The economics of harem maintenance in the sac-winged bat, *Saccopteryx bilineata* (Emballonuridae)

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Abstract *Saccopteryx bilineata* has a polygynous mating system in which males defend females in a harem territory. Harem defense and courtship include energetically costly flight maneuvers and hovering displays. We tested if (1) harem males have a greater field metabolic rate than non-harem males or females and if (2) the field metabolic rate of harem males is correlated with the number of females in a harem territory. We measured the energy budget in 32 *S. bilineata* with the doubly labeled water method and compared these estimates with behavioral observations in the daytime roost. Among adult bats, field metabolic rate varied with body mass by an exponent of approximately two. We found no significant difference in field metabolic rate or mass-specific field metabolic rate between harem and non-harem males. The mass-specific field metabolic rate of harem-males increased with harem size. The latter finding supports the hypothesis that the energy costs of courtship display and territorial defense influence the energy budget of harem males. Overall, field metabolic rates of *S. bilineata* were lower than those of similarly sized bats of the temperate zone and only 2.3 times above the basal metabolic rate recorded for this species. We suggest that male *S. bilineata* did not take advantage of their metabolic capacity because a prudent allocation of energy to activities of harem maintenance is an adaptive strategy for males in this mating system.

Introduction

Models of sexual selection assume that many secondary sexual characteristics of males that are caused by female choice are costly to produce or maintain (Maynard-Smith 1991). Several types of cost that limit the expression of secondary sexual traits have been suggested, such as increased predation, risk of injury or death, and rate of metabolism (summarized by Andersson 1994). Physiological constraints are known to limit the performance of courtship in several species (Halliday 1987; Andersson 1994). For example, males with aerial displays encounter the high energy costs of flight (e.g., Møller 1991; Norberg 1991). The endurance or frequency of aerial displays may reflect the metabolic capacity of an individual and therefore females may select for the quality and quantity of aerial performances by males. Courtship displays are usually fueled by body reserves, which allow high instantaneous increases in metabolic rates [up to 20 times basal metabolic rate (BMR)]. The short-term increase in metabolism that males encounter during displays contrasts with the long-term or sustainable metabolic scope that reflects the upper limit of metabolism over a longer time period. For example, lekking sage grouse (*Centrocercus urophasianus*) experience field metabolic rates (FMRs) that exceed BMR by four times during the mating season (Vehrencamp et al. 1989). To meet the continuous high energy demand of courtship, lekking males usually mobilize fat reserves and increase their nutritional intake (e.g., Clutton-Brock et al. 1982; Vehrencamp et al. 1989). The highest sustainable, i.e., long-term, metabolic rate ever reported in a mammal was seven times BMR (e.g., Hammond and Diamond 1997). Even animals that are exposed to extreme conditions, like human athletes (Westterep et al. 1986) or lactating mammals in cold environments (Toloza et al. 1991; Konarzewski and Diamond 1994) cannot raise their metabolism above this physiological ceiling.
We were interested in knowing to what extent energetically costly courtship displays affect the FMR of competing males in a stable mating system. Our study species, *Saccopteryx bilineata*, has a harem-polygynous mating system (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976), where males defend, over several years, a small roost territory that is occupied by one or several females. Peripheral males without females roost adjacent to harems and occasionally interact with harem males and females. Colonies can reach up to 50 individuals with harem sizes ranging from one to eight females (Bradbury and Vehrencamp 1976; Voigt and von Helversen 1999). *S. bilineata* spends the daytime in well-illuminated buttress cavities of large trees, but they can also be found in or around buildings when human disturbance is low. Individuals typically roost on vertical surfaces and maintain minimum distances of 5–10 cm to each other. Male *Saccopteryx* scent-mark the boundaries of their harem territories and defend this area against intrusions by other males (Bradbury and Emmons 1974). In the daytime roost, females are aggressive toward one another and males, which presumably influences harem size and composition (Bradbury and Vehrencamp 1976). Males are smaller than females and are usually inferior in encounters with females—males move away from aggressive females (Bradbury and Emmons 1974; C.C. Voigt, personal observation). Harem groups are relatively stable throughout the year, but females occasionally move between harems or between colonies, especially between October and February in Costa Rican colonies (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976). Based on these observations, Voigt and von Helversen (1999) suggested that the potential for female choice is high in this mating system. This conclusion was supported by a study of maternity patterns in *Saccopteryx* roosts, which demonstrated that harem males are not the exclusive fathers of the harem offspring (Heckel et al. 1999). However, male reproductive success was on average correlated with harem size (Heckel 2000).

