Original Article

Male greater sac-winged bats gain direct fitness benefits when roosting in multimale colonies

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Social groups that are characterized by the presence of male kin are rare in mammals. Theory predicts that males reproducing in such groups need to overcome the costs of local mate competition, which are supposedly severe in polygynous or promiscuous mating systems. Here, we studied in a polygynous mammal with male philopatry whether male group size renders direct fitness benefits for males that could outweigh the costs of competing with related males for access to territories and mates. We used long-term behavioral observations and genetic data of the greater sac-winged bat to investigate the factors affecting lifetime breeding success (LBS) of harem males living in colonies that contain varying numbers of male residents. We show that tenure of harem males increased with the number of male coresidents and that harem male tenure explained a large proportion of variation in their LBS. Thus, our results provide evidence that males gain direct fitness benefits from a social organization in colonies that include additional harem territories and nonharem males. Immigration of males into colonies was significantly lower when nonharem males (young males that are often related to harem males) were permanently present in colonies, suggesting that larger male groups may be better able to maintain a patriline in a colony and thus also ensure future indirect fitness benefits. *Key words:* female-biased dispersal, lifetime breeding success, male tenure, *Saccopteryx bilineata*, social organization. *[Behav Ecol]*

INTRODUCTION

Social groups that are characterized by the presence of male kin are a rare phenomenon in mammals (Clutton-Brock 1989; Lawson Handley and Perrin 2007). Theory predicts that if competition for mates takes place between kin (local mate competition), this will result in the reduction of inclusive fitness (Hamilton and May 1977; Taylor 1988). The avoidance of local mate competition is, therefore, assumed to be one of the most important selective pressures causing male-biased dispersal patterns in mammals (Dobson 1982; Perrin and Goudet 2001; Lawson Handley and Perrin 2007). Local mate competition may thereby also be seen as a force that can impede the establishment of mammalian social groups that contain several reproducing male kin. Nonetheless, social groups of some mammalian species are characterized by the long-term coexistence of groups of reproducing male kin (e.g., lions *Panthera leo*, Packer et al. 1991; bottlenose dolphins *Tursiops* sp., Krützen et al. 2003). This raises the question of how the potential costs of local mate competition can be overcome to allow multiple related males to reproduce in the same social group. Often, this conflict is solved by the benefits when males of a group cooperate. In general, males form coalitions to defend group territories and/or females. Usually, group males are extremely hostile to foreign unrelated males and the benefits from such behavior accrue to males in terms of indirect and direct fitness benefits (Clutton-Brock 1989; Harcourt 1992; Clutton-Brock 2002; Lawson Handley and Perrin 2007).

The greater sac-winged bat (*Saccopteryx bilineata*) is one of the rare exceptions to the general mammalian dispersal pattern as it exhibits female-biased dispersal (Nagy et al. 2007). Thus far, the only other bat species where female-biased dispersal has been reported is *Carollia perspicillata* (Fleming 1988; Cosson 1994). However, in the study of Fleming (1988), not only males (98%) but also a substantial proportion of females (58%) were found to remain in their natal colony as subadults and adults. In *S. bilineata*, males represent the philopatric sex because about half of the male juveniles becomes residents of their natal colony, whereas all young females disperse (Nagy et al. 2007). As a result of males being faithful to their natal colony, the majority of male colony residents belong to a few patrilines and local mate competition between the related male residents is apparently severe (Nagy et al. 2007). Close kin not only compete over access to harem territories but also over access to females because previous studies showed that up to 70% of juveniles born in the harem of a male may be fathered by other colony males or nonresident males (Heckel et al. 1999; Heckel and von Helversen 2003; Nagy et al. 2007). It is unclear how these costs, which arise from local mate competition, might be overcome in greater sac-winged bats. In theory, the benefits from roosting together with other related males in a colony need to outweigh the costs arising from local mate competition. Similar to males in cooperative

alliances (Bygott et al. 1979), male greater sac-winged bats might gain direct fitness by associating with other males. The perception that kin selection is the sole factor shaping and maintaining social kin groups has been challenged on theoretical (Taylor and Frank 1996; West et al. 2002) and empirical grounds (Clutton-Brock 2002; Spong et al. 2002). Evidence suggests that direct fitness benefits commonly play a prominent role even in specialized cooperative societies and should not be discounted merely because social groups contain kin structures (Clutton-Brock 2002; Spong et al. 2002). One way in which male mammals may profit from the presence of other males is through an increase in their period of reproductive tenure, if higher numbers of males are better able to prevent nonresident males from taking over the female group. Also, the reproductive tenure of males should then be an important determinant of male lifetime reproductive success as demonstrated in lions (*P. leo*, Bygott et al. 1979; Packer et al. 1991) and red-fronted lemurs (*Eulemur fulvus rufus*, Port et al. 2010). Accordingly, we hypothesized that the costs of local mate competition to male greater sac-winged bats are overcome by direct fitness benefits mediated through longer tenure periods when a larger number of male residents are present in colonies.

The greater sac-winged bat is perfectly suited to test whether direct fitness of males is affected by male group size as the number of adjacent harem territories within colonies is highly variable (range 1–12; Bradbury and Emmons 1974; Voigt et al. 2008). Each harem territory is defended by a single male, covers 1–2 m^2 of vertical surface in the colony, and includes 2–3 females on average. Colonies contained up to 60 adult individuals that are distributed in 1–12 such harem territories (Bradbury and Emmons 1974; Voigt et al. 2008). Although male territories in the colony are termed "harem territories" in *S. bilineata*, males follow a resource–defense strategy and defend a roosting territory that is used by females rather than directly defending females (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Larger colonies typically also contain a varying number of nonharem males, which often roost close to but outside of harem male territories in the same colony or sometimes defend a territory of their own but without females permanently roosting in it (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Voigt et al. 2008). Nonharem males queue for harem access. The longest tenured nonharem male will be the first to fill an arising harem vacancy, as has been shown experimentally by temporarily removing harem males from their harem territories (Voigt and Streich 2003). In order to understand the evolution of this complex, mammalian social system that involves male philopatry, detailed knowledge of the factors determining male reproductive success is needed, and the role that the social organization of this gregarious species plays in determining male lifetime fitness must be taken into account.

