Chapter 14
The Wing-Sac Odour of Male Greater Sac-Winged Bats *Saccopteryx bilineata* (Emballonuridae) as a Composite Trait: Seasonal and Individual Differences

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Abstract Male *Saccopteryx bilineata* possess a sac-like organ for the storage and display of odoriferous secretion in their front wing membrane. Since males use the scent in agonistic and courtship activities, and compose it from different secretions of distinct sources, like saliva, urine and gland secretion, we hypothesized that multiple information is encoded in the male scent-profile. We expected that the odour profile of males varies seasonally, giving information on male reproductive status. In addition, the odour profile ought to vary between individuals, thus providing the possibility for individual recognition. We repeatedly collected samples from wing-sac liquids of 20 male *S. bilineata* in five Costa Rican colonies during the mating and non-mating season. Samples were analysed by gas chromatography coupled to mass spectrometry to compare wing-sac contents. Wing-sac odours included various substances such as carboxylic acids, terpenoids and aromatic compounds. Male scent profiles varied (1) between seasons in the relative amount of tetradecanoic and octadecanoic acid, and (2) between individuals in the relative amount of two species-specific substances. These results suggest that the wing-sac liquid of male *S. bilineata* is indeed a composite trait and may be useful for the simultaneous transfer of multiple information.

14.1 Introduction

Selection, natural as well as sexual, may shape signals in various ways when communication signals enhance or reduce the signallers' fitness. Although signals are often associated with a particular message, they often convey several messages. This has been demonstrated for acoustical signals (Runkle, Wells, Robb and Lance 1994), visual signals (Badyaev, Hill, Dunn and Glenn 2001; Basolo and Trainor 2002;

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Grether, Kolluru and Nersissian 2004; Robson, Goldizen and Green 2005) as well as chemical signals (Buesching, Waterhouse and Macdonald 2002a, b). Signals, especially in long living species, in which reproduction is not limited to a single lifetime event and social groups are formed for a long time are often under multiple selective forces. To facilitate individual recognition, signals should carry a predictable individual signature. At the same time, potential mates should prefer signals that present a snapshot of the momentary health and social status of the signaller, selecting for ultimately honest signals (e.g. scents: Penn and Potts 1998). Lastly, hormonal changes during different reproductive status should be encoded in the signal if potential mates aim to assess the reproductive status of a potential mate (Marler 1961). Thus, either distinct signals encoding each type of information separately, or composite traits encoding simultaneously for more than one type of information, are required.

Composite traits have been found in different modalities among several organisms across the animal kingdom, e.g. in green swordtails, *Xiphophorus helleri* (Basolo and Trainor 2002), or the European badger, *Meles meles* (Buesching et al. 2002a, b). Studies on house finches, *Carpodacus mexicanus*, have shown that the plumage colour acts as a composite trait (Badyaev et al. 2001). Several independent components of the ornament, like coloration, pigment asymmetry or patch area asymmetry had different fitness consequences (Badyaev et al. 2001).

In mammals, olfactory cues play an important role in sexual selection, both during matechoice and male contests (Andersson 1994) and as olfactory cues are almost always multi-component, they provide a multitude of possibilities to encode information (Albone 1984) . Chemical signals may provide information about health (Penn and Potts 1998; Kavaliers, Colwell, Braun and Choleris 2003; Zala, Potts and Penn 2004), dominance status (Gosling and Roberts 2001), sex and group membership (Hofer, East, Sämmang and Dehnhard 2001; Safi and Kerth 2003) respectively population affiliation (Hayes, Richardson, Claus and Wyllie 2002).

