RECENT ADVANCES IN THE STUDY OF BATS

Edited by

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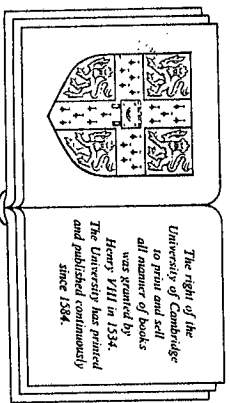
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1987

18   Altruism and co-operation in bats

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Abstract

This paper presents methods for discriminating between the evolutionary mechanisms – kin selection, group selection and reciprocity – which can operate to permit either co-operative (donor and recipient benefit but recipient benefits more) or altruistic (donor pays a cost while recipient benefits) behaviours to persist in a population. The models can be rejected by estimating two parameters, namely the coefficient of relatedness and the probability of being in a situation to behave co-operatively or altruistically in the future. Methods for estimating these variables as well as the cost and benefit of a behaviour are discussed. Then, to obtain a first approximation of the likelihood for kin selection, a modified version of Wright's island model is used to estimate the average level of relatedness within female groups with group sizes, mortality schedules and dispersal rates chosen to be representative of many bat social systems. Data on the demography of five phyllostomid bats – *Desmodus rotundus*, *Phyllostomus hastatus*, *P. discolor*, *Carollia perspicillata* and *Artibeus jamaicensis* – are used in this model to estimate average levels of relatedness. The results show that relatedness correlates with the relative cost of expressing a social behaviour such as food provisioning, communal nursing or social grooming. However, the compositional stability of female groups also correlates with related-

ness. Consequently, the present data support both kin selection and reciprocity as plausible mechanisms for the expression of social behaviour in these phyllostomid bats. Further research on bat social behaviour, particularly on closely related species which differ in the level of relatedness among females within roosting groups, promises to be rewarding.

Introduction

Although the Chiroptera lie second to the Rodentia as the most species – rich order of mammals, bats utilize more resources as food – insects, fruit, leaves, nectar, pollen, vertebrates (including fish, frogs, birds and even other bats) and blood – than any other mammalian order. This variation in feeding habits is matched by a diversity of mating systems (Bradbury 1977a), from monogamy (Vehrencamp, Stiles & Bradbury 1977) to promiscuity (Thomas, Fenton & Barclay, 1979) and lekking (Bradbury 1977b). Much of the variation in mating systems can be attributed to variation in female dispersion pattern (Bradbury & Vehrencamp 1977), particularly to the number of females at a defensible resource such as a diurnal roost. The stability of membership and size of roosting groups of females probably represent adaptations to the spatio-temporal dispersion of food and, to a lesser extent, to the availability of suitable roosting sites. This chapter focuses on those interactions which occur while foraging or inside a roost and which affect an individual's lifetime production of young. As will become apparent, the type of interaction expected within a given roosting group depends on the mating system as well as the size, composition and stability of the group.

To begin discussion and avoid ambiguity I first define some genetic and behavioural terms which I use repeatedly in this chapter. Documented and potential examples of co-operation and altruism in bats are then presented followed by a discussion of the evolutionary mechanisms – kin selection (Hamilton 1964), group selection (reviewed by Wade 1978) and reciprocity (Trivers 1971, Axelrod & Hamilton 1981) – which might explain their evolution and persistence in contemporary populations. Next, I discuss ways by which parameters necessary to test these alternatives may be estimated, and present a simple genetic model to predict the types of social organization in which one would expect high cost altruism or no cost co-operation. Finally, the population structure and social behaviour of the five most well-studied phyllostomid bats are reviewed and compared with the model's predictions.

Definitions

The consequences of an act by a donor are referred to as costs C and to a recipient as benefits B; both are measured in individual fitness units. Here, individual fitness is the number of offspring produced to weaning age during an individual's lifetime. For bats which bear a single offspring, have high fertility and maintain a constant birth interval, female fitness is a function of adult survival and preweaning care. Male fitness in bats without paternal care is determined exclusively by the number of females a given male impregnates. Inclusive fitness of individual A equals A's individual fitness plus or minus A's effect on the fitness of others weighted by the degree of relatedness between A and each individual (Hamilton 1964). Note that A's inclusive fitness does not include any part of the fitness of a relative if A never affects that relative's fitness (Grafen 1982).

The estimate of relatedness used here is the regression coefficient,

$$r = 2f_{xy}/(1 + f_x),$$ 　　(1)

where f_x is the inbreeding coefficient of x, the individual which performs the act, and f_{xy} is the coefficient of consanguinity or kinship between x and y (Hamilton 1972). This coefficient is advantageous because it can be calculated easily (see below) and is often the most appropriate metric to use to formulate kin selection predictions (Michod & Hamilton 1980). The derivation of this coefficient from more exact coefficients of relatedness is presented by Michod & Hamilton (1980).

In this chapter I recognize three types of behaviour. If the outcome of an act results in a benefit to the donor greater than that experienced by the recipient, then the behaviour is selfish. This type of behaviour is expected always to evolve. Co-operative behaviour, on the other hand, refers to acts which benefit both individuals but benefit recipients more. Consequently, the individual fitness of the recipient of a co-operative act is higher than the donor and the fitness of the donor is higher than an individual which never performs or receives a co-operative act. Wilson (1980) has termed this class of behaviour 'weakly altruistic'. Altruistic behaviour requires that the donor pay a cost which lowers its fitness below that of a non-interacting individual while providing a benefit to the recipient.

