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Storage and display of odour by male
*Saccopteryx bilineata* (Chiroptera, Emballonuridae)

Abstract Males of the sac-winged bat, *Saccopteryx bilineata*, actively fill their propatagial sacs with secretions from the genital region, the gular gland, urine and saliva. From our observations and those of Starck we deduce that propatagial sacs in *S. bilineata* do not have a glandular function, but are instead organs for the storage and display of odours. In addition to the already known “salting” and hovering behaviour of male *S. bilineata*, we describe in detail how odour is fanned to roosting individuals during the complex, stereotyped hovering displays. *S. bilineata* males also coat the fur of their backs with saliva using the wing tip and might scent-mark territory boundaries. “Yawning” may represent a visual as well as an olfactory cue. Odour seems to play an important role in the social communication of *S. bilineata* and in other emballonurids, as revealed by the broad distribution of wing sacs in this family. *S. bilineata* males display odour during energetically costly hovering flights in front of females. We demonstrate that the number of hovering displays increases with harem size. The mating effort of *S. bilineata* males comprises a multimodal signalling behaviour. Although males defend harem territories in which females gather, females seem to be able to choose the father of their progeny freely among the males of a colony. This may have led to the evolution of the complex mating displays by male *S. bilineata*.

Key words *Saccopteryx* · Propatagial sacs · Emballonuridae · Odour · Hovering display

Introduction

Olfactory cues, and especially their role in mate choice, have been increasingly investigated by sociobiologists (e.g. Huck et al. 1981; Drickamer 1992; Vollrath and Milinski 1995; Edwards and Hedrick 1998; Penn and Potts 1998). In mammals, the use of scents as a sexually selected trait is supported by the finding that males usually have more and larger glands, especially in polygynous species where male-male competition is expected to be intense (Blaustein 1981; Andersson 1994). The role of olfaction in female choice is probably a common and general phenomenon (Penn and Potts 1998), however, it has been demonstrated only in a few cases (e.g. Reece-Engels 1988; Kavaliers and Colwell 1992, 1995a,b). The reliability of an odour for female choice could result from its being costly to produce or impossible to fake (Penn and Potts 1998). Kavaliers and Colwell (1992, 1995a,b) demonstrated that female mice distinguish between the odour of parasitised and unparasitised males and that they are repelled by experimentally infected males. In addition, olfactory cues may honestly inform females about the genetic compatibility at loci that control the immune response, thereby generating progeny that are more immunocompetent when mating partners are MHC dissimilar (e.g. Wedekind et al. 1995).

Bats are underrepresented in studies of olfactory communication, although they are known to have a wide variety of odour-producing organs (Quay 1970). Almost every part of a bat’s body seems to be suitable for the production of odour. Most glands are located on the head, especially around the mouth, such as the buccal, pararhinal, labial and gular glands (Dalquest et al. 1952; Dabson et al. 1977; Nowak 1994); others are situated on the shoulders and the axillary region (Quay...
Glandular regions are often equipped with large hair tufts, like the erectile interaural crest of male Tadarida chapini (Fenton 1985). Some members of the family Emballonuridae (e.g. Saccopteryx and Balantiopteryx) have evolved sac-like organs on the propatagial wing membrane (Starcck 1958; Goodwin and Greenhall 1961). These propatagial sacs have previously often been considered as glands (Quay 1970; Bradbury 1977; Fenton 1985), although Starck (1958) revealed the absence of secretory cells in the sac epithelia of Saccopteryx bilineata and Balantiopteryx plicata. Bradbury and colleagues investigated the sociobiology and ecology of S. bilineata (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). This species has a seasonal invariable harem-polygynous mating system (Tannenbaum 1975; Bradbury 1977; Bradbury and Vehrencamp 1977). Colonies include up to 50 individuals and are organised into so-called “harem” groups, each consisting of one territorial male and several females (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Harms are sometimes accompanied by peripheral males. Besides defending a harem territory against other males, harem males also attempt to recruit and retain females through various visual, olfactory and acoustic displays (Bradbury 1977).

We studied the behaviour of male S. bilineata with respect to the production and use of propatagial scents. Our observations show that adult males of Saccopteryx transfer secretions from the genital and gular regions in a stereotypic manner into the propatagial sacs, and that males fan the propatagial odour to females during two complex displays. One of these displays consists of complicated stereotypic wing movements during hovering by which males seem to puff odour to a roosting female.

Flight manoeuvres in general and hovering flights in particular are energetically costly (Norberg 1990; Winter 1998; Winger et al. 1998; Voigt and Winter 1999). A costly display of odours could therefore contribute a multimodal signal that contains information on a male’s quality. We tested the hypothesis that harem males with a large number of females in their territory show a higher energetic effort for the display of odours than males with only a few females, by comparing the number of hovering displays and flight manoeuvres of males with different harem size in the same colony.

**Methods**

Behavioural observations were carried out in a colony of S. bilineata near the biological station La Selva of the Organization for Tropical Studies (Costa Rica, Province Heredia, 10°25’N/84°00’ W) from October to December 1994–1996. The colony averaged 50 adult individuals and was located inside an abandoned building. Beginning in 1994, we mist-netted bats as they emerged at dusk from their roost. For identification during the day, we attached numbered or coloured plastic rings (Hughes) around the forearm. We weighed all captured individuals (Pesola scale, accuracy 0.5 g), took morphometric measurements and noted the sex and reproductive condition. For a study of the paternity pattern within the colony (Heckel et al., in press) we took 4-mm-diameter tissue samples from the plagiopatagial membrane using a biopsy punch.

In advance of our study, we habituated the animals in the daytime roost to the presence of human observers. In addition, we never caught bats closer than 5 m from the daytime roost. As a result, the bats allowed us to observe the colony without causing disturbance. Daily activity budgets of colony members were registered with an infrared-sensitive camera (Sony) and a portable VCR (Panasonic). When light levels were low we used an electric torch covered with an infrared filter (750 nm) for illumination.

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The course of a day in a colony of S. bilineata

The first members of the colony approached the day roost from the surrounding forest and flew around the building at beginning of dawn (at approximately 0500 hours), emitting social calls in flight or from a roosting position and occasionally still hunting for insects. Having entered the day roost at approximately 0513 hours (± 5 min SD), most territorial males immediately landed in their territory which usually did not exceed 1 m² of the inner wall of the building (Fig. S1). A few males settled at the periphery of another male’s territory. These “satellite males” often interacted with the harem holder during the whole day, for example through vocal communication or even physical encounters (e.g. flight chases). Both territorial and satellite males performed songs regularly but mostly when a female entered the colony. Other “peripheral males”, especially subadult males, were more passive in the quieter areas of the building near the ceiling.

Females on average appeared in the day roost after the males, at 0524 hours (± 9 min SD). As soon as a