Here, we combine individual life-history data from more than a decade of behavioral observations with paternity data from marked greater sac-winged bats originating from differently sized colonies to examine the factors that influence reproductive success in males of a species with male philopatry and female dispersal. The analysis of factors relevant for defining male reproductive success should also help to shed light on the ultimate causes of male philopatry in other mammals. In particular, we examine the factors that influence the reproductive lifespan (harem male tenure) and fecundity (annual breeding success) of harem males. Finally, we quantify the relative importance of male reproductive lifespan and fecundity in explaining variation in male lifetime breeding success (LBS) and test the hypothesis that male group size has a positive effect on male reproductive success.

MATERIALS AND METHODS

Field methods

Bats in 7 colonies were observed over the course of 4–9 (1994–2011) years at La Selva Biological Station (10°25′N, 84°00′W) in Costa Rica. The population of one colony that used to include approximately 50 adult individuals collapsed in 2002 (BH1) for unknown reasons. When paternity analyses were resumed in 2004, the colony contained 9 adult individuals (BH2, Table 1). For the purpose of our study, we will use these as 2 separate colonies and will therefore refer to 8 study colonies in the remainder of the text. After capture with mist nets, all bats were individually distinguishable using binoculars to identify them by color bands on their forearms in the colony. Overall, 217 adult females and 130 adult males roosted in our study colonies. Of these, 16 adult females (7%) and 1 adult male (0.8%) were not captured and remained unbanded. We used biopsy punches (4 mm) to remove a small piece of the wing membrane for genetic analysis at capture. Capture methods and methods to distinguish harem males from nonharem males and to identify group structure in the field are described in detail in Heckel et al. (1999) and in Heckel and von Helversen (2003). Group structure (colony sizes, harem male identities plus identities, and number of associated females, identities, and number of nonharem males, number of male residents [= the number of harem males plus the number of nonharem males], and number and motherhood of juveniles) was determined on a daily to at least weekly basis in the colonies with binoculars during the following periods: September to October 1995, June to August 1996, October 1996 to February 1997, June to August 1997, June to August 1998, December 1998 to February 1999, June to August 1999, November to December 1999, June to August 2000, December 2000 to January 2001, June to August 2001, December 2001 to January 2002, July to August 2002, November 2002 to January 2003, July 2003 to January 2004, July to August 2004, December 2004 to February 2005, June to August 2005, June to August 2006, June to August 2007, in April, June and August 2008, in January and July 2009, July to August 2010, and April to May 2011. These observation periods include the mating season in December (Voigt and Schwarzenberger 2008; Greiner et al. 2011) as well as the periods of parturition and lactation of the single yearly pup in June to July. See Table 1 for a detailed description of the study periods and group composition for each of the study colonies.

Data analysis

We determined LBS (the number of juveniles a male fathered throughout his entire tenure in the colony with the females roosting therein) for 50 harem males for whom harem male tenure ceased before the end of this study based on paternity analysis of 277 pups. In total, 301 pups were born in our colonies during the respective study periods; of which, 24 pups (8%) were not caught. Empirical studies frequently utilize lifetime reproductive success, which is defined as the number of offspring surviving to breeding age sired by a parent, as a measure for lifetime fitness (see Clutton-Brock 1988a). Because virtually all young females disperse at 2–3 months of age, we were not able to determine survival rates for all offspring of harem males. LBS can, however, be considered as an applicable proxy for lifetime fitness (e.g., Vanpé et al. 2008). Over the course of 17 years, we have never observed a harem male roosting in more than one colony (Nagy M, Knörnschild M, Voigt CC, Mayer F, unpublished data). Reproduction takes place almost exclusively among the residents of a colony, as evidenced by the low proportions of extra colony paternities (Heckel and von Helversen

Table 1

Study periods, group composition, origin of harem males that gained a harem position in the study colonies, and tenure of harem males

Colony	C5	RS	ZOM	C2	BH2	RH	PH	BH1
Study period for estimation of group composition	2004–2005	2004–2005	2007–2011	2003–2006	2004–2011	2004–2011	2003–2011	1996–2001
Average number (per year) of								
Adult individuals	4.5	5.8	5.2	5.5	7.0	9.7	12.9	51.5
Adult females	3.5	4.5	3.8	3.8	4.9	5.7	8.1	30.8
Adult males	1	1.3	1.4	1.7	2.1	4.0	4.8	20.7
Harem males	1	1	1.2	1.3	1.6	2.0	2.6	11.3
Nonharem males	0	0.3	0.2	0.4	0.7	2.0	2.2	9.3
Females per harem	3.5	4.5	3.4	2.4	3.2	2.4	2.9	2.6
Range in number of								
HMs	1	1	1–2	1–2	1–3	1–3	2–4	9–12
N-HMs	0	0–1	0–1	0–1	0–3	1–4	1–5	7–12
Origin of HMs								
Natal males	2	0	3	2	3	7	12	16
Neighboring colony	0	0	0	1	1	0	0	1
Unknown immigrant	0	2	3	1	4	1	2	1
Study period for estimation of HM tenure	2004–2011[a]	2004–2011[a]	2007–2011	2003–2011[a]	2004–2011	2004–2011	2003–2011	1994–2001[b]
Mean HM tenure (years)	0.6	0.9	0.7	1.0	1.3	1.9	1.5	2.9
SD HM tenure (years)	0.1	0.4	0.3	0.6	0.7	1.4	1.0	2.6
Median HM tenure (years)	0.6	0.9	0.7	0.8	1.1	1.7	1.2	2.2
Range in HM tenure (years)	0.6–0.7	0.6–1.2	0.4–1.0	0.5–1.7	0.6–2.2	0.2–4.1	0.6–4.0	0.1–9.2[b]
Sample size	2	2	5	4	7	7	12	25
Mean HM tenure in years (sample size) of HMs still present in 2011	—	—	0.5 (1)	—	0.1 (1)	0.4(1)	1.1 (2)	—

