males has not been predicted, since several studies (e.g. Joermann 1984; Wilkinson 1985) indicate that males violate two of Trivers' (1971) five criteria for the evolution and maintenance of reciprocal altruism: low dispersal rates (which maximize the opportunities for donors to receive reciprocations) and weak dominance hierarchies (which minimize counter-altruistic aggressive behaviour between potential reciprocators). Males are more transient members of vampire colonies than are females (Wilkinson 1988), and strong dominance hierarchies have been reported among adult males (Wilkinson 1984; Park 1991). These behaviour patterns should undermine the stability of reciprocal altruism between male *D. rotundus*.

We conducted a 7-month behavioural study of a captive colony of vampire bats and documented that reciprocal altruism between adult males of low relatedness did occur, was relatively common, and was associated with a very low-intensity, non-linear dominance relationship between males.

The experimental group consisted of two male and four female adult vampire bats of four independent maternal lines. We calculated relatedness between members of the colony from genealogies (Krebs & Davies 1978) using data extending back three generations. We determined maternal contributions directly, and determined paternal contributions probabilistically using the number of available potential sires at the times of conception. Relatedness between the two males (32L and 35R) was 0·26 ($\bar{X} \pm SD = 0{\cdot}15 \pm 0{\cdot}06$ for the whole colony). The males were 51 and 42 months of age, respectively, at the conclusion of the study. Bats were housed in a 0·4-m^3 plywood roost box designed to simulate a hollow tree and provide a variety of roosting options in all three dimensions. We subjected the colony to experimental manipulations (unpublished data) intended to promote blood-sharing behaviour and test the extent of reciprocity and effects of 'cheating' (i.e. non-reciprocation).

We observed blood-sharing regurgitations between males on three occasions, twice from 35R to 32L and once from 32L to 35R. 35R never regurgitated to the females in the colony, even when solicited, and 32L regurgitated only once to a female (47R; relatedness=0·11). The total data set (N=10 regurgitations; 151 solicitations)

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revealed no significant correlation between relatedness and regurgitation for the colony ($r=0{\cdot}288$, $P>0{\cdot}05$). Association time between the two males, defined as the total time a pair of bats were observed in close proximity (less than one body length) as a percentage of the total observation time, was high: 28% of 32L's total association time was with 35R, compared with as little as 1% for some female pairs. Mutual social grooming between males, not previously reported, was relatively common. Also, male–female association and non-aggressive social interactions were much higher than previously reported. We observed aggressive interactions between the two males on only four occasions, resulting in two 'wins' (defined as an unopposed or unreturned aggressive act) each. Aggressive interactions between male–female pairs were much more common. Blood regurgitation from adult females to adult males, also previously unreported, accounted for three of the 10 observed events, with one female (41R) regurgitating to both males. We interpret these results as indicating that the dominance relationships between both male and female colony members were weak.

We conclude that social interactions between captive, socially acclimatized adult male vampire bats in non-crowded conditions are much more frequent and varied than previously reported or supposed, and that adult males participate in reciprocal altruistic food sharing. Indeed, the energetic constraints imposed by foraging failure that favour reciprocal altruism among females also apply to males. The prevailing paradigm in which vampire bat society is dominated by strong resource defence polygyny and strong male–male dominance hierarchies may need to be re-examined.

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