Adult males try to attract females into their harem territory using various acoustic, visual, and olfactory displays. One of the most distinguishing displays is a hovering flight, during which odor is fanned toward roosting females (Bradbury and Vehrencamp 1977; Voigt and von Helversen 1999). The odor is stored in sac-like organs of the propatagial membrane, originating from urine, saliva, and secretions from the genital and gular region (Voigt and von Helversen 1999). During a stereotypic behavior each afternoon, adult *S. bilineata* males blend these odoriferous liquids into their wing sacs. Hovering displays of males can last up to 14 s but, on average, are 2 s in duration. Male *Saccopteryx* perform hovering displays continuously throughout the year although copulations occur only during 2 months (C.C. Voigt, personal observation). The number of hovering displays and flight maneuvers by males in the daytime roost correlated with the number of females in their harem (Voigt and von Helversen 1999). Because of the high energy costs of flight (Winter and von Helversen 1998; Voigt 2000), especially hovering flight (Norberg et al. 1993; Voigt and Winter 1999), we predicted that (1) FMR of males would be correlated with harem size and that (2) FMR of harem males would exceed that of non-harem males or females. We tested these predictions by measuring FMR in *S. bilineata* using the doubly labeled water (DLW) method (summarized in Speakman 1997). In addition, we performed behavioral observations in the daytime roost to quantify harem size and composition.

**Methods**

We evaluated the energy costs of harem maintenance in *S. bilinea-ta* in colonies near the "La Selva" biological station (Organization for Tropical Studies, Costa Rica, Province Heredia, 10°25′ N, 84°00′ W) during November and December 1994, October 1995, November 1996, and December 1998 through early February 1999. None of the experimental days were affected by heavy rainfall. The periods of study correspond to female recruitment or mating in Costa Rican colonies of *S. bilineata* (C.C. Voigt, personal observations). Our three study colonies were located in abandoned cottages surrounded by secondary rainforest or plantations. Most behavioral studies that have been reported by our group in previous papers were conducted in a different colony. Roosts A and C were located adjacent to Rio Puerto Viejo, whereas roost B was situated in the National Park of Braulio Carillo at the border to the La Selva property. Colony size varied during our study but ranged from 10 to 20 individuals in colonies A and B and about 5 in colony C. Starting in 1994, we hand-netted bats in the roosts. On these occasions, we placed colored or numbered plastic bands (Hughes) around the forearm of each bat. Females were banded on the left and males on the right forearm. All captured bats were weighed (Pesola-scale, accuracy 0.1 g), and sex and reproductive condition were recorded. We refer to juvenile males as those individuals that had a propatagial sac without a white lining and containing no odoriferous substance. We refer to juvenile females as those with pink nipples as opposed to the black nipples characteristic of post-lactating females.

Prior to the DLW experiments, we determined the sites of encounters between territorial males to locate the boundaries of each harem (Bradbury and Emmons 1974; Voigt and von Helversen 1999). During the first year of our study, we performed 3–14 censuses in a 3-week period before a DLW experiment to estimate harem size. We found that harem ownership and the number of females in a harem was consistent during subsequent censuses. Thus, we determined harem size in subsequent years only on the day of the DLW experiment, shortly before capturing the bats.

**DLW experiment**

We performed DLW experiments on 17 adult males (22 measurements), 6 subadult males (6 measurements), 5 adult females (6 measurements), and 4 subadult females (4 measurements). We conducted repeated measurements during subsequent years with 4 males and 1 female. Another repeated measurement was performed with a fifth male after the bat changed its social position from a non-harem to a harem male.

To capture individuals for a DLW experiment, we closed all openings of the buildings (A and C), and then hand-netted single individuals from the wall. Because we could not completely close all openings of building B we set up 6- or 4-m mistnets in the building and also hand-netted bats. Captured bats were transferred to a holding cage made out of mosquito netting (0.5 m²). After weighing and marking each bat as described above, we subcutaneously injected a sterile solution of DLW into each bat (volume: 50–100 μl; enriched with oxygen-18 by 15–30 atom% and with
deuterium by 5–9 atom%) at approximately 1000 hours (mean 0948 hours ± 58 mins SD). For equilibration of isotopes in the body water pool, bats were returned to the holding cage for an average of 1.5 h (±20 min SD). From each bat we took approximately 40–50 µl of blood into a hematocrit tube. All tubes were immediately flame-sealed and stored at about -4°C until analysis. After blood sampling and weighing, bats were released in their daytime roosts. On the following morning, the procedure was repeated and blood was taken at approximately the same time as on the previous day.

