

Selection on social traits in greater spear-nosed bats, *Phyllostomus hastatus*

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Abstract Many studies assume that selection molds social traits and have investigated the manner in which this occurs, yet very few studies have measured the strength of selection on social traits in natural populations. In this paper, I report results of phenotypic selection analyses on two social traits – the size of social groups and the frequency of group foraging – in *Phyllostomus hastatus*, the greater spear-nosed bat. I found significant positive directional selection on individual group foraging frequency, but no directional selection on individuals in different-sized social groups. These results have implications for the structure of social groups, cooperative behavior among group mates, and maternal investment strategies. I argue that combining studies of natural selection on wild populations with experiments to identify the agents and mechanisms of selection can do much to increase our understanding of social evolution.

Keywords Social evolution · Selection analysis · Reproductive success · Group foraging · Group size

Introduction

Female social groups are common among mammals and typically are composed of related individuals (e.g., Wrangham 1982; Sterck et al. 1997; Gompper et al. 1998; Spong et al. 2002). The evolution of such matrilineal social structure frequently depends, at least in part, on kin selection. Kin selection theory (Hamilton 1964a,b) has been enormously successful at explaining variation in sociality and cooperation among relatives (reviewed in Bourke and Franks 1995; Reeve and Keller 1996; Frank 1998). However, kin selection is not always a sufficient explanation (Cockburn 1998; Clutton-Brock 2002; Griffin and West 2002; West et al. 2002; Sachs et al. 2004) and is unlikely to contribute significantly to cooperation, stable social groups, and social evolution in taxa where groups are not formed of close relatives.

Finding that the female greater spear-nosed bats, *Phyllostomus hastatus*, live in stable social groups is in keeping with the common mammalian pattern of female-based societies. However, in contrast to the common pattern, the average relatedness among females within groups is near zero (McCracken and Bradbury 1977, 1981; McCracken 1987). Low relatedness values result, in part, because all offspring disperse from their natal group. Matrilineal social structure, thus, has no chance to develop. Given the low relatedness within stable social groups, this social structure is not likely to be maintained by kin selection. Low average colony relatedness has been found for several other bat species (Burland et al. 2001; Burland and Wilmer 2001; Kerth et al. 2002; Rossiter et al. 2002), some of whom also live in stable groups (Kerth et al. 2002). Such groups appear to consist of multiple related pairs (mother and offspring or siblings). Despite low average relatedness, kin selection could be important in these

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species if individuals recognize kin and preferentially direct cooperative behavior towards them. There is no evidence that greater spear-nosed bats do this (McCracken and Bradbury 1981; Porter and Wilkinson 2001; Boughman JW and Wilkinson GS, unpublished).

Group living in this species is instead likely to depend on the ratio of benefits and costs that accrue independently of relatedness (Connor 1995a,b; Clutton-Brock 2002; Johnson et al. 2002). These benefits can include improved foraging (Caraco 1980, 1981; Clark and Mangel 1984, 1986; Ranta et al. 1993; Beauchamp and Fernandez-Juricic 2005), improved defense of limiting resources (Cheney 1981; Emlen 1991; Jerome et al. 1998; Dubois and Giraldeau 2003; Dubois et al. 2003; Vucetich et al. 2004), or decreased predation risk (Lima and Dill 1990), and all these benefits can add up to higher offspring production (Stacey and Koenig 1990; Woolfenden and Fitzpatrick 1990; Clutton-Brock et al. 2001). However, in many species, the potential benefits of sociality may be offset by costs (Griffin and West 2002). Groups are not entirely cooperative entities. Dominant individuals can impose costs on subordinates by reducing access to food and suppressing reproduction (Caraco 1980; Barnard and Sibly 1981; Schneider 1984; Armitage 1986; Caraco et al. 1989; Caraco and Giraldeau 1991; Rood 1990; Sherman et al. 1991; Creel and Macdonald 1995; Kutsukake and Clutton-Brock 2006). Competition among group mates for resources and breeding opportunities can be fierce (West et al. 2002). In addition to these subtle tug-of-wars, high-density living can enhance the transmission of disease and parasites (Brown and Brown 1996, 2004).

Simply put, we expect sociality to evolve when the benefits exceed the costs. However, estimating the strength of selection via the above mechanisms and identifying the specific ecological conditions that promote sociality is not a simple task. One way to do this is to estimate selection acting on social traits using the classic methods of selection theory, which measures the covariance between a trait and fitness (Lande and Arnold 1983; Arnold and Wade 1984). These methods have a rich history in evolutionary biology (reviewed in Endler 1986; Wade and Kalisz 1990; Kingsolver et al. 2001) and are considered a powerful approach to measure the way that natural selection acts in natural populations. This approach is useful because selection can act in complex ways. Selection can be directional – either increasing or decreasing a trait, or stabilizing – resulting in an optimum value. Selection can also change trait values either directly via various selection agents or indirectly via correlation with other traits. Thus, estimating selection on a target trait helps to reveal whether selection is acting at all, and if so, whether it is positive, negative, or stabilizing. Another contribution of selection analysis is to quantitatively translate measured

benefits and costs into the common currency of fitness. In many studies of social behavior, benefits and costs are hard to equate because they are in different currencies (e.g., energy gain vs predation risk).

