NOTE / NOTE

Duration of courtship displays corresponds to social status in male greater sac-winged bats (*Saccopteryx bilineata*)

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Abstract: In species with complex courtship displays, male courtship performance is often used by females to assess male quality. The greater sac-winged bat (*Saccopteryx bilineata* (Temminck, 1838)) lives in a harem-based resource-defence polygyny. Courting males perform complex hover displays in front of roosting females. Males differ in their social status by having females permanently or sporadically in their day-roost territory (harem males vs. nonharem males). We compared the frequency and duration of hover displays from harem and nonharem males in free-living colonies. Male social status was correlated with male age and the number of females being courted; thus, these two effects were removed to compare the frequency and duration of hover displays for harem and nonharem males. The frequency of hover displays per hour did not differ between harem and nonharem males, whereas the mean duration of hover displays was linked to male social status, with harem males exhibiting significantly longer hover displays than nonharem males. When analysing each social status separately, the hover display duration of both harem and nonharem males was neither influenced by the number of competing males nor by the number of females being courted. Male age did not influence the hover display duration of nonharem males; however, it had a significant effect on the hover display duration of harem males, with older harem males hovering significantly longer than younger harem males. Because females are free to choose in which male territory to roost, they might use the duration of hover displays to evaluate the quality of courting males.

Résumé : Chez les espèces qui affichent des comportements de cour complexes, les femelles utilisent souvent la performance de la cour faite par un mâle pour évaluer la qualité de ce mâle. Le grand saccopteryx rayé (*Saccopteryx bilineata* (Temminck, 1838)), vit dans une polygynie de défense des ressources basée sur un harem. Les mâles qui courtisent entreprennent des étalages compliqués de vols stationnaires devant les femelles perchées. Le statut social des mâles diffère selon qu'ils ont des femelles en permanence ou seulement sporadiquement dans leur territoire de perchage de jour (mâles avec harem vs. mâles sans harem). Nous avons comparé la fréquence et la durée des vols stationnaires chez des mâles avec et sans harem dans des colonies libres en nature. Le statut social des mâles est en corrélation avec l'âge du mâle et le nombre de femelles courtisées; nous avons donc retiré ces deux effets afin de comparer la fréquence et la durée des étalages de vol stationnaire chez les mâles avec et sans harem. La fréquence horaire des étalages de vol stationnaire ne diffère pas chez les mâles avec et sans harem; cependant, la durée moyenne des vols stationnaires est reliée au statut social, car les mâles avec harem accomplissent des vols stationnaires significativement plus longs que ceux des mâles sans harem. Dans une analyse séparée de chacun des statuts sociaux, la durée du vol stationnaire chez les mâles avec ou sans harem n'est pas influencée par le nombre de mâles compétiteurs, ni par le nombre de femelles courtisées. L'âge du mâle n'influence pas la durée du vol stationnaire chez les mâles sans harem; il a toutefois un effet significatif sur la durée du vol stationnaire des mâles avec harem, car les mâles avec harem plus âgés ont un vol stationnaire significativement plus long que celui des mâles avec harem plus jeunes. Puisque les femelles sont libres de choisir le territoire mâle où se percher, elles utilisent peut-être la durée des étalages de vol stationnaire pour évaluer la qualité des mâles qui les courtisent.

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Introduction

In many species, male reproductive success is regulated by the number of females a male can access and by his ability to secure matings with them (Maynard Smith 1991; Andersson 1994; Andersson and Iwasa 1996). Because females normally invest more in producing offspring than males, they are choosy about which males to accept as mating partners (Clutton-Brock and Parker 1992; Clutton-Brock and McAuliffe 2009). Active precopulatory mate choice by females creates selective pressures on male traits, which can lead to diverse male courtship displays such as large vocal repertoires, bright coloration, or complex behavioural displays (Andersson 1994; Andersson and Iwasa 1996; Gil and Gahr 2002). Hence, the design of signals used during male courtship displays is strongly influenced by sexual selection (Kodric-Brown and Brown 1984; Andersson 1994; Getty 2006) and male courtship performance may function as an indicator by which females can assess the quality of potential mates (Andersson 1994).

The greater sac-winged bat (*Saccopteryx bilineata* (Temminck, 1838)) is a neotropical insectivorous mammal living in a harem-based resource-defence polygyny where males acquire and defend small territories in the day roost (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976). Males try to persuade females to roost in their territory and mate with them, but they cannot monopolize females (Heckel et al. 1999) because of their smaller body size and relative smaller physical strength (Bradbury and Emmons 1974). Hence, female mate choice plays an important role (Voigt et al. 2008). Up to eight females can roost in an individual male's territory and form his "harem" (Bradbury and Emmons 1974). Colonies can consist of up to 60 adults distributed in 1–12 adjacent harems. Harem males are very faithful to their territories and defend them year-round. Males that defend a territory but only sporadically (e.g., only for a few hours on some days) have females roosting in their territory are called nonharem males; they are often found in the vicinity of harem territories as well, especially in large colonies (Voigt et al. 2008). These nonharem males are often young males that are queuing for harem access in their natal colony (Voigt and Streich 2003), which results in a patrilineal structure of colonies (Nagy et al. 2007). Male *S. bilineata* use visual, auditory, and olfactory signals (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976; Voigt et al. 2008) to attract females and retain them in the male's territory but cannot keep them from moving freely within the colony (Bradbury 1977). Hover displays are the most conspicuous aspect of the complex multimodal courtship behaviour of males (Bradbury and Emmons 1974; Voigt and von Helversen 1999; Behr and von Helversen 2004). Courting males hover in mid-air in front of roosting females and perform stereotypic wing movements to fan odour from sac-like organs in their front wing membranes towards the females (Voigt and von Helversen 1999). In addition, both individuals utter social calls while the male is hovering (Behr and von Helversen 2004). Males perform hover displays year-round, but rates increase during the mating season (Voigt et al. 2001, 2007). Hover displays can be observed throughout the day but are most prevalent after colony members have entered the day roost at dawn and before flying out at dusk (Voigt

and von Helversen 1999). A male courts females only when they are roosting, however briefly, in his respective territory and not when they are roosting in a neighbouring territory (Voigt et al. 2008).