Greater sac-winged bats, *Saccopteryx bilineata*, have a large behavioural repertoire that involves among others the use of odour (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). Males possess, in contrast to females, a pouch in their front wing membrane, which is used to store and display odour (Voigt and von Helversen 1999). The wing sacs are free of secreting cells (Starck 1958; Scully, Fenton and Saleuddin 2000) but contain an odoriferous liquid (Bradbury and Emmons 1974). Male greater sac-winged bats show a unique behaviour during which they clean and actively refill the wing-sacs daily during a stereotypic time-consuming two-stage process with various odoriferous secretions from different body regions (Voigt and von Helversen 1999; Voigt 2002, 2005). Microbial analysis of the wing pouches showed that males have on average fewer microbes in the wing-sac than females in their rudimental pouch, and that every male has on average two out of 40 different microbes in their wing-pouch, possibly indicating an individual microbial flora (Voigt, Caspers and Speck 2005). The mating system of greater sac-winged bats has been described as harem-polygynous (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976), since the basic social unit within a colony comprises of a single adult male and a varying number of females. In the remainder of the text we refer to these social units as harems and to the territorial male as the harem male. Harem males display their wing-sac odour throughout the year during aerial displays and also when roosting next to a colony member or in agonistic male-male encounters. The most frequent odour display is a hovering flight during which males remain airborne in front of a female for a few seconds (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Voigt and von Helversen 1999; Voigt, von Helversen, Michener and Kunz 2001; Voigt 2005). This behaviour can be observed throughout the whole year, although it is more often performed by males prior and during the mating season (Voigt and Schwarzenberger 2007). Voigt and von Helversen (1999) argued that the potential for female choice in *S. bilineata* is large, because females are larger than males and have control over copulations (Tannenbaum 1975). This is also reflected in a high percentage (70%) of extra harem paternities (Heckel, Voigt, Mayer and von Helversen 1999). Thus, it is very likely that the chemical signals of male greater sac-winged bats may be shaped by sexual selection.

The wing-sac odour of male greater sac-winged bats is involved in several behaviours, is a mixture of several secretions from different body regions, and filled into a specialized storage organ, which makes *S. bilineata* a suitable subject for the study of compositional chemical traits. We hypothesized that the wing-sac odour of male *S. bilineata* is a compositional trait. We collected wing-sac secretion of 20 male individuals during different reproductive seasons, analysed the volatiles using a gas chromatograph linked to a mass spectrometer (GC-MS) and predicted that scents ought to carry information about (1) reproductive status and (2) individuality in male greater sac-winged bats.

14.2 Material and Methods

14.2.1 Study Population

All samples were collected from a population of greater sac-winged bats at La Selva Biological Station administered by the Organization for Tropical Studies (OTS) in Costa Rica. La Selva Biological Station (10°25’ N, 84°00’ W) is surrounded by tropical lowland rainforest at an elevation of approximately 100 m. Odour samples were collected during three field seasons (September 2003 to January 2004, August 2004, and December 2005 to March 2005) from individuals of five different colonies, all located in abandoned cottages surrounded by primary and secondary growth forest. Individuals were mist-netted in the morning between 0500-0600 hours, when they returned to their day-time roost or alternatively in the daytime roost, close after they returned early in the morning (0600-0830 hours) using nylon mist-nets (Avinet, CH2, Mist Net, 38 mm mesh in 50 denier, 2-ply nylon, 4 shelves, net size 2.6 m). We collected odour samples from all caught males, weighed them, and noted sex and reproductive condition. For individual recognition all individuals were marked with coloured plastic bands (Hughes, size XCL) on the forearm. Immediately afterwards all bats were released at the site of capture. None of the captured individuals disappeared from the daytime roost after data and sample collection.

14.2.2 Sample Collection

Odour samples were collected from *S. bilineata* by wiping out the wing-sac with a piece of cotton (Hartmann DIN 61640-CO, 100% cotton). Female odour samples were taken by wiping out the rudimental part of the wing sac (for pictures of the wing-sac and the wing-sac rudiment see Voigt et al. 2005). The cotton was washed with dichlormethane and dried prior to taking odour samples. We wiped out only one wing-sac each time we took a sample and alternated the wings between subsequent sampling events to ensure that the impact of sample collection was as low as possible and had minimal influence on the subsequent sample of the same individual. Samples were stored in Teflon-capped glass vials (2 ml) and 100 µl of dichlormethane were added to each sample for preservation. In total 41 samples from 20 different males in five colonies were analysed.

To test for seasonal variation of wing-sac odours, we collected odour samples from seven different males. Each of the seven males was caught once during the non-mating season (August 2004) and once during the mating season (December 2003 – January 2004 or December 2004 – January 2005). To test for the individuality of wing-sac odours, samples from adult males caught at least three times were used.