Very little research on social evolution has measured selection acting on social traits using selection theory until recently (but see Wolf 2003, for a review). Most studies of social evolution have used the methods of behavioral ecology, measuring specific benefits and costs and correlating these with variation in group size or structure, or developing and testing optimality models (e.g., Packer et al. 1990; Higashi and Yamamura 1993; Bourke and Franks 1995; Brown and Brown 1996). These studies provide important insight into the nature of benefits and costs and identify potential selective agents that act to create selection. They have done much to clarify social evolution. Even so, they do not provide a complete picture.

Combining approaches can be powerful (Moore and Boake 1994; Carriere and Roitberg 1996). We can use behavioral ecology methods to measure specific costs and benefits of particular traits and identify the agents that impose selection, and use selection theory to determine how these combine to create selection on the traits. The two approaches are complimentary; taken together, a more complete picture of how social traits are shaped by selection is likely to emerge. This is, in part, because behavioral ecology explores the action of selection differently than selection theory. Behavioral ecology focuses on the adaptive value of traits whereas selection theory focuses on the strength and form of selection (Grafen 1988). We are often interested in both aspects.

In this paper, I study selection on two social traits—the size of social groups and group foraging by social group members. Selection on group size could take several forms. Many studies expect there to be an optimal group size; however, it has been noted that optimal group size may be unstable (Sibly 1983; Giraldeau 1988; Giraldeau and Caraco 2000). This is because solitary individuals can increase their fitness by joining a group; thus, the evolutionarily stable group size should be the size at which fitness is equal for solitaries and group members (reviewed in Giraldeau and Caraco 2000). At this size, individuals will have lower fitness than they would at the optimal size. Therefore, group members should be selected to deter solitaries from joining. An important determinant of whether groups are at the optimal or stable size is the extent of outsider vs insider control over group membership (Higashi and Yamamura 1993). That is, whether solitaries are free to join groups (outsider control) or group members restrict such joining (insider control). Stable group sizes are expected with outsider control and

optimal group sizes with insider control. In either case, individuals in groups closer to the optimum should have higher average fitness than individuals in groups at the stable size; thus, variation in group size may have fitness consequences.

Selection on group foraging could also take several forms. Many studies expect that group foraging should improve food finding or defense (Howell 1979; Clark and Mangel 1984, 1986; Brown and Brown 1996; Laland et al. 1996). However, food sharing and increased competition between group members over access to food may lower food intake (Ranta et al. 1993). Thus, group foraging could either increase or decrease fitness.

This study's objective was to use selection theory to estimate the strength of natural selection on social traits in the greater spear-nosed bat, *P. hastatus*. Good information is available from previous studies on social structure and on the potential benefits and costs to group living. Female greater spear-nosed bats live in stable social groups of about 18 unrelated adults (McCracken and Bradbury 1977, 1981). Group membership appears to be obligatory as adults of both sexes are never observed roosting alone. Colonies consist of between 4 and 40 stable female groups and several more transient 'bachelor' male groups (McCracken and Bradbury 1981). Female bats both acquire and defend food resources in groups. Females forage with one to five group mates on many resources (Wilkinson and Boughman 1998) and with larger groups on extremely concentrated resources such as large fruiting trees (Greenhall 1965). Foraging in groups reduces search time when food is patchily distributed (Wilkinson and Boughman 1999) and may improve the ability to defend resources against conspecific competitors (Wilkinson and Boughman 1998, 1999). We have successfully used to date a behavioral ecology approach to investigate potential benefits and costs to group living in greater spear-nosed bats. The benefits we have measured are direct and immediate, but we do not currently know whether variation in group foraging or group size has fitness consequences. This paper aims to fill that gap.

In this paper, I test current selection on group living by measuring the fitness effects of variation in group size and group foraging. I measure two fitness correlates that estimate offspring production: the probability of pup survival to independence and the condition of pups at independence. I use these measures because juvenile condition correlates with first-year survival in many mammals (Festa-Bianchet et al. 1997; Loison et al. 1999; Cote and Festa-Bianchet 2001) and in birds (Potti et al. 2002) and can affect reproductive value (Clutton-Brock and Godfray 1991). I take this approach to investigate the nature of selection acting on group foraging behavior and social group size.