Altruistic and co-operative behaviours in bats

Until recently few people suspected that some bats perform co-operative or altruistic behaviours. The ultimate altruistic act, failing to reproduce in order to aid another individual, has not yet been docu-

mented in any bat species. One explanation, however, for the persistent presence of an adult-size, non-reproductive *Vampyrum spectrum* with an adult pair and nursing young (Vehrencamp et al. 1977; personal observations) is that the fourth individual is delaying its own reproduction to help provision the new offspring. Further research is needed on this and other apparently monogamous, family-living carnivorous bats (see, for example, Sazima 1978) to explain their social organization. The next most costly altruistic behaviour is providing another individual with nutrients which could be used to increase personal fitness. This category includes provisioning by regurgitation (Schmidt 1978, Mills 1980, Wilkinson 1984) or by exchange of prey items (Vehrencamp et al. 1977; personal observations of *V. spectrum*) and communal nursing (Brossett 1962, Watkins & Shump 1981, McCracken 1984). Other potentially altruistic behaviours include remaining at a roost with non-volant young while mothers feed (O'Farrell & Studier 1973), retrieval of fallen young (McCracken & Bradbury 1981) and mobbing a predator which has caught a conspecific (August 1979).

Potentially co-operative acts include constructing tents by chewing the midribs of broad-leaved tropical plants (reviewed by Kunz 1982), following previously successful foragers to locations where food can be found and forming dense roost aggregations in which individuals in the center of a cluster gain greater energetic savings by increased insulation than individuals on the periphery (Trune & Slobodchikoff 1978). The latter is suggested by observations indicating that aggregation lowers metabolic rate below that experienced by a solitary individual (Howell 1976). Foraging in cohesive flocks (see, for example, Bradbury & Vehrencamp 1976, Sazima & Sazima 1977, Howell 1979) may involve co-operation if foraging path overlap is reduced (Cody 1971). Finally, social grooming (Wilkinson 1986) may reduce the number of ectoparasites on a group member and thereby decrease the number of ectoparasites which could infect other members of the group, including the groomer. Social grooming is not considered altruism here because there is no evidence, at least from primate studies (Dunbar & Sharman 1984), that the groomer incurs any measurable cost.

Evolutionary models for altruism and co-operation

Traditional Darwinian natural selection makes an economic assessment of a trait's evolutionary value: will the trait increase in frequency when rare and persist despite attempted invasion by another trait and become an evolutionary stable strategy or ESS (Maynard Smith & Price 1973). According to this definition, altruistic and co-

operative behaviours present evolutionary dilemmas because both should be out-competed by selfish behaviour. The three evolutionary mechanisms – kin selection, group selection and reciprocity – which have been proposed to solve these dilemmas are discussed below.

Kin selection

In an important paper, Hamilton (1964) showed that altruism should evolve when

$$rB - C > 0, \qquad (2)$$

where r is the coefficient of relatedness. As Grafen (1984) points out, the great utility of Hamilton's rule (equation 2) lies in its ability to analyse the consequences of interactions between any two individuals rather than to analyse what will happen in a group of individuals.

Numerous population genetic models (see review by Michod 1982) have analysed the assumptions underlying Hamilton's rule. Although there are some situations – such as strong selection (i.e. large difference between C and B), inbreeding and overdominance – which affect the genetic basis of the behaviour, including quantitative inheritance (Yokoyama & Felsenstein 1978, Boyd & Richerson 1980, Aoki 1982, Engels 1983), and the form of the fitness function. Although much less work has examined the expected relation between C, B and r at equilibrium, some quantitative genetic models suggest that Hamilton's rule may still obtain (Boyd & Richerson 1980) or may need to be modified slightly such that $rB - 2C > 0$ (Engels 1983). In sum, the theoretical justification for use of kin selection to explain the evolution and persistence of altruistic and co-operative behaviour is overwhelming. Although this fact probably accounts for the frequent use of kin selection as a *post hoc* explanation for altruism, it does not exclude the possibility that other models may also operate.

Group selection

Since Wynne-Edwards' (1962) proposition that selection should act on traits affecting the survival and reproduction of groups rather than individuals, many people (see, for example, G.C. Williams 1966, Maynard Smith 1976) have argued that group selection is an unlikely force in evolution. Most theoreticians and field workers currently agree that differential extinction of groups is not important relative to individual selection except perhaps for the evolution of decreased virulency in

some parasites (Gilpin 1975). Models of group selection based on differential productivity of groups (see review by Wilson 1983), on the other hand, can favour co-operation if animals assort randomly after mating into groups with respect to their predisposition to behave co-operatively (Wilson 1977). Altruism, however, is only favoured under highly non-random dispersal (Charlesworth 1979). If assortative dispersal among unrelated animals is dismissed as being unlikely, this type of group selection becomes algebraically equivalent to a kin selection model where individuals dispense aid according to the average level of relatedness within the group (Wade 1980). Wade's kin-group selection differs from Hamilton's kin selection, though, in that it uses the average degree of relatedness within a group for accounting purposes. One would expect, then, random distribution of aid within the group. If there is variation in the degree of relatedness among group members and some way to identify close from distant relatives, Hamilton's rule predicts that altruism will be directed preferentially to close relatives.

Reciprocity

Trivers (1971) proposed reciprocity as an alternative to kin selection to account for co-operation and altruism among distantly related individuals. The paucity of convincing examples and presumed susceptibility to cheaters precluded acceptance of this idea until Axelrod & Hamilton (1981) demonstrated that once established in a population, reciprocity is an ESS. They envisioned tit-for-tat (TT) reciprocity in which a TT individual always co-operates with another individual on the first opportunity, but only continues to co-operate if that individual reciprocates. If the opportunity to be a donor and recipient reverses on each subsequent act, then for reciprocity to be advantageous, the probability w of being in a situation to behave co-operatively (or altruistically) must be sufficiently high such that

$$wB - C + wC > 0 \qquad (3)$$

(Axelrod and Hamilton 1981). Obviously, when $w = r$, reciprocity provides a greater benefit than kin selection. Since TT cannot increase in frequency when rare, Axelrod & Hamilton (1981) suggest that this behaviour might be favoured initially in kin groups. This idea suggests that kin selection and reciprocity may operate concurrently to favour the persistence of an altruistic or co-operative behaviour.