14.2.3 Chemical Analysis

Odour samples were analysed by GC and GC-MS using a Hewlett-Packard 5890 gas-chromatograph equipped with a 30 m J & W (J&W Scientific, Folsom, CA) DB5-coated capillary column and a linked Hewlett-Packard mass selective detector (MSD; 70eV EI). Dichlormethane extracts of the cotton samples were concentrated to approximately 5µl prior to analysis. Data were collected under the following GC conditions: 1.5µl split-less injection, helium as carrier gas, 60°C inlet temperature, 3 min initial time, 10°C/min rate, 280°C final temperature, 20 min final time. In addition, GC-MS chemical ionisation and high resolution experiments were performed with a VG 70-250 SE mass spectrometer on 30 m DB5MS and 50 m CPSil88CB capillary columns. For analyses the proportion of each peak area to the total peak area was calculated in percent (%). The following criteria were applied to choose substances for more detailed analysis: a) male specificity, b) fatty acids, and c) steroids. Substances fulfilling these criteria were compared using the relative contribution of their peak area in relation to the total peak area of all selected substances.

14.2.4 Statistical Analysis

Statistical analyses were performed with SPSS 8.0. We used a Wilcoxon signed ranks test to test for seasonality. To test for individuality we used a general linear model (GLM) with either individual or colony as a fixed factor. All tests were two-sided. For the parametric tests we used only homogenous and normally distributed data, transforming data using natural logarithms (1+ln) prior to statistical analysis if necessary.

14.3 Results

In total, 185 substances were found in the wing-sac liquid of male *S. bilineata* from a Costa Rican population. For a more detailed analysis the relative peak area of thirteen focus compounds was compared (Table 14.1). Of these nine were male-specific substances (indole, indol-3-carboxaldehyde, indole-3-carboxylic acid, 2-aminoacetophenon, anthranilic acid, 5H,10H-dipyrrolo[1,2-a:1′,2′-d]pyrazine-5,10-dione (pyrocoll), indolo[2,1-b]quinazoline-6,12-dione (tryptanthrin), 2,6,10-trimethyl-3-oxo-6,10-dodecadienolide, and a compound $C_{15}H_{24}O_2$ of unknown structure), three were fatty acids (tetradecanoic acid, hexadecanoic acid, and octadecanoic acid), and one a steroid (cholesterol). On average, the cumulative peak area of these substances made up 62.5 ± 20.7% of the whole chromatogram area.

14.3.1 Seasonality

Odour samples of seven males were compared between the non-mating season (August) and the mating season (December). None of the thirteen analysed substances was absent during either season. However, there was a significant differ-

Table 14.1 The thirteen focus scent compounds found in the wing-sac secretion of male *S. bilineata* sorted by their mean relative contribution (%) to the cumulative peak area of the focus substances. The table also shows the results of the GLM (fixed factor: individual) we used to compare the variances within the individuals and between individuals.

Substance	Mean±Std	Min-Max	*P*
Cholesterol	24.9 ± 12.0	0 - 62.6	0.02
Hexadecanoic acid	23.9 ± 14.7	6.9 - 67.4	0.19
$C_{15}H_{24}O_2$	17.1 ± 8.0	0 - 30.0	0.001***
Tryptanthrin	9.3 ± 4.7	1.9 - 18.5	0.52
Pyrocoll	6.4 ± 9.1	0 - 42.2	0.015
Octadecanoic acid	6.0 ± 4.7	0 - 21.8	0.34
2,6,10-trimethyl-3-oxo-6,10-dodecadienolide	4.9 ± 2.4	0 - 8.6	$<$ 0.001***
Anthranilic acid	2.8 ± 4.0	0 - 20.1	0.40
Indole-3-carboxylic acid	1.3 ± 1.8	0 - 4.1	0.15
Indole	1.3 ± 1.1	0 - 5.1	0.65
Indole-3-carboxaldehyde	1.2 ± 1.1	0 - 4.2	0.16
Tetradecanoic acid	0.8 ± 0.9	0 - 3.7	0.48
2-Aminoacetophenon	0.1 ± 0.2	0 - 0.7	0.06