Materials and methods

Study species

I studied *P. hastatus* in Guanapo Cave, Trinidad, West Indies. In Trinidad, many female greater spear-nosed bats begin to reproduce at 2 years of age and nearly all females attempt reproduction by age 3 years. Banding records indicate very low adult mortality and females can live more than 20 years in the wild (McCracken and Bradbury 1981; McCracken et al., unpublished). The details of group formation are not well understood. Group mates synchronize parturition (Porter and Wilkinson 2001). Females give birth to a single young at the beginning of the rainy season and nurse these pups for about 70 days. Pups begin to fly at 45 to 50 days, and by 55 to 60 days they begin to forage on their own (Stern et al. 1997). Approximately 40% of juveniles do not survive to independence (Stern 1996). Juveniles are preyed upon by opossum (*Didelphis virginiana*), tegu lizard (*Tupinambis teguixin*), bullfrog (*Rana catesbeiana*), and screech owl (*Otus choliba*) (personal observation). Pups sometimes fall from the cave ceiling and, if not retrieved, they die. Other sources of mortality are not directly known, but pups who looked starved or with extremely heavy parasite infestations have been observed. Observational work suggests that group mates share offspring care by protecting pups against predators (personal observation).

Food competition among adult group members appears to be weak when resources are divisible, as several group mates routinely fed on the same food items during foraging experiments with no aggression (Wilkinson and Boughman 1999). However, prized and indivisible food such as large-bodied beetles can be hotly contested (personal observation). Competition between groups is more intense, as resident females will repel intruders (Wilkinson and Boughman 1999; Boughman JW, unpublished).

Group captures

I captured bats at three different times during lactation: (1) the first 10 days after birth (mean pup age at capture in 1994=9 days; in 1995=3 days), (2) before pups began flying (mean pup age at capture in 1994=31 days; in 1995=27 days), and (3) before pups were fully weaned and independent (mean pup age at capture in 1994=67 days; in 1995=53 days). These times were chosen to include the period of highest pup mortality, which occurs when pups begin to fly or become volant (Stern 1996).

I conducted nightly visual censuses in Guanapo cave from April 1 to 23 in 1994 and April 6 to 28 in 1995, noting new pups and maternal identity. During the first week after birth, I caught pups at night when adults

were out foraging. This caused minimal disturbance but did not allow me to verify maternal identity. I caught entire social groups during the day by encircling the group with a bucket and gently dislodging bats. These captures enabled me to identify mother–pup pairs and to collect data on group size and maternal condition. I calculated maternal condition with data from these early captures and not later captures, as maternal condition is expected to change throughout lactation. I re-captured groups before pups began to fly (i.e., pre-volancy) and before weaning.

At each capture, I collected data on group identity and group size. I sexed bats, assessed female reproductive status, weighed bats to the nearest 0.1 g, and measured forearm length to the nearest 0.02 mm. Forearm length is highly repeatable and correlates strongly with overall body size and pup age (Stern 1996). I estimated adult age class by the extent of toothwear on a scale of 1 to 5 (McCracken and Bradbury 1981; Wilkinson and Boughman 1998). A score of 1 corresponds to 1 to 3 years; 5 corresponds to at least 12 years of age. I also counted the number of ectoparasitic streblid flies (*Trichobius* spp. and *Euctenodes mirabilis*) on adults and pups. All bats were individually marked with a numbered metal band placed on their forearm. Group identity was indicated by a second metal band covered with colored reflective Scotchlite (3M) tape. This enabled me to track bats as they moved throughout the cave. All bats were released at the point of capture within 2 h.

I calculated condition as the residuals from a regression of body weight on forearm length. I calculated relative condition for pups by dividing a pup's absolute condition by the average for its sex in the year it was caught. I used sex-specific condition because size dimorphism appears early in pup growth (Kunz and Stern 1995). I assessed mortality through direct observation of dead pups and also considered a pup dead if it disappeared before volancy when the pup's mother remained in the group. After pups became volant, they were more likely to leave the roost group temporarily, so I conducted visual censuses of marked bats not roosting with their natal group. If pups were not located during these censuses, I considered them to be dead and in no case were these pups resighted. Dispersal between caves is rare and likely occurs when juveniles are somewhat older; therefore, these missing pups had probably not dispersed. Over 10 years of banding nearly 3,000 individuals, we have only eight records of bats dispersing between colonies, although McCracken and Bradbury (1981) report several dispersal events between caves of yearling females. This amount of dispersal appears to be sufficient to prevent significant genetic structuring among caves (McCracken 1987).