If the probability p that the donor-recipient identity will switch on the next opportunity for co-operation is not 1, then the required inequality becomes

$$wpB - C + wpC > 0 \qquad (4)$$

(Axelrod & Hamilton 1981). Schaeffer (1978) recognized that reciprocal food sharing will be favoured only when environmental variability creates a surplus for one individual (low cost) and a deficit in another (high benefit) at one point in time which subsequently reverses. A stable system of reciprocity will be favoured when this environmental oscillation is predictable yet unavoidable. The term w then depends not only on the likelihood of encountering the same individual in the future, but also on the probability that there will be an ecological need for an altruistic behaviour at that time. Consequently, reciprocity should be expected only for behaviours which occur frequently during the lifespan of all individuals.

Although reciprocity may occur within kin groups, it still can be detected when kin selection operates. As long as w is not perfectly correlated with r, reciprocity predicts that aid will be dispensed preferentially to individuals with relatively high values of w in addition to high values of r.

Testing the models

At least three levels of analysis can be used to assess these models of social evolution. First, one can discriminate between kin, kin-group and reciprocity selection by determining how aid is distributed within the group. If aid is dispensed at random, then a kin-group selection model is supported. If altruism is observed between individuals with relatively high values of w, reciprocity is supported, and if it occurs between pairs with high values of r, kin selection is implicated. Wilkinson (1984) used this approach to demonstrate that blood sharing among vampire bats can be explained only by the simultaneous operation of kin selection and reciprocity.

The second level of analysis estimates the relative selective importance of each mechanism in maintaining altruism. One can obtain this information by comparing the predictive abilities of the two variables, r and w. For blood sharing by vampire bats this comparison revealed equal predictive ability of the two variables. Alternatively, the relative importance of these two mechanisms can be obtained by estimating r and w and then comparing the quantities obtained from equations (2) and (4) after substitution while holding C and B constant.

The most rigorous analysis involves calculation of the intensity of selection on a given behaviour produced by each mechanism. This permits estimation of the direction, and sometimes the rate, of evolution and is discussed below. Although estimation of C and B for a given behaviour is not necessary to conduct the first two levels of

analysis, it is necessary for the third. Methods for estimating these parameters are discussed below.

Estimation of w

In most situations, some measure of the frequency with which two individuals interact in the recent past will provide an estimate of the probability that they will encounter each other in the future. The measure used will depend on whether the data consist of observations in a roost or while foraging and on where the behaviour in question occurs. Two indices of association based on roost census data and one based on radio-telemetry data of foraging are discussed by Wilkinson (1985a). To estimate w, an association index must vary between 0 and 1 and be weighted by the probability that one individual will be in need of aid and the other in a position to help. For the vampire bat this probability depends on the frequency with which individuals fail to obtain a blood meal. Since adults fail to feed on 7 % of all nights (Wilkinson 1984), the required weighting for two adults would be $0.93 \times 0.07 = 0.065$ while the weighting between an adult feeding a juvenile would be $0.93 \times 0.33 = 0.31$ since juveniles miss meals every third night.

To use equation (4), p must be estimated in addition to w. One estimate of p is the number of times an individual received a benefit divided by the number of times it donated aid. Unless many instances of altruistic aid are observed, p probably will have to be estimated by pooling individuals within an age/sex category. If there are too few data to estimate p reliably and there is no reason to expect asymmetry in the propensity to share, then p could be assigned a value of 1 until further information becomes available.

Estimation of r

To calculate r between a pair of individuals, sufficient genea- logical information must be available to estimate the coefficient of consanguinity,

$$f_{ij} = \sum_{x=1}^{k} (1/2)^{n_x+1} (1+f_x)$$ (5)

where individuals i and j share k common ancestors, n is the number of genealogical connections between them through common ancestor x and f_x is the inbreeding coefficient of each common ancestor. The coefficient of relatedness can then be calculated from equation (1). In some situations pedigrees can be reconstructed from genotypic inform- ation by excluding some pathways. Thompson (1976) presents the maximum likelihood procedures for such estimation.

If genealogical information is not available, an average within-group estimate of r can be calculated as a genotypic regression (Pamilo & Crozier 1982). This technique can be used when there are multiple alleles at a locus (Pamilo 1984), but only estimates obtained by averag- ing over several loci from at least five groups (Wilkinson & McCracken 1985) are accurate. When there is no inbreeding, the fixation index $F_{st} = f_{ij}$ (Pamilo & Crozier 1982) and equation (1) can be used to estimate r.

If no genetic information is available then average r can be estimated from demographic data by making certain assumptions about the struc- ture of the population and the mating system (Bertram 1976, Seger 1977, Murray 1985, Wade 1985). Murray (1985) has generalized Wright's island model of population structure to estimate average r within groups. A modified version of Murray's model is presented below to illustrate how variation in a few key demographic parameters can be expected to influence average r.