Abbreviations in the top line represent different colonies. HM, harem male; N-HM, nonharem male.

[a] Colonies C5, RS, and C2 were observed until 2011, but bat populations of these colonies disintegrated between 2005 and 2006 (C5 and RS) and between 2006 and 2007 (C2).

[b] Two harem males allotted to the BH1 defended their harems from 1995 until 2003 and from 1995 until 2004. These 2 harem males were allotted to the BH1 as they had spent the largest part of their tenure in the BH1.

2003; Nagy 2010). Therefore, we are confident that we have a reliable estimate of LBS by counting all juveniles a male fathered in his resident colony. Nine of the 25 harem males roosting in the largest of our study colonies (BH 1) were already adult when captured between 1995 and 1996, and it is likely that their harem tenure in the BH1 started before our study period. Therefore, and because we were not able to catch 10 juveniles of this colony over the 6-year study period, LBS of several males in our largest colony remained underestimated. According to our hypothesis, these males should

be the longest tenured males and achieve the highest LBS, and therefore, the underestimation of their LBS should make our conclusions conservative. Another 14 juveniles growing up in the harems of 8 harem males were not sampled (Table 2). As these 8 harem males succeeded in fathering 85% of the sampled pups born in their harems, we assigned paternity of the 14 unsampled pups to the harem male with which the respective mother roosted. In contrast, paternity loss for males from the BH1 was substantially higher (Nagy 2010).

Table 2

Study periods over which juveniles were sampled, sample size, and assignment results for paternity analysis

Colony name	BH1	BH2	C2	C5	RH	RS	PH	ZOM	
Study period	1996–2001	2004–2008	2003–2005	2004–2005	2004–2008	2004–2005	2003–2007	2007–2008	Total
Number of									
Juveniles born	170	28	16	9	26	9	33	10	301
Juveniles typed	160	25	13	5	23	8	33	10	277
Juveniles with known mother[a]	160	25	13	5	20	8	24	8	263
Fathers (95% confidence[b])	47[c]	24	9	4	20	7	29	4	144
Fathers (80% confidence[b])	18[c]	0	0	0	0	0	1	0	19
Juveniles with unknown father	12	1	4	1	3	1	3	6	31

[a] Mothers were determined by observation of nursing and confirmed with Cervus 2.0 (Marshall et al. 1998) or Cervus 3.0 (Kalinowski et al. 2007).

[b] We allowed 1 mismatch with the mother as well as with the father of juveniles.

[c] Values refer only to paternity analysis for the years 1999–2001 of the BH1. Paternity assignment results for the years 1996–1998 of the BH1 are described in more detail in Heckel and von Helversen (2003). Paternity assignment was carried out with Cervus 2.0 (Marshall et al. 1998) as results were already published in Heckel and von Helversen (2003) and Nagy et al. (2007).

Paternity analysis

Eleven polymorphic microsatellite loci (Heckel et al. 2000) were used to genotype a total of 862 individuals caught over the course of 15 years (1994–2008; Table 2) at La Selva Biological Station (OTS, Costa Rica). Of these, 153 were adult females and 105 were adult males roosting in our study colonies. Furthermore, a total of 277 juveniles born in our study colonies were typed. The remaining genotypes came from individuals caught in the vicinity of our study colonies ($N = 377$, 44%). Genetic samples were not obtained from 12 adult females (7%; total number of adult females = 165), 1 adult male (1%; total number of adult males = 106) as well as from 24 juveniles (8%; total number of juveniles = 301) born in our study colonies during the periods of paternity data acquisition denoted in Table 2. All individuals were genotyped at least at 10 loci and genotypes were 99.4% complete.

Paternity analysis was performed as described in Heckel and von Helversen (2003), with the exception that paternity was inferred using Cervus 3.0 (Kalinowski et al. 2007) for all juvenile cohorts starting with the year 2003. We performed paternity analysis for each juvenile cohort separately. Maternity was determined by nursing observations in the field and affirmed by genetic analysis with the exception of 14 pups, whose mothers were not sampled genetically. All adult males captured were treated as putative fathers (unless their death was known) for the paternity assignment of pups with known ($N = 263$) or without known ($N = 14$) mothers. With Cervus 3.0 (Kalinowski et al. 2007), we simulated 100 000 offspring with an error rate of 0.01 (based on 103 known mother–offspring pairs error rate was estimated to be 0.006). Although we had sampled 99% of the males roosting in our study colonies, we used a proportion of 90% sampled candidate males to account for the approximately 10% of pups that were fathered by nonresident males (Heckel and von Helversen 2003). Simulations were performed for 2 confidence levels (80% and 95%). We allowed 1 mismatch per parent–offspring pair and assigned the most likely males as fathers. Table 2 gives a detailed overview of sample sizes and assignment results of paternity analysis per study colony.

Statistical analysis

Generalized linear models

We used generalized linear models (GLMs) using the R statistical package 2.13.0 (R Development Core Team 2008) to assess the influence of different explanatory variables on tenure and annual breeding success of harem males.