Group foraging

A number of previous studies report that *P. hastatus* forage in groups, primarily on rich and patchy food resources. These studies include observations of groups departing from caves and traveling towards feeding areas (Goodwin and Greenhall 1961), observations of groups at food trees (Greenhall 1965; McCracken and Bradbury 1981), and radio tracking where social group mates joined together on feeding areas (McCracken and Bradbury 1981). Our previous work showed that foraging groups are often composed of females from the same social group (Wilkinson and Boughman 1998, 1999). To investigate foraging group composition, we used infrared (IR) video focused outside the cave entrance to record bats departing from and returning to the cave. We then used bout analysis to test for clustering. Bout analysis uses nonlinear regression to test for clustered departures and returns by determining whether the frequency of intervals between events is linear (no clustering) or nonlinear (significant clustering) (Sibly et al. 1990). If significant clustering is found, it then estimates the interval corresponding to clustered events. Our earlier data showed that bats departed from and returned to the cave in twos and threes, and that 30 s is the interval for paired departures and returns (Wilkinson and Boughman 1998). We investigated next the composition of these groups by attaching differently colored light-emitting diodes (LEDs) and reflective Scotchlite (3M) bands to all females from six groups. We then monitored roosting groups inside the cave using IR video to determine when females departed or returned with group mates, using the 30-s interval estimated by bout analysis as our criterion for paired departures and returns, and found 26% of LED-marked females departed together. We combined these data with observations at the cave entrance of LED-marked bats departing, circling, and returning to the cave. Those observations found that females from the same group were together significantly more often than expected by chance and estimated that 24% of females depart with group mates on first foraging flights while 40% of females do so on subsequent flights (Wilkinson and Boughman 1998). To verify that females leaving the cave with group mates actually forage together, we used mist nets to catch bats at feeding sites and found that 26% of females were captured with one or more group mates (Wilkinson and Boughman 1998). There are additional unpublished radio tracking data that corroborate these findings (Wilkinson GS, unpublished). The estimated proportion of females seen with group mates is approximately equal with all our methods, suggesting that these methods are measuring the same thing.

For this study, I estimated how often individuals foraged in groups by using an IR video camera to

monitor paired departures of marked females from each group's roost site inside Guanapo cave. When capturing entire social groups, I marked females individually by bleach-marking distinctive and unique patterns on their shoulders that were visible under IR illumination. I used bleach marks because they last longer than LEDs or Scotchlite bands. A Javelin CCD camera (model JE-7362) fitted with a 16-mm lens generated the image under IR illumination provided by a covering a headlamp with a Kodak Wratten 87 gel filter. I recorded onto a portable Panasonic video recorder (model AG-1200) driven by a 12-V car battery. I videotaped groups for approximately 6 h on each of five to seven nights per group. These tapes were later scored to determine the identity of individuals, age class, and the number of single and paired departures from and returns to the roost site. I considered two bats to be together if they left the roost within 30 s, based on our earlier bout analysis (Wilkinson and Boughman 1998). I feel confident that estimating group foraging proportion with paired departures using IR video of marked females in roosting groups gives an unbiased estimate of actual group foraging, based on the similarity of estimates using multiple methods. Throughout the paper, the term 'group foraging' refers to such paired departures.

I obtained data on condition and mortality for 273 pups and their mothers from 20 social groups and group foraging data on 13 of these social groups. I analyzed group means because values for individuals within social groups are not entirely independent and the two social traits cannot be measured on individuals. Group size and frequency of group foraging are traits that emerge from the phenotypes of individuals within groups who may vary in their tendency to forage with others or in their joining behavior. The analysis estimates average selection on the females in each group. In essence, it asks, what is the average effect of being in a social group of this composition? I do not intend an analysis of group selection and do not compare selection within and between groups because the focus is on the fitness consequences to individuals of their own and group mates' behavior. Although I endeavor to measure many traits, there may be other unmeasured sources of selection that could strengthen or oppose the selection measured here. This is a potential problem with selection studies (Mitchell-Olds and Shaw 1987). The results must be interpreted cautiously in light of this. The data estimate reproductive success in 2 years and, therefore, are a snapshot of how social traits can affect fitness in this long-lived species. Few studies of long-lived taxa measure lifetime reproductive success, and these studies are primarily of closed populations (reviewed in Clutton-Brock 1988).

Analysis

I analyzed data with the classic methods of selection analysis. I described the distribution of phenotypes and fitness by calculating trait means and standard deviations for each social group. Opportunity for selection (I) is the variance in relative fitness based on these values (Arnold and Wade 1984). Phenotypic correlations among measured traits and fitness components are basic information in studies of the strength and form of natural selection. I calculated Pearson correlation coefficients for all traits.

I estimated standardized selection differentials by calculating the covariance between the standardized trait and the fitness correlates measured on individuals and averaged for each group (Lande and Arnold 1983; Phillips and Arnold 1989). Standardized differentials were considered nonzero if the Pearson correlation coefficient was significantly different from zero. Selection differentials estimate the extent to which fitness is correlated with each trait and include both direct selection on the trait and indirect selection through traits correlated with the target trait. Thus, they indicate the net strength of selection but provide no information on mechanisms or causal links. If indirect effects oppose direct effects, correlations and differentials can mask directional selection. Linear selection gradients estimate the direct effects.