In the following equations, which apply to dioecious diploids with overlapping generations and migration, N_f refers to the number of reproductively active females within a group and N_m is the number of males which mate randomly with the N_f females. Unequal paternity is not permitted but has relatively small effects on r. Wade (1985) dis- cusses a similar model which allows unequal paternity. S_j and S_a are the annual survival probabilities for juveniles and adults, respectively, and m_m and m_f are the proportion of juveniles of each sex which leave the natal group before reaching sexual maturity. If N_f remains constant over time, then the number of young produced per year (L), the proportion of newborns which are female (R) and S_a specify S_j because the number of juvenile female recruited (N_{jf}) plus the number of adult females surviving (N_{af}) should equal N_f:

$$N_f = N_f L R S_j + N_f S_a.$$ (6)

Migration does not affect N_f since each group receives as many immi- grants as it loses emigrants. After rearrangement, equation (6) becomes

$$S_j = (1 - S_a)/L R.$$ (7)

Average r among adult females in a group can be found from equation (1) after calculating the adult female coefficient of consanguinity, f_{af}. This requires determining the juvenile female coefficient of consanguinity,

$$f_{jf} = (N_f + N_m)/[2N_f N_m (m_f + m_m)(4 - m_f - m_m) + N_f(1-m_m)^2(1+m_f)+N_m(1-m_f)^2(1+m_m)].$$ (8)

and the adult female inbreeding coefficient,

$$f_f = f_{fj}(1 - m_f)(1 - m_m). \qquad (9)$$

The adult female coefficient of consanguinity is then

$$f_{af} = \frac{(1-m_f)^2 \{f_{fj}N_f(N_f-1)(N_f-1)N_f(N_f-1) + 2N_{fj}N_{af}4N_f^2(N_f-1)\}}{1-[N_{af}(N_f-1)/N_f(N_f-1)]-N_{fj}N_{af}/N_f(N_f-1)+N_{fj}N_{af}/(N_f^2(N_f-1)]} \qquad (10)$$

The estimates of r obtained from equations (1) and (10) can be substituted into equation (2) to provide the criteria for testing kin-group selection. Figure 1 illustrates how multiple paternity affects r within a group in which all males disperse ($m_m = 1$), all females remain within the group ($m_f = 0$), annual fecundity is 1 offspring/female and the primary sex ratio is ½. Three relations can be noted from this figure. First, r decreases asymptotically with the size of the group even though females are philopatric. Second, multiple paternity appreciably lowers r only when complete harem dominance ($N_m = 1$) is compared to shared paternity between two or more males; this effect becomes more pronounced as group size increase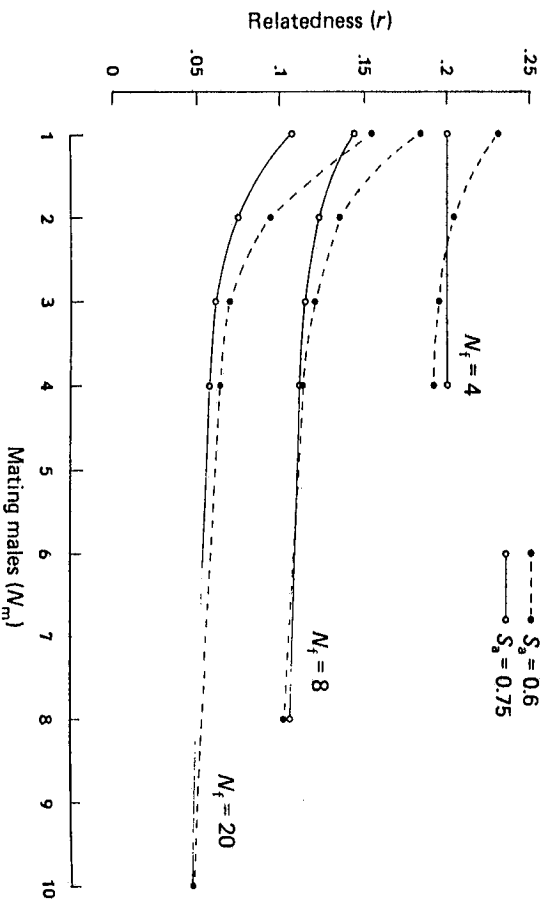s. And third, a decrease in adult female survivorship results in an increase in r. The third result appears counterintuitive until one realizes that a decrease in S_a causes an increase in S_j (equation 7) thereby allowing more female daughters to survive for recruitment into their natal groups.

The effect of female dispersal is shown in figure 2. As expected, increasing female dispersal lowers r until complete dispersal results in a group of unrelated females. The magnitude of the effect depends on the group size and adult survivorship as in figure 1. Retaining adult males rather than females within the group has a negligible effect on average r among adult females, although it can dramatically increase the average r among the juvenile cohort, particularly if few males mate.

Estimation of C and B

Recently, Cheverud (1985) and Wade (1985) proposed quantitative genetic methods for estimating the intensity of kin selection. They argue that the selection differential (a measure of the difference in some character, such as tendency to be altruistic, before and after a selection episode), as measured by the covariance between the phenotype and relative fitness, is the best way to estimate C and B. Altruism can be defined to occur whenever the selection differential between families S_b

Figure 1. Average within-group estimates of relatedness calculated by the island model (see text) as a function of the number of mating males. N_m, the number of females in each group; S_a, adult survivorship. All females remain in their natal group and have one offspring per year, and all males disperse.
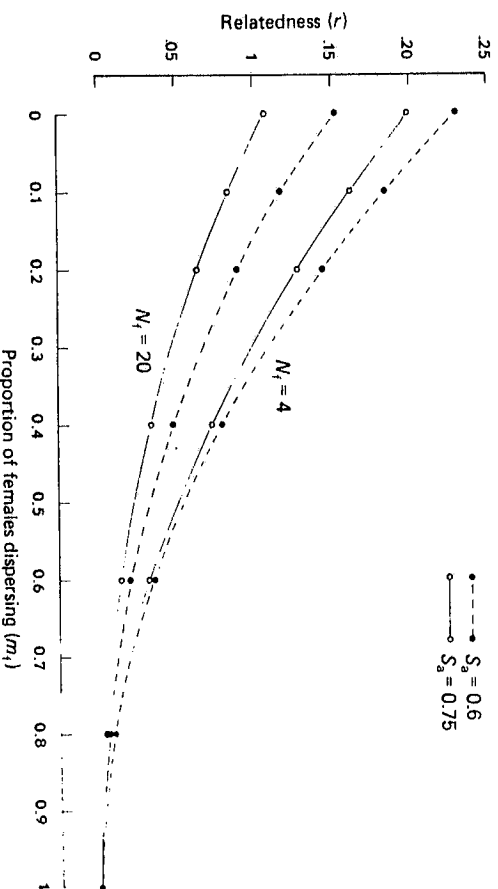