DLW experiments were conducted over 23.9 h (±0.4 h SD). In two cases, we sampled blood after 48 h. We define the daily change in body mass as the difference in the two measurements of body mass at the time of blood sampling. Total body water was measured for five sacrificed individuals. After weighing and euthanizing the bats, we dried the carcasses at 90°C for 2 days to constant dry mass. Percent total body water averaged 72.5% (±3.1% SD). Background samples of oxygen-18 and deuterium isotopes were taken from at least two individuals during each study period (mean for oxygen-18 = 0.19963 atom%, n = 17; mean for deuterium = 0.15227 atom%, n = 17).

Blood samples were distilled after Nagy (1983). We used the guanidine-hydrochloride method described by Wong and Klein (1986) and Wong et al. (1987a, 1987b) for the preparation of isotopic oxygen and deuterium concentrations (Coleman et al. 1989; Kendall and Coplen 1989) for the preparation of hydrogen isotopes. Samples were analyzed at least in duplicate using a Finnigan Delta-S isotope mass spectrometer in Boston University Stable Isotope Laboratory. After every sixth sample, we analyzed a laboratory standard in duplicate. We assumed that the evaporative water loss of S. bilineata is similar to that of same-sized temperate insectivorous bats (25% of total water flux; Speakman 1997) and calculated FMR with Eq. 7.17 in Speakman (1997). The carbon dioxide production rate (CO2, mol h⁻¹) was converted to FMR after Lusk (1976) assuming a respiratory quotient of 0.8 and by multiplying the result by the duration of the experiment. All calculations were performed with Microsoft Excel (Version 97). Statistical analyses were performed with SPSS (Version 4.00) on mean values for individuals.

**Results**

A total of 32 S. bilineata (38 measurements) were used for DLW experiments in this study. Body mass for adult males averaged 7.7 g (±0.3 g SD, n = 17) and 8.0 g (±0.2 g SD, n = 6) for adult females. Adults were heavier than subadults of the same sex (subadult females: 7.2 g ±0.6 g SD, n = 4; subadult males: 7.2 g ±0.5 g SD, n = 6). We found differences in body mass by age but not by sex (two-way ANOVA, age: F1,32 = 12, P < 0.005; sex: F1,32 = 0.02, P > 0.05; interaction: P > 0.05). Body masses of harem males and non-harem males were not significantly different (t-test, t17 = 0.44, P > 0.05). Bats did not lose significant amounts of body mass during the DLW experiments (0.06 ±0.21 g day⁻¹ SD; two-tailed t-test, t32 = 1.45, P > 0.05).

The mean ratio between oxygen-18 and deuterium washout rate (ko/kd) was 1.38 (±0.10 SD). Adult male Saccopteryx had a mean FMR of 15.4 ±2.9 (SD) kJ day⁻¹ (n = 17) compared to 13.5 ±3.0 kJ day⁻¹ (n = 6) for subadult males. Similarly, FMR was slightly higher in adult females (17.0 ±2.9 kJ day⁻¹, n = 6) compared to subadult females (16.0 ±2.2 kJ day⁻¹, n = 4). FMR was significantly correlated with body mass among adult individuals (Fig. 1). We therefore controlled for body mass when comparing FMRs...
Fig. 3 Mass-specific field metabolic rate (mFMR; kJ g$^{-1.97}$ day$^{-1}$) of male *S. bilineata* in relation to harem size. Harem size explains 38% of the variability in FMR. The regression equation for the correlation between mFMR and harem size is: mFMR=0.226 (±0.019 SE)+0.019 (±0.007 SE)×n (with n=number of females in a harem). The slope of the regression line was significantly different from zero (see text).

between individuals. Neither FMR nor mass-specific FMR was significantly correlated with sex or age (two-way ANOVA, age: $F_{1,32}$<1.5, $P$>0.05, sex: $F_{1,32}$<3.2, $P$>0.05, interaction: $P$>0.05; Fig. 2). The average FMR of harem males was 14.9±1.4 (SD) kJ day$^{-1}$ (n=13) or 0.27±0.04 (SD) kJ g$^{-1.97}$ day$^{-1}$ (n=13) and for non-harem males 16.6±2.8 kJ day$^{-1}$ (n=5) or 0.30±0.04 kJ g$^{-1.97}$ day$^{-1}$ (n=5) (Fig. 2). The mean FMR and mass-specific FMR were not significantly different between harem and non-harem males ($t$-test, $t_{16}$<1.3, $P$>0.05; Fig. 2).