I used the methods of Lande and Arnold (1983) and Arnold and Wade (1984) to calculate standardized directional selection gradients (slope estimates of the strength of selection on each trait). I used ANCOVA to analyze selection separately for each year and found a significant year effect but no interaction. This means that there are mean differences between years (significantly different intercepts), but the relationship between each trait and the fitness measures is constant (parallel slopes). Therefore, I present estimates of selection gradients pooled across years. Multiple regression analysis assumes that all predictors having direct effects on fitness are included in the model and then estimates direct effects by statistically controlling for those other effects. Multicollinearity is a frequent problem in selection studies (Mitchell-Olds and Shaw 1987), so I assessed the degree of collinearity in the data by calculating condition indices and variance inflation factors (Petraitis et al. 1996). These data are not plagued by high collinearity, as the largest condition index was less than 2 (values are recommended to be less than 30; SAS 1991), and all variance inflation factors were very close to 1 (values are recommended to be less than 10; SAS 1991; Sokal and Rohlf 1981). I determined normality of residuals by Shapiro–Wilks test and did not find substantial deviations from normality; thus, data are analyzed on a non-transformed scale. Checks for outliers revealed no

observations that unduly influenced results (all studentized residuals were less than 2.5; Freund and Littell 1991).

Results

Group variation

Social groups varied in all traits. Group size ranged from 10 to 22 with an average of about 17 adult females. The data estimated group size over six years (1990 to 1995) for four populations in Trinidad including Guanapo cave which is the focus of this paper (16.4 ± 3.87 , $n=22$ groups). The others are Tamana (15.0 ± 4.97 , $n=7$ groups), Caura (14.9 ± 4.61 , $n=5$ groups), and Lopinot (16.4 ± 5.97 , $n=22$ groups) caves. These estimates are very close to McCracken and Bradbury's (1981) estimate of 18 females, suggesting that mean group size has remained stable over this time period. Group foraging frequency varied from 0 to 0.52 with a mean of 0.26, indicating that, on average, females foraged with group mates about one quarter of the time. The make-up of social groups influenced how frequently individuals foraged together. The females in medium-sized groups (14 to 17 adults) foraged together more often than those in small (10 to 13 adults, $t_7=2.34$, $p=0.05$) and large (18 to 23 adults, $t_7=1.95$, $p=0.09$) groups. The females in older groups foraged socially more than females in young groups ($t_8=-3.0$, $p=0.017$).

Social groups also varied in pup survival and relative condition at weaning. Just less than half of pups survived (49%). In three groups, all pups survived, while only 15% survived in the group with the highest mortality. The variation in relative condition at weaning was also substantial, from -2.71 to 4.78 . This variation provides ample opportunity for selection ($I=0.11$ for survival, $I=7.88$ for relative condition at weaning).

Average parasite load varied from 2 to 14.4 flies per pup (mean=7.1, CV=87.8). Average maternal condition varied from -4.11 to 1.92 (CV=3.96), indicating that the females in some groups were in much better condition than in other groups. Maternal age, as estimated by toothwear, also varied among groups from 1.9 to 3.3 (mean=2.5, CV=33.1). Maternal age was not correlated with group size ($r=-0.01$, $p=0.82$) nor were maternal condition ($r=-0.02$, $p=0.75$) or birthdate ($r=0.16$, $p=0.5$). There is no evidence of sex bias in maternal investment as neither maternal age ($t_{2,266}=-0.15$, $p=0.5$) nor maternal condition ($t_{2,166}=-0.07$; $p=0.5$) differed with offspring sex. The females in older groups gave birth earlier than the females in younger groups ($F_{1,13}=10.3$, $p=0.007$). There was no relationship between maternal condition and birthdate ($F_{1,13}=0.1$, $p=0.8$) nor was there an effect of maternal age on pup survival ($F_{1,13}=0.07$, $p=0.8$).

Phenotypic correlations and selection differentials

The two traits that showed large phenotypic correlations with fitness measures were parasite load and maternal condition, both of which were negatively correlated with fitness (Table 1). With a sample size of 13 groups, correlations below 0.53 are not significant. It was surprising that maternal condition was significantly negatively associated with pup condition pre-volancy, although this association was gone by the time pups reached independence (Table 1). Therefore, mothers in good condition did not necessarily produce pups with early good condition. Some mothers may instead have maintained their own condition at a cost to pups. Some mothers may have alternatively invested so heavily in pup condition that their own condition was depressed. Further work is required to investigate these possibilities.

The estimated selection differentials showed that parasite load depressed condition at weaning (Table 1).