Figure 2. Average within-group estimates of relatedness calculated by the island model (see text) as a function of the proportion of females m_f, which disperse away from their natal group. Symbols as in figure 1. All males disperse and all females are mated by a single male.

is positive and the within family differential S_w is negative. Cheverud (1985) points out that for altruism to be favoured,

$$S_b h^2_b > |S_w h^2_w|,$$

(11)

where h^2_b and h^2_w are the between and within family heritabilities of the behaviour.

Cheverud (1985) discusses how to estimate S_b and S_w from regressions of total fitness on the phenotype. If total fitness cannot be calculated, then some component of fitness can be used although the results then pertain only to that component. This method provides the most rigorous test of models of social evolution. However, difficulties arise when individuals do not interact in discrete groups. Sometimes it may be possible to identify interacting sets of individuals within roosting groups (Wilkinson 1985a) and to use a measure of association to identify appropriate groups on which to make fitness comparisons. But to test the kin selection model rather than the kin-group selection model, group size should be reduced to two when performing the analysis. Reciprocity can be compared to kin selection by using equation (3) or (4) in combination with equation (11).

When total fitness or even a component of fitness cannot be estimated for the interactants, in some situations it may be possible to estimate a parameter which correlates with a component of fitness, and then use it to measure C and B. Wilkinson (1984) adopted this approach when analysing food sharing among vampire bats by estimating the number of hours remaining before starvation as a correlate of survivorship. Since vampire bats slow their metabolic rate as they approach starvation at a constant relative body weight, Wilkinson (1984) discovered that a donation of blood received a few hours before starvation will result in more hours gained than lost if the donor recently had fed.

Social behaviour and structure in phyllostomid bats

The results presented above suggest demographic situations in which kin-group selection should favour co-operative or altruistic behaviour. High cost altruistic behaviours should be found in those species which show little female dispersal and have relatively small groups and high juvenile survivorship (figure 2). Polygyny will favour altruism by kin selection further only if paternity is limited to a single male (figure 1). In this section I discuss what is known about the demography and social behaviour of five species of Neotropical phyllostomid bats in order to compare average r as estimated by Murray's model with the expression of co-operative and altruistic behaviours, thereby making an indirect test of the kin-group selection model (table 1).

Desmodus rotundus

The vampire bat *Desmodus rotundus* feeds exclusively on blood, most often that of domesticated mammals (Turner 1975). In north-western Costa Rica, groups of 8 to 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 neighbouring groups (figure 3). These groups form by restricted female dispersal; on average, one female transfers between groups every two years. In contrast, all juvenile males disperse three or more kilometres prior to attaining reproductive maturity (Wilkinson 1985b). The mating system is resource defence polygyny: adult males fight for access to the top of 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 seven variable enzymes reveal that maximum paternity of top males is less than 50 % (Wilkinson 1985b). Since top males are deposed, on average, every 1.5 years, female dispersal causes a relatively low average r within female groups. Pedigree analysis gave $r = 0.11$ (Wilkinson 1984) and $2F_{st} = 0.098$, and the genotypic regression gave $r = 0.02$ (Wilkinson 1985b). Given adult survivorship of 0.76 and one offspring per female every 10 months (Wilkinson 1985b), the island model predicts that $r = 0.104$ to 0.077, which is consistent with both the pedigree and F_{st} estimates of r. The low genotypic regression reflects how this method often underestimates r when few groups are used (Wilkinson & McCracken 1985).

Although communal nursing has been described for this species in captivity (Schmidt & Manske 1973, Mills 1980), all 42 banded pups nursed only from the known mother (Wilkinson 1985b). Provisioning by blood regurgitation, on the other hand, was observed on 110 occasions during 400 h of behavioural sampling. Seventy-seven of these observations involved a mother feeding her dependent offspring while 33 occurred between two adults or an adult and offspring. Regurgitations between bats other than mothers and their young did not occur at random but were distributed preferentially both to close relatives and individuals which had frequently shared a day roost in the past (Wilkinson 1984). These results, in conjunction with observations of reciprocal blood exchanges among captive unrelated roostmates, support reciprocity, in addition to kin selection, as an explanation for this altruistic behaviour (Wilkinson 1984).