We performed two repeated measurements with four males and three measurements with a fifth male. All these repeated measurements were conducted during different years, except for one male. The intra-individual variation of FMR was low for most of these males and the size of the specific harem was stable between days of measurement. The variation of FMR for the male with three data points was significantly lower than the overall variation among all adult males ($F_{19,2}$=157, $P$<0.05). In two males, we found a considerably large range of FMRs. M21 had a high FMR of 15.3 kJ day$^{-1}$ (equivalent to 0.266 kJ g$^{-1.97}$ day$^{-1}$) as a subadult bat compared to the next year’s measurements as an adult (FMR=14.0 kJ day$^{-1}$; mass-specific FMR=0.252 kJ g$^{-1.97}$ day$^{-1}$). The repeated measurement for M22 was taken in the same year. As a non-harem male, M22 had an FMR of 16.2 kJ day$^{-1}$ (mass-specific FMR=0.273 kJ g$^{-1.97}$ day$^{-1}$) and 1 month later as a harem male defending a single female, an FMR of 12.8 kJ day$^{-1}$ (mass-specific FMR=0.228 kJ g$^{-1.97}$ day$^{-1}$).

The following comparison of mass-specific FMR between males with varying harem size is based on mean values of adult males. We consider males without females in their territory as a separate group because the underlying cause of female absence may be a different reproductive strategy compared to harem males. Mean values of mass-specific FMR were positively correlated with the number of females in a male’s territory (Fig. 3).

The slope of a regression line calculated with the least-squares method was significantly different from zero ($r^2$=0.38; $t$-test: $t_{12}$=2.6, $P$=0.024). Thus, mass-specific FMR of males was correlated with the number of females defended by a male in his territory.

**Discussion**

Male *S. bilineata* usurp and defend territories in their daytime roosts, and females roost within these territories (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Males also recruit and retain females in their harem with energetically costly flight maneuvers (e.g., hovering flight: Voigt and Winter 1999; horizontal flight: Winter and von Helversen 1998; Voigt 2000). The number of hovering flights and flight maneuvers performed by a male each day correlates with the number of females in his harem (Voigt and von Helversen 1999). Thus, we predicted the FMR of harem males to be correlated with the number of females in a territory and that harem males would have a higher FMR compared to non-harem males. To test these hypotheses we conducted DLW experiments and compared individual FMR with behavioral observations in the daytime roost.

In support of our first prediction, we found that the mass-specific FMR of harem males was correlated with harem size (Fig. 3). This increase in energy turnover may have resulted from the necessity to defend a harem and to recruit females on the wing. In contrast to our second prediction, the mean mass-specific FMRs of harem and non-harem males were not significantly different (Fig. 2). The variation in mass-specific FMRs was large for both groups of adult males. Some of the variation in FMR among harem males resulted from a varying number of females in the harem and the associated increase in energy costs (Fig. 3). Most non-harem males roosted in close proximity to a harem (see also Bradbury and Emmons 1974; Bradbury 1977; Voigt and von Helversen 1999) and interacted frequently with adjacent males and females. Bradbury and Emmons (1974) also suggested that during nightly foraging, males cover large areas that include foraging patches of females. Although we lack quantitative data on nightly foraging behavior, we suggest that male *Saccopteryx* possibly exhibit alternative costly mate-searching tactics similar to those found, for example, in the common shrew (Stockley et al. 1994, 1996). In a population of the common shrew, Stockley and colleagues found that the majority of males established large overlapping ranges in areas of relative high female density, while a minority occupied small exclusive ranges and made repeated long-distance movements to visit female ranges. Because of the high epididymal sperm counts of the latter group, Stockley and co-workers suggested that these males compensate their lower competitive ability in direct combat by increasing their sperm production, i.e., by competing indirectly through sperm competition. Analysis of reproductive success by DNA fingerprinting revealed that males with such a
strategy indeed gained reproductive success, although the mean success of the dominant males was greater. Similarly, Heckel (2000) found that peripheral males of *S. bilineata* father offspring in colonies of *S. bilineata* and that harem males are on average most successful. At least during the night, *Saccopyrtex* individuals are widely dispersed and males may therefore be unable to monopolize their mating partners. Thus, sperm competition could be a component of the *Saccopyrtex* mating system. Sperm numbers, mobility, and the ability to win direct combats may be important determinants for mating success in *S. bilineata*. Differences in the flight activity among males in the daytime roost may not be mirrored in daily energy expenditure of males if those individuals that are less active in the roost cover larger distances during the night in search of potential mating partners.

