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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 (BMR) 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.

**Keywords** Doubly labeled water · Field metabolic rate · Harem · *Saccopteryx bilineata*

**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 (Westerterp 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 paternity 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 Emmons 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. bilineata 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 from mosquito netting (0.5 m³). 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...