Several lines of evidence suggest that individual *D. rotundus* exchange information about the location of preferred hosts. Small female-biased groups of two to four bats often leave a roost together (Wilkinson
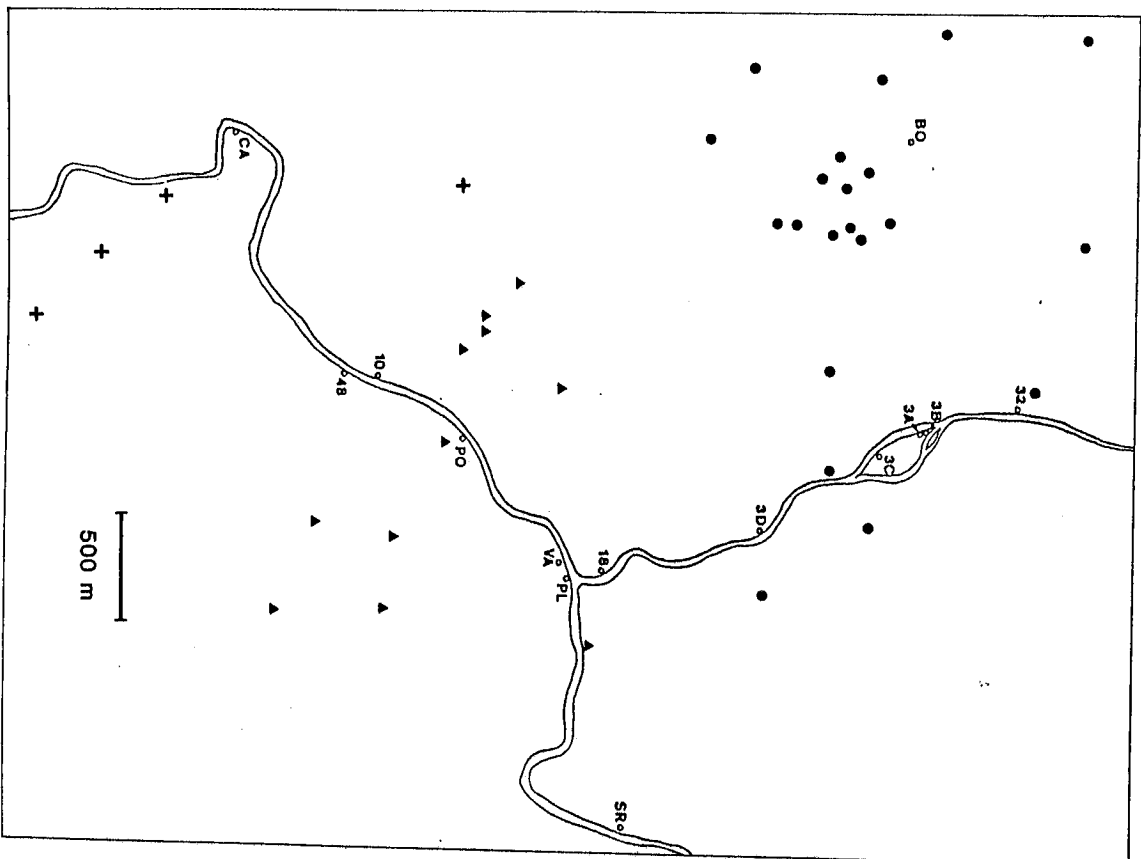

Figure 3. Geometric activity centers of 36 radio-tagged vampire bats at the La Pacifica study site, Costa Rica. Each point represents a minimum of 3 nights of triangulations taken at 10 min intervals during only the time each bat was outside its roost. ○, Roosts; activity centers for: ●, the UP group; ▲, the MD group; +, the DN group.

Table 1. *Summary of demographic data and estimates of relatedness.*

species	N_f	N_m	m_f	S_a	S_j	L	r
Desmodus rotundus	8–12	3	0.05	0.76	0.48	1	0.104–0.077
Phyllostomus hastatus	7–25	1	0.20?	0.84	0.32	1	0.82–0.045
Phyllostomus discolor	2–15	1?	0.5?	0.75?	0.25	2	0.083–0.019
Carollia perspicillata	2–18	2?	0.58	0.79	0.30	2	0.058–0.010
Artibeus jamaicensis	3–14	1?	0.97	0.60	0.40	2	0.0002–0

1985a), and groups of two to six bats arrive at a corral and circle prey before feeding (Greenhall, Schmidt & Lopez-Forment 1971; personal observations). Most direct observations of bats feeding on prey suggest that solitary feeding or occasional simultaneous feeding by a mother and her recent young (Wilkinson 1985a) is the rule; however, observations of up to seven bats feeding sequentially from a single wound (Greenhall *et al.* 1971, Young 1971) suggest that occasionally some individuals obtain a blood meal without taking the time (up to 40 min) to make a wound (Greenhall 1972). The relatively high incidence of failed feeding attempts (see above) attests to the difficulty involved in obtaining a blood meal. Not all bats share a wound site, however, since most interactions between bats on prey are agonistic involving audible vocalizations, lunges and chases (Greenhall *et al.* 1971, Wilkinson 1985a).

These observations suggest that vampire bats may share wound sites with kin or roost-mates although the small amount of overlap in utilized foraging range between most group members implies that this behaviour probably occurs infrequently (Wilkinson 1985a). One interpretation of these results and of figure 3 is that female groups form to defend preferred feeding areas from other groups. Further study of this aspect of the social behaviour of *D. rotundus* is certainly warranted.

Social grooming occupies, on average, 5 % of adult female roosting time. Both close kin and frequent roost-mates groom each other preferentially even when mother-infant pairs are excluded (Wilkinson 1986). The rate of social grooming is independent of roosting site while self-grooming rate varies significantly with roost identity. Since ectoparasitic bat fly densities are known to vary between roosts (M.L. Higgins & G.S. Wilkinson unpublished observations), self – but not social – grooming probably occurs in response to bat fly infestations. Rather than control ectoparasites, social grooming may function to identify future aid-giving partners and/or to monitor the potential for giving or receiving blood. In support of this proposition, social grooming occurs more often than expected before but not after food sharing episodes and correlates with

regurgitation frequency (Wilkinson 1986). Since much social grooming occurs near a partner's stomach and these bats can fill their highly distensible stomach with their body mass (30–35 g) in blood (Wimsatt 1969), social grooming may provide a method for assessing the recent feeding history of roostmates. Social grooming, therefore, could facilitate identification of cheaters, a necessary requirement for a stable reciprocity system.