We found that the FMR of *S. bilineata* varied with body mass by an exponent of approximately two. The scaling relationship of FMR and body mass between bat species (inter-specific comparison) has a lower mass exponent of approximately 0.73 (Speakman and Thomas, in press). The few studies focusing on intra-specific variation in FMR indicate that among other species as well, FMR varies with a mass exponent greater than one. Berteaux et al. (1996), for example, found that the FMR of a rodent varied with a mass exponent of 1.25. This is consistent with the general pattern found in vertebrates. Energy expenditure varies to a greater extent with body mass when individuals of the same species are compared than when different species are compared (e.g., McLean and Speakman 2000; Voigt 2000).

On average, bats did not loose body mass during the DLW water experiments. This suggests that the treatment did not affect the time or energy budget of the study animals. Similar to other DLW studies, the variability in the data was relatively large. Despite biological factors such as individual activity patterns, or varying microclimatic conditions, other factors may have contributed to this variability. Most DLW studies exhibit variability that is presumably caused by the sampling protocol or the procedure of isotope analysis (Speakman 1997). In the present study, the most important potential sources for errors were (1) variation in background isotope concentration, (2) variation in total body water content, and (3) variation in the extent of fractionated-water loss. With our experimental design, we could not control for these factors in individual bats. However, C.C. Voigt, O. von Helversen, R.H. Michener and T.H. Kunz (unpublished data) conducted a validation study with the nectar-feeding bat *Glossophaga soricina* and showed that the DLW method provides accurate estimates of FMR with bats in a humid environment.

Despite the high species richness of the order Chiroptera (>920 species; Koopman 1993), FMR has been measured in only 9 species (summarized in Speakman and Thomas, in press). Our experiment with *S. bilineata* represents the first measurement of FMR in the family Emballonuridae. *S. bilineata* showed the lowest of all FMRs in bats measured to date and only half of the FMR of similar-sized, lactating *Pipistrellus pipistrellus* (7.6 g; Racey and Speakman 1987). This difference may reflect the fact that the pipistrelle bats under study experienced metabolic stress when nursing their young. In addition, *P. pipistrellus* roosts provide lower average roost temperatures compared to *Saccopyrtex* roosts [17°C for *P. pipistrellus* in Speakman and Racey (1988), compared to approximately 28°C in *Saccopyrtex* colonies (C.C. Voigt, personal observation)]. Neither our behavioral observations nor the study of thermoregulatory abilities (Genoud and Bonaccorso 1986) indicate that *S. bilineata* is capable of torpor. Thus, the low FMR of *S. bilineata* cannot be explained by metabolic suppression. The daily metabolic scope (ratio between FMR and daily BMR) of male *S. bilineata* averaged only 2.3, which was lower than the average value for all other bat species studied to date using the DLW method (mean=3.8, calculated from values in Speakman and Thomas, in press). In a similar study, Kunz et al. (1998) found that harem-defending male *Phyllostomus hastatus* (Phyllostomidae) had a daily metabolic scope of 4.8 [calculated from FMR in Kunz et al. (1998) and BMR from McNab (1969)]. This more than twofold difference may be explained by the greater size of *Phyllostomus* compared to *Saccopyrtex* and the associated increase in metabolic scope with size (Hammond and Diamond 1997). However, male-male competition in *Phyllostomus* could also have contributed to the larger metabolic scope. Vehrencamp et al. (1989) found that FMR of lekking male grouse was on average by four times greater than BMR, which they noted was probably close to the maximum sustainable rate. Given that mate competition is presumably high in *S. bilineata*, and other similarly sized species exhibit higher rates, the low metabolic scope of male *S. bilineata* is unusual.

An explanation for this finding may be that males invest cautiously in activities associated with harem maintenance. An important influence in the mating system of *S. bilineata* is probably endurance rivalry (the persistence of males at the breeding site; see Andersson 1994). In stable colonies of *S. bilineata* it may be advantageous for males to allocate energy economically to activities associated with female recruitment and territorial defense if this enables them to persist in the colony over a prolonged period. Prudence and persistence could create a higher lifetime reproductive success compared to energetic extravagance and early death.

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