Table 1 Correlations among phenotypic traits and standardized selection differentials

	Group foraging	No. of adults	Parasite load	Maternal condition	Pup condition at volancy	Pup survival	Pup condition at weaning
Group foraging		0.34	-0.09	-0.14	0.002	-0.34	0.31
No. of adults			-0.32	0.43	0.11	0.02	-0.03
Parasite load				-0.05	-0.36	0.28	-0.54*
Maternal condition					-0.54*	-0.42	-0.08
Pup condition at volancy						0.17	0.32
Pup survival	-0.02	0.03	0.34	-0.12	0.003		0.05
Pup condition at weaning	0.14	-0.36	-6.19*	-0.23	0.07		

Phenotypic correlations are shown on the upper diagonal (critical value of $r=0.532$). Selection differentials are shown on the lower two rows (see text for details)

* $p<0.05$

The selection differentials for group foraging and group size were not significantly different from zero for either fitness measure. Selection differentials estimate the total strength of selection. Conflicting selection can be masked by such measures if positive and negative selection are approximately equal in magnitude. This will occur if benefits equal costs. Thus, the lack of significant selection differentials does not necessarily mean that selection is absent. The action of conflicting selection can be revealed by estimating selection gradients.

Selection gradients

Linear selection gradients (Table 2) indicate that relative condition at weaning was significantly enhanced by group foraging (Fig. 1a). Group size had non-significant negative effects on pup condition (Fig. 2a). Pup condition in 1995 was significantly lower than that in 1994 (Table 2). This is due to a difference in means (intercepts) rather than a difference in gradients (slopes). The model explained over 40% of the variation in pup condition at weaning.

The selection gradients for group foraging and group size on survival were near zero (Table 2; Figs. 1b and 2b). Survival was again lower in 1995 than in 1994 (Table 2), suggesting that 1995 was a particularly harsh year. This model explained over 60% of the variation in pup survival, but this was primarily due to mean differences between years. These selection analyses reveal potential ways that natural selection can shape social behavior in this species.

Table 2 Standardized selection gradients for survival and relative condition at weaning

Factor	β	γ	SE
Relative condition at weaning			
Year		-0.56*	0.248
Proportion group foraging	0.49*		0.799
Group size	-0.24		0.028
R^2 ($df=3, 13$)	0.41*		
Survival			
Year		-0.66**	0.022
Proportion group foraging	-0.32		0.071
Group size	0.08		0.025
R^2 ($df=3, 13$)	0.62**		

Selection gradients less than 0.48 were not significant at $\alpha=0.05$.

Although significant year effects were detected, this was due to a difference in means (intercepts). The gradients (slopes) were similar across years (see text for details)

β linear selection gradient pooled across years, γ difference in mean fitness between years, SE standard error, R^2 proportion of variance explained by the full model

* $p<0.05$; ** $p<0.01$

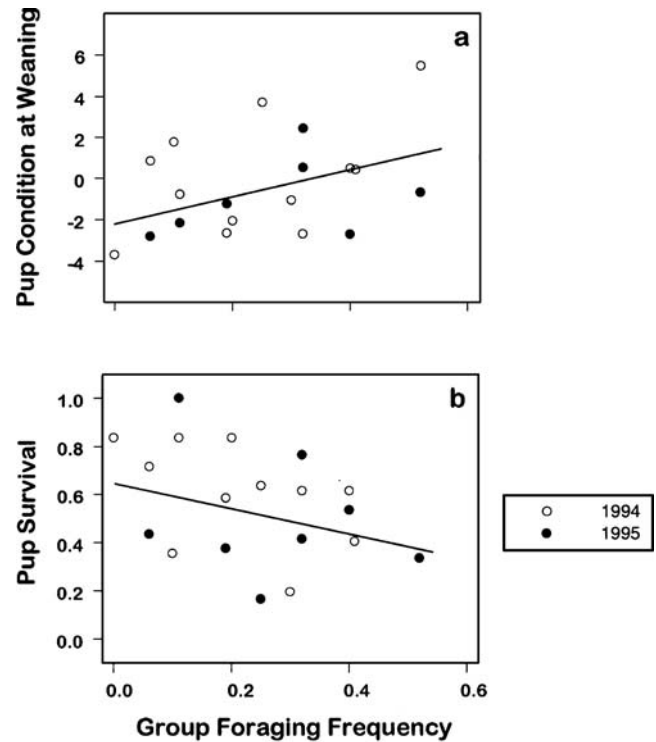


Fig. 1 Relationship between frequency of group foraging and fitness measures. The values plotted are corrected for differences between years and lines indicate selection gradient averaged for 1994 and 1995. **a** Relative condition of pups at weaning; **b** survival of pups to weaning