Phyllostomus hastatus

In contrast to *D. rotundus*, all female *P. hastatus* leave their natal groups and disperse shortly after weaning. Each year, female young disperse from several different roosting clusters to form new groups. Single males defend these stable groups of 7 to 25 equal-aged females for up to 3 years and usually father most, if not all, of their synchronously produced young each year (McCracken & Bradbury 1977, 1981). Electrophoretic analysis of five blood enzymes provides a genotypic regression estimate of $r = 0.037$ and $2F_{st} = 0.062$ (McCracken this volume). The most plausible explanation for this nonrandom structure is that female half-sibs occasionally disperse together to form a new group. Although G.F. McCracken (personal communication) never observed two marked half-sibs in the same cluster, he resighted few (less than 5 %) dispersing females. The genotype data do not support the alternative explanation of occasional inbreeding due either to sister-brother or mother-son matings. To obtain $r = 0.05$ by using the island model with $N_f = 20$, $S_a = 0.84$ and $L = 1$, only 20 % of a group's female offspring should end up in different groups. To keep population size constant, $S_j = 32$ % from equation (7), which means that only three female offspring will survive from each cluster to disperse together.

These computations suggest that roosting clusters of *P. hastatus* may contain several subgroups of two to four half-sisters. Unfortunately, little quantitative information on the social behaviour of this species is available to relate to this inference. In contrast to earlier reports (McCracken & Bradbury 1981), recent observations made using a night vision scope of marked individuals within caves have revealed that one to four week-old young occasionally nurse from more than one female and that adult females frequently groom cluster-mates (personal observations). Young also licked the mouths of their mothers to obtain fluid, but food sharing was never observed between mothers and non-young, and it could not be induced between two adult female cluster-mates, one of which had been starved previously (J.W. Bradbury personal communication).

Considerable evidence suggest that these 90–100 g omnivorous bats sometimes aggregate at rich food sites. During most of the year, individual females maintain exclusive foraging areas which adjoin the foraging areas of cluster-mates (McCracken & Bradbury 1981). Occasionally, though, radio-tagged females have been observed to congregate at a single site (McCracken & Bradbury 1981). Although much of this species' diet is comprised of sequentially ripening fruit such as *Cecropia peltata* (Fleming 1982), swarms of alate leaf cutter ants, *Atta cephalotes*, and flowering *Hymenaea* trees provide temporary rich food sources that may favour co-operative foraging (McCrcken & Bradbury 1981). Furthermore, Bloedel (1955) reports a group of 30 *P. hastatus* feeding on swarming termites, and Goodwin & Greenhall (1961) describe feeding on the aril of sapucaia nuts (*Lecythis zabucajo*) while making loud, audible vocalizations. These relatively low frequency sounds may be used to advertise the location of rich food sources. The size of these flocks suggests that if this behaviour is an example of co-operation, then kin selection cannot provide a sufficient explanation. However, kin selection may prove important in understanding the occurrence of communal nursing and social grooming in this animal.

Phyllostomus discolor

Little information on the demography of this species is available. It is included here because of evidence which suggests that this 45 g, primarily nectarivorous bat performs several types of co-operative behaviour. This bat forms groups of 2 to 15 adult females which are actively defended by single males (Bradbury 1977a). Five to ten such groups can be found in a roost, such as a hollow tree (personal observations), and sometimes entire colonies switch roosts (Bradbury 1977a; personal observations). *P. discolor* often forages in flocks of 2–12 bats around flowering trees (Heithaus, Opler & Baker 1974; Sazima & Sazima 1977). Typically, two to six bats fly in single file, each bat occasionally drinking from, and often draining, a flower which is never visited subsequently (Heithaus et al. 1974; personal observations). Such groups spend 5–15 min at a tree, disappear for an hour or more, and then return to feed from that tree again (Heithaus et al. 1974; personal observations). Simultaneous radio-tracking of 10 *P. discolor* (8 males and 2 females) from one colony in Costa Rica during January 1983 revealed that females forage nonrandomly (personal observations). The two radio-tagged adult females flew together over a 20 km circuit and visited seven flowering trees on at least three successive nights. At one

particularly large balsa tree (*Ochroma lagopus*), we used a night vision scope and infra-red light to observe the two radio-tagged females and 4 unmarked *P. discolor* visit flowers while flying in single file.

Hungry males presented with the task of finding one out of 16 cups containing accessible food in a large flight cage make fewer exploratory flights and locate the food in less time if an experienced bat is present. The gain in time is further decreased, although not significantly so, if two experienced bats are present (D. Bolger unpublished results). These observations indicate that individual *P. discolor* learn the location of food from other bats but do not reveal how they acquire that information. Communal nursing and provisioning have not been described in this species, but no systematic observations have yet been conducted on marked animals. Females within groups frequently groom each other (personal observations). Given the potential for stable female groups which may or may not contain relatives and obviously complex foraging interactions, this species will undoubtedly prove fascinating to study in greater detail.

Carollia perspicillata

Adult females of this 20 g frugivorous species form groups which vary in size from 2 to 18 individuals in caves and hollow trees in northwestern Costa Rica (Williams 1986) Groups of two to four adult females have been observed in captivity (Porter 1979). In both captive and wild populations, adult females frequently move between clusters (Porter 1979, Williams 1986); in the wild each female moves, on average, between 3.8 clusters every 6 months but spends 62 % of its time in one group (Williams 1986). Although these bats move from a cave roost to hollow trees during the dry season in Costa Rica, 58 % of the individuals in a particular cluster return 2 to 4 years later (T.H. Fleming personal communication). These clusters occupy areas on the cave ceiling which are actively defended by adult males, sometimes for 4 years (T.H. Fleming personal communication). In captivity, adult females become more site faithful from birth to weaning (Porter & McCracken 1983). Although this behaviour may increase the chance that a harem male will impregnate his females after the March/April birth peak owing to a post-partum oestrus, to father all of a female's young each year a harem male must also copulate with that female during the October/November oestrus, well after the July/August birth peak (Porter & McCracken 1983). Paternity exclusion analysis with five variable enzyme systems indicates that harem male reproductive control is not complete; some females have young with genotypes incompatible

with the harem male (Porter & McCracken 1983). Although few data are available, 58 % of yearling females return to their natal cave (Williams 1986). If all of these females joined their natal groups, r is between 0.058 and 0.010, given $S_a = 0.79$, $R = 0.35$ (T.H. Fleming personal communication) and $N_m = 2$.