We fitted the number of mating seasons a harem male was present as the dependent variable in a GLM to investigate the factors influencing harem male tenure duration. The following explanatory variables were tested: age at harem acquisition (years), forearm length (mm; for details on measurement procedures see Voigt et al. 2005), harem size (average number of females a male defended throughout his harem male tenure), and number of resident males (average number of harem and nonharem males a harem male roosted together within a colony throughout his harem male tenure). Harem sizes and numbers of resident males were determined as 1 value per observation period and then averaged over the number of observation periods a harem male was present. We used a fidelity index F (Heckel et al. 1999) to estimate harem sizes and numbers of resident males. F corresponds to the proportion of censuses during which a bat was present in the territory where it was observed in the majority of census. Only individuals that were present in the colony at least during half of the censuses were included in the estimate of harem size and number of resident males. F equals 1 if an individual was

observed in the same territory during all observations and F equals 0.5 if a bat was present in a territory during half of the census observations. On average, females showed high fidelity to their harem territories (mating period: $F = 0.80 \pm 0.18$, $N = 114$; parturition period: $F = 0.84 \pm 0.16$, $N = 140$) and, with few exceptions, harem males were always present in their harem territories (mating period: $F = 0.98 \pm 0.06$, $N = 38$; parturition period: $F = 0.96 \pm 0.09$, $N = 61$). Nonharem males were present in their colonies on 86% $\pm$ 17% ($N = 30$) of census counts during the mating season and on 87% $\pm$ 15% ($N = 50$) of census counts during the parturition period. Age at harem acquisition was slightly correlated with the number of resident males (Pearson's correlation: $N = 64$, $r_p = 0.30$, $P = 0.017$), harem size was slightly correlated with the number of resident males ($N = 64$, $r_p = -0.21$, $P = 0.09$), and harem size was also slightly correlated with forearm length ($N = 44$, $r_p = -0.25$, $P = 0.1$). The GLM was fitted using a Poisson error distribution and a log-link function. We were able to estimate harem male tenure durations for 64 harem males. However, data on forearm length were available only for approximately 70% of harem males (44 of 64). Because forearm length had no effect on harem male tenure durations (see Supplementary Table 1a and 1b), we ran a new analysis excluding forearm length as an explanatory variable but with the full sample size of 64 harem males.

To investigate the factors affecting harem male fecundity (annual breeding success), we determined the mean number of pups a harem male fathered per mating season present, transformed it into an integer, and fitted it as the dependent variable in a GLM. The explanatory variables tested were the same as in the analysis of harem male tenure duration, also including forearm length of harem males (see above). The GLM was fitted using a negative binomial error distribution with a log-link function (function in R: glm.nb in the MASS Package; Venables and Ripley 2002). Data on annual breeding success of harem males were gained from 50 harem males and 42 harem males for which forearm length was available were included in the model.

Initially, we used generalized linear mixed models with colony affiliation fitted as a random factor to account for harem male tenure and annual breeding success measures gathered from males originating from the same roost. Because the variance contribution of colony affiliation in both modeling attempts turned out to be zero, the random factor was omitted and we fitted GLMs, which yielded identical results. Model selection was carried out using Akaike's Information Criterion (AIC) and the stepAIC function (MASS library) utilizing the backward selection procedure. In Tables 3a and 4a, we present candidate models selected with this procedure, their respective AICc values, delta AICc values, and Akaike weights. AICc is the second-order AIC and is recommended for models with small sample sizes (Burnham and Anderson 2002). Model estimates for explanatory variables in models that had considerable support (delta AICc < 2; Burnham and Anderson 2002) were averaged. Model averaging was conducted by weighing estimates and the standard error (SE) of parameters for each model by their respective Akaike weights. Finally, unconditional 95% confidence intervals were calculated using the model-averaged estimate and the unconditional SE (Burnham and Anderson 2002).

Variance components of LBS

We used a widely utilized method by Brown (1988) to estimate the variance in LBS of harem males (see also Coltman et al. 1999 for a detailed description of this method). This analysis decomposes the variance in LBS into the individual contributions of reproductive lifetime (L, harem male tenure measured as the number of mating seasons a male defended his

Table 3

(a) Model selection statistics for factors affecting the length of harem male tenure for 64 harem males

(a)

Models	K	AICc	Delta AICc	Akaike weights	Residual deviance	Residual DF
3. No. MR	**2**	**222.33**	**0**	**0.69**	**61.29**	**62**
2. No. MR + HS	**3**	**224.51**	**2.18**	**0.23**	**61.26**	**61**
1. No. MR + HS + Age HM	4	226.79	4.45	0.07	61.26	60

(b)

	Model-averaged estimate	Unconditional SE	Unconditional CI (95%)
Number of male residents	**0.04**	**0.01**	**0.02 to 0.06**
Harem size	−0.01	0.06	−0.13 to 0.11
Intercept	0.37	0.19	−0.01 to 0.7

Model averaging was performed for models highlighted in bold and results of model averaging are presented in b. No. MR, Number of male residents; HS, Harem size; Age HM, Age at harem acquisition. Table presents the results of GLMs with a poisson error distribution and log-link function. Colony affiliation of harem males fitted as a random term explained zero variation in the number of mating seasons present and was dropped from the analysis.

harem position) and fecundity (*F*, number of pups a harem male fathered per mating season present) as well as the contribution of the product of $L \times F$. The relative contribution of $L \times F$ will be the effect over and above the effect of the individual components *L* and *F*. The contribution from the covariation between components of LBS can turn out positive or negative, where a negative contribution could mean that one component cancels the effect of another. However, a negative contribution of $L \times F$ could also be caused by the fact that fecundity is overestimated in individuals that die early and vice versa (Brown 1988; Clutton-Brock 1988b). Only individuals that sired at least 1 pup can be included in the above model. To estimate the contributions of nonbreeding harem males (LBS = 0) to the total variance in LBS, we used the following equation by Brown (1988) giving the overall variance in LBS among breeding and nonbreeding harem males: $pV(\text{LBS}) + p(1-p)\,\text{LBS}^2$. Here, *p* denotes the proportion of breeders and $1-p$ the proportion of nonbreeders. *V*(LBS) and LBS denote the variance and the mean in LBS. The first term in the expression is the proportion of variation explained due to breeders and the second the variation in LBS explained due to nonbreeders.