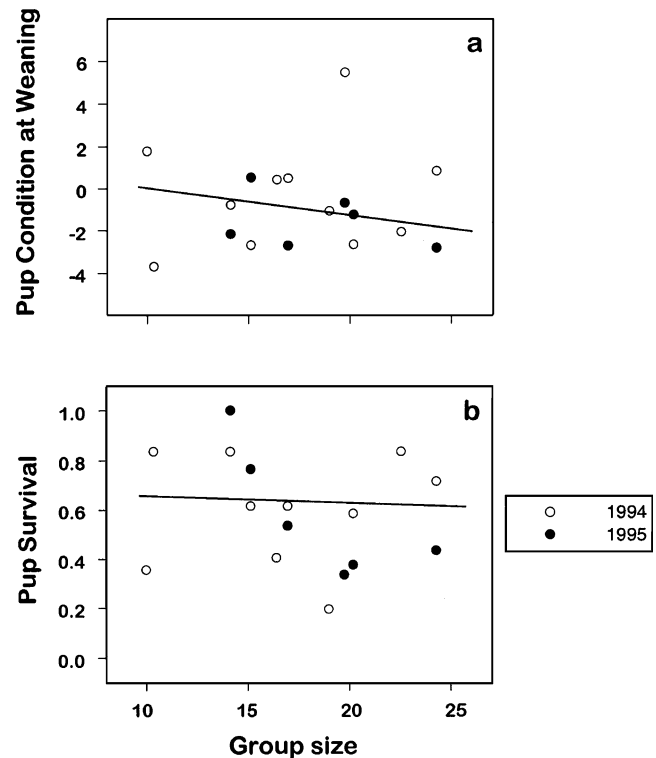


Fig. 2 Relationship between social group size and fitness measures. The values plotted are corrected for differences between years and lines indicate selection gradient averaged for 1994 and 1995. **a** Relative condition of pups at weaning; **b** survival of pups to weaning

Discussion

Selection on group size

Females in varying size groups differed very little in fitness measures. Thus, directional selection does not appear to be currently acting on group size behavior. Stabilizing selection could be acting but, unfortunately, cannot be directly tested here because the sample size is too small to allow sensitive tests of nonlinear selection. The lack of directional selection is consistent with the stability of estimates reported here and from work done 15 years earlier (McCracken and Bradbury 1981). It could be that no selection acts on group size. However, the absence of variation in fitness for different-sized groups is expected if groups vary in member or territory quality such that the groups vary in their optimal or stable group size (Giraldeau and Caraco 2000). In this case, selection would be acting to keep each group at its optimum or stable size. Data on territory quality would be very valuable for testing this hypothesis but is not currently available and would be very difficult to obtain. One way to investigate the potential effect of member quality is to determine whether groups of different sizes contain individuals with different attributes. Using the data reported here, I considered data on group stability (average tenure of females in a group) and composition (female age, parity, body size, condition, and tendency to cooperate) and found no correlations with group size except for one: females in medium-sized groups forage socially more. So, perhaps group foraging contributes to patterns of group size. The absence of other effects suggests that most aspects of member quality do not differ among groups of varying size, but additional data are required to test this definitively.

Selection on group foraging

The positive selection gradient for group foraging suggests that it significantly improved the relative condition of pups at weaning. This suggests that females could experience selection to increase their frequency of group foraging. Group foraging had weak, nonsignificant effects on pup survival, which suggests that pup survival does not depend directly on social foraging. The mean frequency of group foraging is 0.26, which is approximately equal to a previous estimate of 0.24 (Wilkinson and Boughman 1998). Group foraging is certainly not obligatory or fixed. If it were, there would be no variation on which selection could act. Group foraging is likely a facultative behavior and is predicted when food is patchily distributed in rich clumps (Bradbury and Vehrencamp 1976; Clark and Mangel 1986; Giraldeau and Beauchamp 1999; Beauchamp and Fernandez-Juricic 2005). Under such resource distribution, individuals who

forage in groups are expected to have higher net energy gain. When food is distributed more uniformly, group foraging is not predicted to yield such benefits because of the costs of food sharing and competition among group mates (e.g., Clark and Mangel 1984). Consistent with these predictions, *P. hastatus* forage in groups more when food is more patchily distributed (Wilkinson and Boughman 1998, 1999).

Resource abundance could also affect pup condition, which is likely to be higher when food is abundant. Parturition in this and other bat species (Heideman 1995; Arlettaz et al. 2001) appears to be timed to coincide with high resource abundance for mothers (Porter and Wilkinson 2001) or pups (Cumming and Bernard 1997), which should increase pup survival and female fitness. However, resource patchiness (which should promote group foraging) and abundance are not necessarily correlated and, therefore, group foraging and abundance may have independent effects on pup condition. Resource abundance will only explain the correlation between group foraging and pup condition to the extent that group foraging and resource abundance are correlated for groups. We currently lack data on this correlation for *P. hastatus* and, thus, cannot address this issue directly. However, data for cliff swallows (Brown 1988) and spiders (Spiller 1992) suggest that the differences in social foraging, not differences in resource abundance between colonies, explains differences in adult foraging success and offspring body mass. If this pattern holds for *P. hastatus*, both group foraging and resource abundance may influence pup condition, but they may do so independently. Further work is required to clarify this issue.