***significant after Bonferoni correction

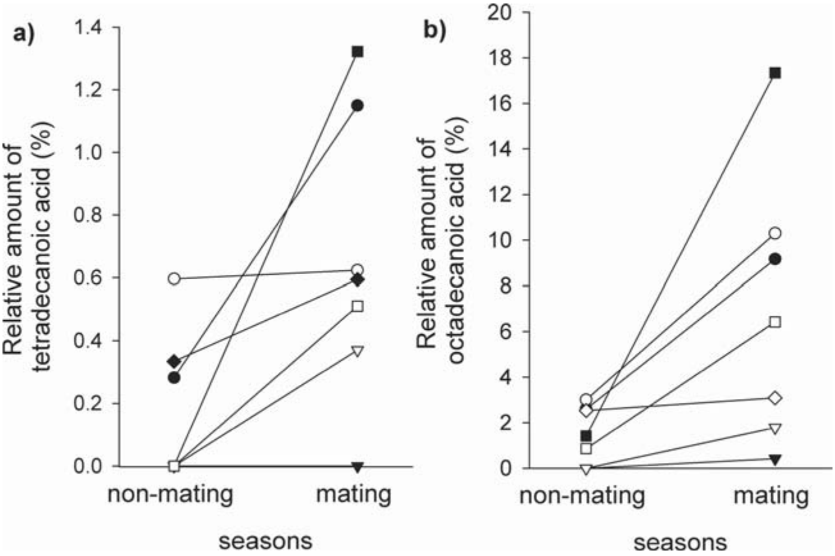

Fig. 14.1 The percentage peak area of tetradecanoic acid (a) and octadecanoic acid (b) in relation to the other twelve focus substances in the wing-sac liquid of seven male *S. bilineata*. Samples of the same individual from the non-mating season (July-August) and the mating season (December) are connected by a line. Individual symbols indicate samples from individual males

ence in the relative peak area of tetradecanoic acid (Wilcoxon signed ranks test: $n = 7$, $Z = 2.2$, $p = 0.028$) and octadecanoic acid (Wilcoxon signed ranks test: $n = 7$, $Z = 2.4$, $p = 0.018$) between seasons. The relative amount of both substances was significantly higher during the mating season than during the non-mating season (Fig. 14.1). For all other substances we found no seasonal differences in the relative contribution to individual odour profile.

14.3.2 Individuality

We compared the odour samples of seven adult male *S. bilineata* that were caught at least three times (four individuals three times, two individuals four times and one individual eight times). None of the substances was detected only in a single individual. The average relative portion of 2,6,10-trimethyl-3-oxo-6,10-dodecadienolide (GLM: $F_{6,21} = 14.99$, $p < 0.001$), and $C_{15}H_{24}O_2$ (GLM: $F_{6,21} = 5.95$, $p = 0.001$) differed significantly between individuals (Table 14.1). On two occasions, we had two males of the same colony in our analyses. Males from the same colony had different, unique, non-overlapping levels of 2,6,10-trimethyl-3-oxo-6,10-dodecadienolide (minimum – maximum values for Colony 1: male A 5.5 - 6.7% and male B 1.6 - 4.4%; Colony 2: male A 2.6 - 6.3% and male B 6.2 - 8.1%). Levels of $C_{15}H_{24}O_2$ showed much overlap between males from the same colony (Colony 1: male A 18.2

- 24.4% and male B 13.3 - 25.9%; Colony 2: male A 0 -20.2% and male B 15.8 - 30.0%). No significant differences were found for the relative peak areas of the other eleven substances.

14.4 Discussion

Male greater sac-winged bats have a specialized storage organ, the wing-sac in their front wing membrane, which they fill with substances from various body regions during a unique perfume-blending behaviour (Voigt and von Helversen 1999; Voigt 2002). The wing-sac odour of male greater sac-winged bats contains substances, such as fatty acids, terpenoids and aromatic compounds. This is consistent with the hypothesis that the wing-sac liquid of male *S. bilineata* might combine information: 1) on reproductive status and 2) on individuality.