Neither low values of r nor unstable female groups favour co-operation or altruism. Although communal nursing has been observed a few times it is extremely rare (Williams 1986). Provisioning and allogrooming have not been observed despite extensive observations on captive and wild animals in roosts. Radio-telemetry, mist-netting and baiting with fruits all indicate that these bats prefer fruits that are regularly distributed and reliably produced (Fleming, Heithaus & Sawyer 1977; Heithaus & Fleming 1978; Fleming 1982). Bachelor males and females visit two to six feeding areas every night, independent of weather or moon condition (Heithaus & Fleming 1978) and females from the same cluster forage independently of each other and the harem male (Fleming 1982). Thus, there is no evidence that these bats share information or co-operate in any other way while foraging. Although Porter (1979) suggests that harem males behave paternally by guarding offspring, a more parsimonious explanation for this behaviour is male defence of the female cluster area.

Artibeus jamaicensis

Adult female *A. jamaicensis* form groups of 3 to 14 individuals in tree hollows (Morrison 1979) or solution cavities in caves (Kunz, August & Burnett 1983) while solitary non-harem males occupy foliage roosts (Morrison 1979). Non-harem male groups also occur in caves (Kunz *et al.* 1983). The mean group size in caves and trees is about six adult females (Morrison 1979, Kunz *et al.* 1983). In Panama, only one of 31 marked juveniles was ever captured as an adult in her natal group (Morrison 1987). Dispersing females join existing groups rather than establish new groups as in *P. hastatus* (Morrison 1987). The probability of recapturing an adult female at a roost is 53 % (D.W. Morrison personal communication). Single males defend tree hollows from other males at the time of parturition (Morrison & Morrison 1981) presumably to mate with the resident females during their biannual post-partum oestrus (Fleming 1971). The reproductive success of these harem male is unknown; however, female roosts never contain more than a single male (Morrison 1979, 1987). so complete reproductive control is possible. With $S_a = 0.6$ (Morrison 1979) and the parameters mentioned above. the island model predicts $r = 0.0006$ to 0.

There are no published descriptions of interactions within day roosts, so whether communal nursing, provisioning or allogrooming occur in the wild is unknown. Extensive radio-telemetry studies indicate, though, that these bats never form flocks while foraging. In all study locations (Heithaus, Fleming & Opler 1975; Morrison 1978a; August 1981), figs are the primary, if not only, food eaten by this bat. Although many *A. jamaicensis* often feed in a fruiting fig on a given night, each bat arrives and departs independently (Morrison 1978a). Furthermore, captive females do not groom each other (E. Mayrand personal communication). The only potentially altruistic or co-operative behaviour which these bats are known to perform is mobbing in response to distress calls given by a captured individual (August 1979). Predation is undoubtedly a strong selective force on the behaviour of this 50 g species since individuals avoid flying during the moonlit portion of the night and carry figs away from a fruiting tree to a feeding roost (Morrison 1978b). Barn owls (Wetmore & Swales 1931) and opossums (Morrison 1978b) are known predators. Given the absence of association between cluster-mates while foraging, it would be very surprising if this behaviour involved a substantial cost to the mobbing individual.

Conclusions

The data described in the previous section show that the behaviours with the highest costs, communal nursing and provisioning, occur in those bats, *D. rotundus* and *P. hastatus*, with different levels of relatedness but similar stabilities of group membership. Those species which form female groups with low average r and relatively low compositional stability (*C. perspicillata* and *A. jamaicensis*) exhibit virtually no altruistic or co-operative behaviours. What little data are available suggest that *P. discolor* may be intermediate in expression of costly behaviours. Whether female groups in this species are also intermediate in average r and stability of association must await further study. Since average r within a group of bats will always be less than some of the pairwise values of r, it is unlikely that average r will be sufficiently large to favour high cost behaviours by kin-group selection. Consequently, kin selection and reciprocity are more plausible explanations for the social behaviour of *P. hastatus* than kin-group selection. Furthermore, given the established potential of some of these bats to discriminate individuals (Schmidt 1972, Rother & Schmidt 1985), kin-group selection is an unlikely explanation for co-operation or altruism in any of these species. Unfortunately, data indicative of discrimination between kin selection and reciprocity are only available for the vampire bat. The

strong evidence for reciprocity in this species and the apparent similarity within the stability of female groups between vampire bats and *P. hastatus* further support reciprocity as a likely explanation for co-operation in the latter species.

This review has indicated some potentially rewarding research possibilities on bat social behaviour. Determination of how aid is distributed among group members in other species is of the utmost importance for deciding if reciprocity is limited to a few special cases or is indeed a common force in the evolution of social behaviour. Although this review focused on five phyllostomid bats, other species, such as those that are carnivorous and could therefore provide substantial nutrients by provisioning, should not be overlooked. The next stage in the quantitative evaluation of social evolution models will almost certainly entail estimation of the selection intensities caused by kin selection and reciprocity. The survey of the available information presented here should illustrate that in many respects, bats present useful systems for attempting such work. Some species, such as *D. rotundus* breed readily in captivity and, therefore, even present the opportunity for estimating the heritability of some behaviours. Given the obvious potential of this work, I am certain that future research on interactions between bats will continue to provide important information about how social behaviour is shaped by evolution.

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