Group foraging may affect pup condition indirectly because it improves maternal energy gain, but it may also affect pup condition directly, which can also increase female reproductive success. Once pups become volant, they begin to forage for themselves and, thus, may gain from foraging with group mates. Group foraging may be especially important to pups just learning to find their diverse and widely dispersed food (Kerth et al. 2001; Rossiter et al. 2002; Schmidt-French and Whitaker 2005). Naive pups may benefit from following adults to foraging sites (Gopukumar et al. 2003) or by searching for food with other pups. Preliminary evidence indicates that pups frequently follow adults out of the roost and that they also forage with other pups (Boughman JW and Wilkinson GS, unpublished).

Maternal condition and maternal investment

Maternal condition can modify reproductive effort with consequent effects on offspring condition and subsequent survival (Price and Grant 1985; White et al. 1987; Larsson

and Forslund 1992). Maternal effects are typically most pronounced when offspring are young (Price 1998; Gendreau et al. 2005); however, offspring condition at independence can persist long enough to affect age at first reproduction, clutch size, and body size in birds and mammals (Price and Grant 1985; Clutton-Brock and Godfray 1991; Schluter and Gustafsson 1993; Festa-Bianchet et al. 1998). Thus, variation in pup condition at independence is likely to contribute to variation in pup survival, which affects adult female fitness.

The selection differentials for maternal condition are unexpectedly weakly negative for both relative condition at weaning and survival. These effects were nowhere near significant but nonetheless are puzzling. The negative relationship between maternal and pup condition was stronger pre-volancy. Two related processes could explain this pattern: competition between mothers and their pups, and maternal reproductive strategies. Competition could involve conflict over how much milk pups get or competition at feeding sites over how much food pups eat. Stern et al. (1997) studied lactational output and found variation among individual females in foraging time and the composition and quantity of milk. They also found variation in pup growth but unfortunately did not report data on the relationship between individual lactational output and either female condition or pup growth. A lab-based study of social foraging suggested feeding competition in adult–pup pairs, but not for pup pairs. This study showed that pups foraged less vigorously when paired with an adult than when paired with another pup (Boughman JW and Smith C, unpublished). So, pups may follow adults to feeding sites to find food, but competition with adults might then force them to search in the vicinity for their own food source. This is consistent with findings for other taxa, where subordinates often lose out in social foraging (Caraco et al. 1989; Ranta et al. 1993). Given that the magnitude of the negative relationship dropped off as the pups aged, the latter hypothesis is less likely.

Long-lived animals with many chances to reproduce are expected to invest relatively little in any one reproductive effort (Clutton-Brock and Godfray 1991; Festa-Bianchet et al. 1997, 1998). Their primary means to maximize reproductive success is to maximize their own survival, thus ensuring many opportunities to produce offspring. Thus, females may exercise reproductive restraint during years of low food abundance or when they are young and have high residual reproductive value (Clutton-Brock 1991), especially if this increases life span (Ransome 1995). Greater spear-nosed bat females can live upwards of 20 years in the wild (McCracken et al., unpublished) and begin reproducing as early as age 2 years; thus, they may conform to this pattern.

Conclusions

This study adds to our emerging picture of group foraging behavior in *P. hastatus*. Prior work used the methods of behavioral ecology to investigate the ecological conditions favoring group foraging and the mechanisms that bats use to form foraging groups. That work determined that female social group mates actively form foraging groups (Wilkinson and Boughman 1998) and actively deter individuals from other social groups (Wilkinson and Boughman 1999; JW Boughman, unpublished). Thus, foraging groups are composed of members of the same social group. Females form foraging groups by following group mates from the roost (Wilkinson and Boughman 1999) and by using a group-distinctive vocalization to facilitate group formation outside the roost (Boughman 1997; Boughman and Wilkinson 1998; Wilkinson and Boughman 1998). Foraging in groups decreases search time and may enable bats to defend rich resources from conspecifics. The benefits of social foraging are restricted to females foraging with long-term group mates (Wilkinson and Boughman 1999). Group foraging is more common during the times of year when food is patchily distributed, which is when it should be most beneficial. Group foraging is less common when food is widely and uniformly dispersed or food items cannot be shared (Wilkinson and Boughman 1998, 1999). These are conditions when the costs of sharing may outweigh the benefits of food finding and defense. Thus, we know something of the benefits and potential costs of group foraging. The selection analysis approach used in the current work adds to this picture, because now we know that group foraging can have fitness consequences and may be under directional selection to increase. This suggests that one advantage to group living in this species is the opportunity to forage socially.

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