14.4.1 Reproductive status/Seasonality

Analysis of hormonal metabolites in the faeces of *S. bilineata* showed most females were in oestrous in early December, suggesting that *S. bilineata* has a mating season of only approximately a few weeks each year (Voigt and Schwarzenberger 2007). In *S. bilineata,* odour is involved in several courtship or greeting displays, such as hovering flights (Bradbury and Emmons 1974; Voigt and von Helversen 1999; Voigt et al. 2001; Voigt 2005). The hovering flights can be observed most frequently in the morning after the bats have returned to the daytime roost and in the evening shortly before the bats emerge from the roost (Bradbury and Emmons 1974; Voigt and von Helversen 1999; Voigt 2002). Aerial greeting displays can be seen during the whole year in the daytime roost, although males hover more frequently prior to and during the mating season, indicating that the hovering flight and therewith the wing-sac content is part of the courtship behaviour (Voigt and Schwarzenberger 2007).

Our study shows that the composition of the wing-sac odour changes between non-mating and mating seasons. The relative amount of tetradecanoic acid (C14) and octadecanoic acid (C18) is higher during the mating season, suggesting that females could use fatty acids for assessing the reproductive status of a male. The importance of fatty acids for olfactory communication has already been shown in several mammals, such as spotted hyenas, *Crocuta crocuta* (Hofer et al. 2001) and the Indian mongoose, *Herpestes auropunctatus* (Gorman 1976).

A possible explanation for seasonal variation in odour profiles might be temporal changes in the bats' insect diet. Possibly males feed on different insect species during the mating season than during the non-mating season. Alternatively odour profiles may vary seasonally according to fluctuating hormone levels. Since hormones such as testosterone are known to vary with reproductive activity (bats: Hosken, Blackberry, Stewart and Stucki 1998) and since plasma androgen levels influence glandular secretion in mammals (Ebling 1977), it is possible that androgen-controlled glandular secretion causes seasonal changes in the odour profile of male greater sac-winged bats.

14.4.2 Individuality

None of the 185 substances detected in the male wing-sac odour occurred only in a single individual. Although most substances were shared by all males, we detected inter-individual difference in the composition of the wing-sac liquid. The relative contribution of 2,6,10-trimethyl-3-oxo-6,10-dodecadienolide and $C_{15}H_{24}O_2$ (species-specific substances, unpublished data) was constant throughout season, and differed between individuals.

Harems of *S. bilineata* are stable over several years (personal observations; Voigt 2005). Each morning, males "greet" returning females by hovering in front of them (Bradbury and Emmons 1974; Voigt and von Helversen 1999). We suggest that individual recognition based on odour might be important for the group maintenance in this social system. Individual recognition based on olfactory cues is a well-documented phenomenon in mammals (Halpin 1980, 1986; Johnston, Derzie, Chiang, Jernigan and Lee 1993), although the exact mechanisms are poorly understood. Buesching et al. (2001) analysed subcaudal gland secretions of badgers, *Meles meles,* and compared the variation between samples collected repeatedly from individuals. In badgers individual variation of subcaudal gland secretions was lower than seasonal variation, suggesting that the subcaudal gland secretion in badgers encodes information about badger individuality. To facilitate recognition, each individual ought to exhibit unique identity information in its odour. Thus, for individual recognition males ought to differ in the relative peak area of at least one odour compound. Individuals that can be mistaken, e.g. individuals of the same colony should have individual distinct, non-overlapping ranges of the relative amount of this substance. In our study, the relative amount of 2,6,10-trimethyl-3-oxo-6,10-dodecadienolide and $C_{15}H_{24}O_2$ differed between individuals. Individuals of the same colony had unequal levels of 2,6,10-trimethyl-3-oxo-6,10-dodecadienolide, making individual recognition based on the concentration of one substance possible.

14.4.3 The Wing-Sac Odour as a Composite Signal

A storage and display organ, in which a scent bouquet is actively blended from secretions of various body areas, has so far only been described for the greater sac-winged bat in mammals (Voigt and von Helversen 1999). The combination of information in such a specialized organ may be an adaptation to the specific needs of the social system of *S. bilineata*. *S. bilineata* is polygynous and females maintain a minimum distance to their neighbours within the harem territory. Aerial displays are the only possibility for males to bring females in contact with their scent from a distance since females respond aggressively to approaching males. Male greater sac-winged bats use a single morphological structure, the wing-sac, as the organ to display the scent. Here we showed that multiple information is potentially encoded in the odoriferous liquid, namely seasonality and individuality. Whether this information is used in intraspecific communication remains to be proven.

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