Correlations

Correlations were carried out in SPSS 11.5, means are presented with 1 standard deviation (±SD) unless stated otherwise, and statistical tests are 2-tailed. Because several variables were present in more than 1 correlation, we applied sequential Bonferroni corrections (Rice 1989) and present the adjusted α-levels together with the respective tests in the RESULTS section.

RESULTS

Harem acquisition and origin of harem males

During the observation period between 1994 and 2011, the number of males per colony remained almost constant over a long period of time irrespective of the size of the colony (Supplementary Figure S1). Only 1 roost (BH; Supplementary Figure S1) experienced a singular and sudden decline in size. The majority of males that took over a harem were natal males born to females and resident males of the respective colony (45 of 62 males, 73%; Table 1). Three immigrant harem males turned out to descend from individuals of a neighboring

Table 4

(a) Model selection statistics for factors affecting annual breeding success (fecundity) for 42 harem males

(a)

Models	K	AICc	Delta AICc	Akaike weights
3. HS + No. MR	**3**	**198.27**	**0**	**0.61**
2. HS + No. MR + Age HM	**4**	**199.79**	**1.52**	**0.28**
1. HS + No. MR + Age HM + FA	5	201.77	3.50	0.11

(b)

	Model-averaged estimate	Unconditional SE	Unconditional CI (95%)
Harem size	**0.26**	**0.1**	**0.06 to 0.45**
Number of male residents	**−0.033**	**0.017**	**−0.07 to −0.001**
Age at harem acquisition	0.18	0.17	−0.16 to 0.52
Intercept	0.11	1.07	−1.20 to 2.21

Model averaging was performed for models highlighted in bold and results of model averaging are presented in b. HS, Harem size; No. MR, Number of male residents; Age HM, Age at harem acquisition (years); FA, Forearm length (mm). Table presents the results of GLMs with a negative binomial error distribution and log-link function. Colony affiliation of harem males fitted as a random term explained zero variation in annual breeding success of harem males and was dropped from the analysis. Annual breeding success was transformed into an integer. For details see MATERIALS AND METHODS.

colony (4%), and 14 harem males (23%) were unknown adult immigrants, which did not descend from members of the colony they gained a harem position in (Table 1). Of the 17 immigrant harem males, 8 harem males (47%) were never observed as being nonharem males and were thought to have taken over harems immediately at immigration. The proportion of non-natal harem males was significantly larger in colonies that occasionally did not harbor any nonharem males (12 of 22 harem males, 55% in 5 colonies RS, C2, ZOM, C5, and BH2) as compared with colonies that were permanently inhabited by at least one nonharem male (5 of 40 harem males, 12.5% in BH1, RH, and PH; Fisher's exact test, $P <$ 0.001). Colonies with a higher number of harem males were also inhabited by a larger number of nonharem males (Kendall Tau correlation: $N = 8$, Tau-b = 0.89, $P = 0.004$, $\alpha = 0.025$). Also, colonies that were larger (total number of adult individuals) were inhabited by a larger number of male residents (Kendall Tau correlation: $N = 8$, Tau-b = 0.86, $P = 0.004$, $\alpha = 0.008$).

Harem male tenure

Tenure of nonharem males averaged 0.89 ± 0.82 years (range: 0.0–3.3 years, $N = 52$) before these males gained a harem territory. Mean and SD are based only on nonharem male tenures from males that were juveniles at capture ($N = 44$) or that were known to immigrate as adults ($N = 8$) into our study colonies. Tenure as a harem male, measured from males whose tenure ended before the end of data acquisition but for other reasons than colony disintegration, was 1.9 ± 2.0 years and ranged from 0.1 up to 9.2 years ($N = 64$). The number of mating seasons individual harem males were present (used as a measure of their harem male tenure) was not affected by the age at which males gained a harem, their average harem size, or their forearm length but was predicted by the average number of males (harem and nonharem males) a male roosted with throughout his tenure (Table 3). Accordingly, median tenure of harem males was longer in colonies with a larger number of resident males (Figure 1A; Kendall Tau correlation: $N = 8$, Tau-b = 0.79, $P = 0.009$, $\alpha = 0.010$). In contrast, there was no significant relationship between median tenure of females per colony (the period of time a female roosted in a colony) and the number of male residents (Figure 1A; Kendall Tau correlation: $N = 8$, Tau-b = -0.19, $P = 0.61$, $\alpha = 0.025$) or the size of the colony (Kendall Tau correlation: $N = 8$, Tau-b = -0.11, $P = 0.80$, $\alpha = 0.05$). There was no significant relationship between the study period of individual colonies and median harem male tenure (Kendall Tau correlation: $N = 8$, Tau-b = 0.54, $P = 0.09$, $\alpha = 0.05$) or the mean number of male residents (Kendall Tau correlation: $N = 8$, Tau-b = 0.77, $P = 0.015$, $\alpha = 0.013$). Queuing periods (= median tenure as nonharem male) were not significantly longer when a larger number of male residents were present (Kendall Tau correlation: $N = 8$, Tau-b = 0.57, $P = 0.07$, $\alpha = 0.017$), although there was a tendency toward shorter queuing periods when fewer male residents were present.

Annual breeding success (fecundity) of harem males

Annual breeding success was estimated as the number of pups a male fathered per mating season present as harem male. Harem males that defended a larger harem across their period of tenure succeeded in gaining higher annual breeding success. We also found a negative effect of the average number of males present in the colony on annual breeding success of harem males, whereas forearm length and the age at harem acquisition had no effect on annual breeding success (Table 4). Accordingly, annual breeding success of these
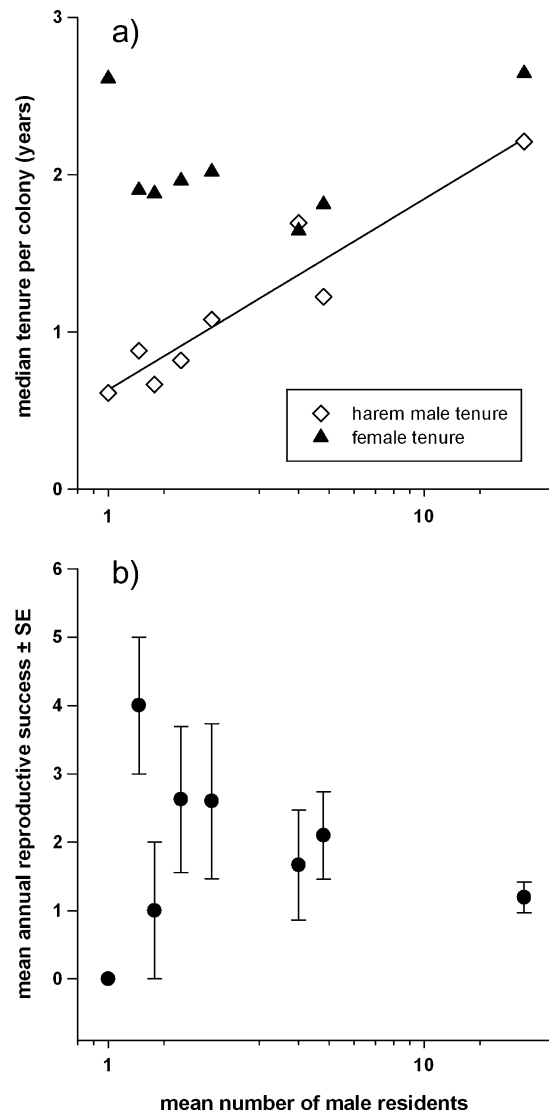

Figure 1
(a) Relationship between the mean number of male residents per colony and median harem male tenure and median female tenure per colony. (b) Annual breeding success of harem males (mean± SE) per colony as a function of the mean number of male residents present in the respective study colony. The x axis is presented in logarithmic scale in both graphs. The solid line in (a) depicts a linear regression.

individuals tended to be lower as the number of male residents increased. We found a trend toward smaller average harems when the average number of harem males increased in a colony (Kendall Tau correlation: $N = 8$, Tau-b = -0.59, $P = 0.06$, $\alpha = 0.05$). Annual breeding success of harem males per colony was independent of the average number of males roosting in a colony (Figure 1B; Kendall Tau correlation: $N = 8$, Tau-b = -0.04, $P = 1$, $\alpha = 0.05$).

Variance components of harem male LBS

LBS of 50 harem males, whose tenure ended before the end of our study period, averaged 4.2 ± 4.2 juveniles per harem male (range: 0–15) with a standardized variance (variance/mean^2) of 0.97. Fourteen of these harem males did not sire any offspring (28%), and thus, 40% of variation in male LBS can be attributed to nonbreeders (Table 5). Nonbreeding harem

Table 5

Percentage contributions of breeding lifespan (L) and annual breeding success (F, fecundity) to variance in LBS of harem males

Component	L	F
L	79.1	
F	−103.5	84.1

N = 36 breeding harem males
Proportion of breeders, 0.72
Percentage of variance due to nonbreeders, 40.2
Percentage of variance due to breeders, 59.8

L = breeding lifespan expressed as the number of mating seasons a male defended his harem; F = fecundity expressed as the average number of pups a male sired per mating season present. Please note that the sum of the single variance contribution of L and F and the contribution from covariance between L and F (L × F) add up to the percentage of variance due to breeders. The percentage of variance due to breeders plus the percentage of variance due to nonbreeders add up to 100%.

males retained their harem territory for 1.1 ± 0.3 mating seasons, which was significantly shorter than the average tenure of harem males, which fathered at least 1 pup (3.0 ± 1.9 mating seasons, Mann–Whitney U test: $N_1 = 14$, $N_2 = 36$, $U = 52.5$, $P < 0.001$). Breeding harem males ($N = 36$) sired 2.3 ± 1.5 pups per mating season present in the colony. Partitioning variance in LBS of breeding harem males into its 2 components (tenure as a harem male and annual breeding success per mating season) showed that annual breeding success accounted for 84% and harem tenure for 79% of variance in LBS (Table 5 and Figure 2). The large negative covariance between harem tenure and annual breeding success (-103.5%) is attributable to their strong negative correlation (Spearman rank correlation: $N = 36$, $R_s = -0.382$, $P = 0.021$, $\alpha = 0.025$). The 14 nonbreeding harem males had to be excluded from this analysis of variance in LBS due to statistical reasons (see MATERIALS AND METHODS section). However, if these 14 nonbreeding harem males were incorporated into the analysis, annual breeding success correlated positively with the number of mating seasons a harem male was present (Figure 3; Spearman rank correlation: $N = 50$, $R_s = 0.341$, $P = 0.015$, $\alpha = 0.017$). These contrasting results suggest that the negative covariation between annual breeding success and male reproductive lifespan represents an artifact of the

systematic removal of nonbreeding harem males that had short reproductive lifespans (1.1 ± 0.3 mating seasons) and no reproductive success.

DISCUSSION

Our detailed analysis of individual life-history variables in *S. bilineata* demonstrates that in a mammalian species with a harem polygynous, male philopatric social system harem males may gain direct fitness benefits by roosting in colonies that contain other adjacent harem males and nonharem males. Direct fitness benefits to harem males are most likely mediated through increased harem male tenure duration as the latter proved to be an important component explaining variation in a harem male's lifetime fitness.

In polygynous male mammals, variation in reproductive success has been attributed primarily to variation in annual breeding success (e.g., red deer *Cervus elaphus*, Clutton-Brock et al. 1988; elephant seals *Mirounga angustirostris*, LeBoeuf and Reiter 1988; soy sheep *Ovis aries*, Coltman et al. 1999). For greater sac-winged bats, our results show that harem male tenure is similarly important (79%) as annual breeding success (84%) in explaining variation in LBS. Reproductive lifespan was also shown to explain a significant amount of fitness variation in roe deer (33%), whereas variation in annual breeding success contributed 56% to variation in LBS in this species (Vanpé et al. 2008). Similar to greater sac-winged bats, bucks of the roe deer defend resources rather than females. Roe bucks return to the same territories every mating season, and competition in the form of dangerous combats is supposedly low once they have established their first territory (Owen-Smith 1977; Vanpé et al. 2009). In *S. bilineata*, males commonly gain their harem position by queuing. An arising harem vacancy will usually be filled by the longest tenured nonharem male in the queue (Voigt and Streich 2003). Probably, because of this queuing, the level of fighting between resident males might be reduced in the greater sac-winged bats (Voigt and Streich 2003); similar to the social system of roe deer (Vanpé et al. 2009) but opposed to those of most other mammal species like elephant seals (*M. angustirostris*, LeBoeuf and Reiter 1988) or red deer (*C. elaphus*, Clutton-Brock et al. 1988). In elephant seals and red deer, males are successful in reproduction for only a few years of their lifetime, and thus, their reproductive lifetime
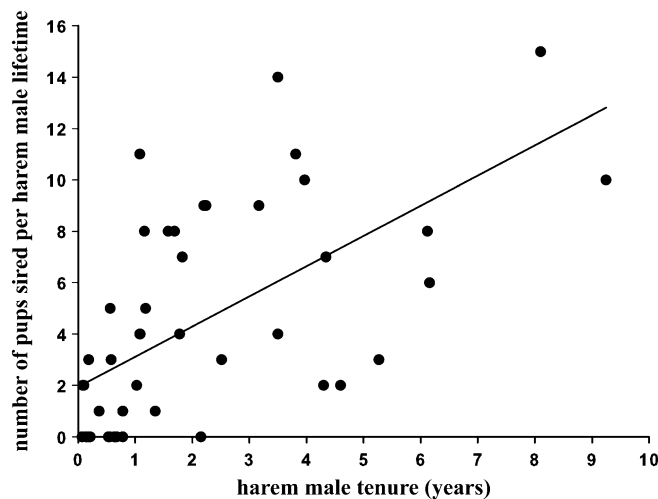
Figure 2
Individual LBS of 50 harem males plotted against their tenure duration. See MATERIALS AND METHODS for details on estimation of LBS. The solid line depicts a linear regression.
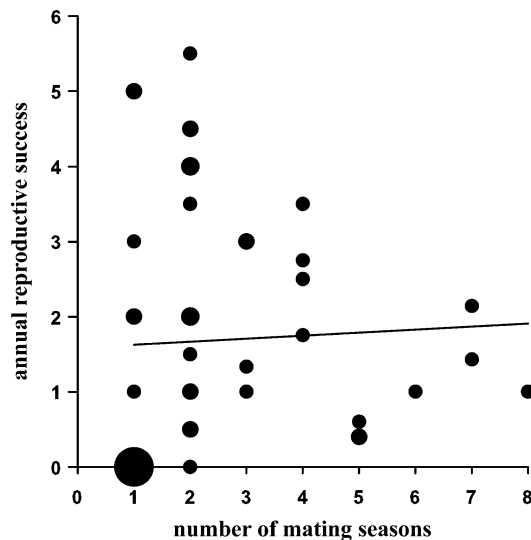
Figure 3

Relationship between number of mating seasons and annual breeding success of 50 harem males that roosted in the 8 study colonies. Individual circles are adjusted in size, encoding the number of males. Please note that the largest circle corresponds to the 14 nonbreeding harem males. The solid line depicts a linear regression.

is not relevant in explaining fitness variation among males (Clutton-Brock et al. 1988; LeBoeuf and Reiter 1988). Engh et al. (2002) showed that reproductive success of male spotted hyenas is determined by their tenure and somewhat less by social rank. In this social carnivore, males (like in greater sac-winged bats) acquire social status by queuing, social rank is not correlated with body mass or size (East and Hofer 2001), and male–male fighting is rare (Engh et al. 2002). Likewise, in greater sac-winged bats, there are no morphological differences between nonharem and harem males (Heckel and von Helversen 2002; Voigt and Streich 2003), and male tenure duration was not affected by the length of a harem male's forearm. Taken together, these results might indicate that harem male status and harem male tenure are not influenced by male fighting ability in *S. bilineata*.

Intriguingly, the duration of harem male tenure of greater sac-winged bats increased with the number of male residents present in a colony and was not related to the number of females a male defended in his harem or his forearm size. Comparisons among mammalian species suggest that intense competition between males commonly has direct and negative effects on the duration of male reproductive tenure in polygynous species (Clutton-Brock and Isvaran 2007). For example, in mandrills (*Mandrillus sphinx*), the duration of alpha male tenure declined with the number of male rivals in the group (Setchell et al. 2006). Also, the number of females defended has been repeatedly shown to affect male tenure duration negatively (Gosling 1986; Packer et al. 1988; Steenbeek 2000). For example, in Thomas' langurs (*Presbytis thomasi*), the frequency of male takeovers increased in groups with more females (Steenbeek 2000). Evidence for positive relationships between reproductive tenure of males and the number of males in a group or group size comes exclusively from species, which are known or suspected to cooperate in female or territory defense (e.g., lions *P. leo* Bygott et al. 1979; meerkats *Suricata suricatta*, Spong et al. 2008; red-fronted lemurs *E. fulvus rufus*, Port et al. 2010). We have reason to assume that *S. bilineata* colony males may likewise form mutualistic cooperative alliances that exclude non-natal males from settlement. Interestingly, the proportion of immigrant harem

males was significantly larger in smaller colonies that did not contain permanent nonharem males. As longer tenure periods occur in larger colonies, males should prefer to immigrate into larger colonies. The observation of contrasting patterns suggests that colony males actively prevent immigration of non-natal males. However, as yet, we were not able to witness attempts of males to immigrate into colonies and/or to expel harem males from their territories, probably because such events are rare and short and hence difficult to observe. Further tentative evidence for a possible role of cooperation between colony males is provided by a learned vocal group signature that reliably associates males to their natal colony and allows the recognition of non-natal males (Knörnschild 2009).

The positive effect of the number of male residents on harem male tenure may appear to be confounded by shorter study periods of our smallest colonies (C5, ZOM, RS, and C2; Table 1). Short study periods might have prevented us from recording longer tenured harem males in our smallest colonies. However, several arguments speak against such a bias in our data. We did not find a significant relationship between the study periods for individual colonies and the number of male residents or the tenure duration of harem males. Indeed, 7 of 8 colonies (C5, RS, C2, BH2, RH, PH, and BH1; Table 1) were observed for 7–9 years and the seemingly short study periods (2–3 years) of the small colonies C5, RS, and C2 are caused by the disappearance of the bat populations of these colonies. As we show in Table 1, tenures of harem males whose tenure had not ceased at the end of our study are shorter than mean tenures of the harem males from the respective colonies whose tenure had already ended. In conclusion, we are therefore confident that 7–9 years of observation of 7 of 8 study colonies are sufficient for estimating reliable measures of harem male tenures for smaller and larger colonies.

It is unlikely that survival effects or habitat quality confounded the observed relationship between harem male tenure and the number of male coresidents per colony. Average number of males per colony and average colony size were highly correlated. This could indicate that prolonged tenure of males is a result of increased survival in larger colonies. To account for this possible confounding effect, we also estimated tenure durations for females roosting in our colonies. However, median female tenure per colony did not correlate with the mean number of males present per colony (Figure 1A) or with colony size. Furthermore, in 1 roost (BH), colony size dropped substantially within 1 year probably due to a disturbance event within the colony. Interestingly, harem male tenure was longer for males that roosted in the BH colony before 2002 (when the colony was larger: see BH1 in Table 1) when compared with harem males that roosted in the much smaller colony after 2002 (BH2). Also, differences in foraging habitat between study colonies cannot be severe because most colonies are found in close proximity (less than 2km) and *S. bilineata* easily overcomes such short distances when flying (Hoffmann et al. 2007). Therefore, we doubt that survival effects or variation in quality of foraging habitats confounded our analysis.

Harem males that defended territories with larger numbers of females succeeded in gaining higher annual breeding success. This is in accordance with results obtained by Heckel and von Helversen (2003) who, however, were not able to use measures of annual breeding success determined over the lifetime of harem males and who used data from only a single study colony. Also, our results may indicate that annual breeding success of harem males is lower when the number of males increases in a colony. This effect could be explained by our result that harem size tended to be smaller in colonies with

larger numbers of males. The GLM analysis (Table 4) suggests a negative effect of the average number of male residents on annual breeding success of harem males, whereas no such relationship was found between average annual breeding success of harem males per colony and the average number of resident males of a colony (Figure 1B). These contradicting results are probably due to the fact that the GLM was performed on individual bats, whereas the correlation analysis used colonies instead; if the average number of male residents indeed influenced annual breeding success of harem males, this effect was probably rather small. The fact that annual breeding success and harem male tenure were equally important in explaining variation in harem male LBS and that the number of male residents could have opposite effects on annual breeding success and harem male tenure suggests the possibility of a trade-off between tenure duration and annual breeding success as male numbers increase. Maybe there exists an optimal male group size in *S. bilineata*.

In conclusion, our results provide evidence that the social organization into several adjacent harems with associated non-harem males renders direct fitness benefits to males of the greater sac-winged bat. These direct fitness benefits are apparently large enough to offset the costs that accrue to males from competing with kin. Where permanent nonharem males were present, harem succession in the colony was significantly more often accomplished by natal (related) males. In addition, the maintenance of a patriline in a colony over long periods of time will benefit males in terms of indirect fitness when roosting together with several related male coresidents. Therefore, our results indicate that male direct and indirect fitness is positively affected by the social organization of this species and add to the tentative evidence that colony males may cooperate in excluding non-natal males from settlement. By taking into account an important feature of the social organization of greater sac-winged bats, our study sheds new light on the understanding of an exceptional and complex mating system in mammals and provides a basis that will allow us to better understand the evolution of male philopatry in polygynous and promiscuous mammals.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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