Because hovering is energetically costly (Winter 1998; Winter et al. 1998; Voigt and Winter 1999), male hover performance may function as an indicator of male quality in *S. bilineata*. In this study, we compared the duration and frequency of hover displays from harem and nonharem males. If hover displays are used by females to assess male quality, the duration and frequency of displays should correspond to the social status of a male (i.e., females should prefer to roost in the territories of males with superior courtship performance). Several additional factors might influence hover display performance, namely the number of females being courted, the number of competing males, and male age. The number of females being courted could influence the duration and frequency of hover displays because males might need to adapt the frequency and duration of their displays according to the number of females they need to court. There is evidence that the presence of rivals affects male courtship in other species (Ridgway and McPhail 1987; Travis and Woodward 1989; Fisher and Rosenthal 2007); correspondingly, males with many male competitors in the colony might hover longer and more often than males with few or no competitors. Male age might have an influence on courtship performance as well. Because nonharem males are, on average, younger than harem males (Heckel and von Helversen 2002), they might display poorly owing to youthful inexperience. We predicted that harem males are capable of hovering longer and more often than nonharem males. In addition, we tested whether male age, the number of females being courted, and the number of other competing males influence the duration or frequency of male hover displays.

Materials and methods

We monitored five different colonies at two field sites (Biological Station La Selva (10°25′N, 84°00′W) and National Park Santa Rosa (10°50′N, 85°37′W)) in Costa Rica from January to February 2009. The research permission for fieldwork was allocated by the Costa Rican authorities (Ministerio de Ambiente y Energía, 076-2008-SINAC). We observed male hover displays in the bats' day roosts, which were located in or on the outside of abandoned buildings. All colonies consisted of at least one harem with a harem male and up to eight females plus one or more nonharem males. Two colonies had one harem male and one or two nonharem male(s) each; one colony had two harem males and five nonharem males; one colony had three harem males and three nonharem males; and one colony had six harem males and five nonharem males. Harem males and nonharem males were distinguished based on behavioural observations during the daily census by mapping individual territories and counting the females (if any) roosting in there. Prior to this study, bats were captured with mist nets (Ultrathin Mist Nets M-14; Ecotone, Gdynia, Poland) and banded with plastic bands on their forearms (size XCL; A.C. Hughes Ltd., Middlesex, UK), which rendered them individually discernible from a distance. The banding procedure is well established as part of a long-term study since

Fig. 1. Hover display durations for all male greater sac-winged bats (*Saccopteryx bilineata*) in our study. Values are means ± 1 SD. Harem males (■) hovered almost 2 s longer than nonharem males (◇). The distribution of individual variance in hover display duration did not differ from an equal distribution (Kolmogorov–Smirnov test: $N = 18$, $P = 0.234$).
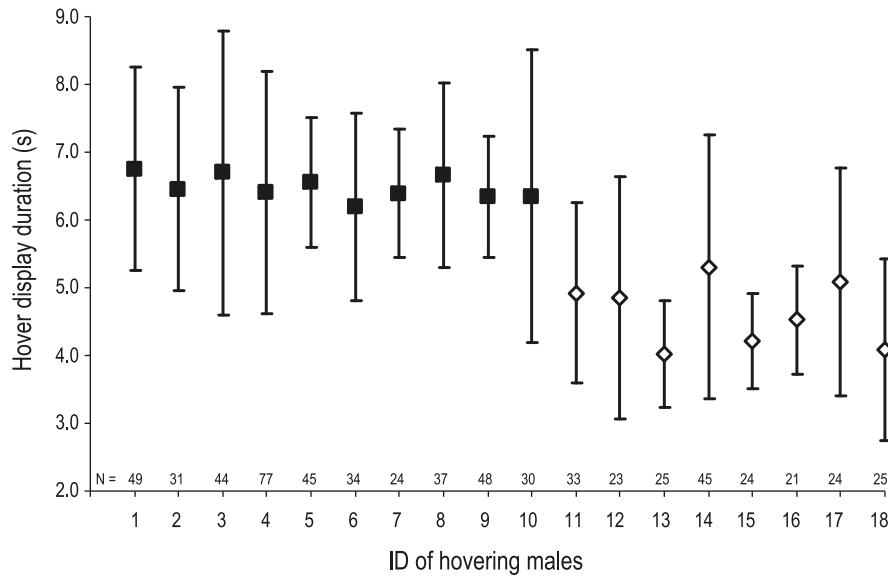
1994 (for details see Voigt and von Helversen 1999). The age in years for all but one male was determined as well. Individuals that were banded as juveniles or subadults were born in the year of capture, whereas individuals that were banded as adults were assumed to be at least 1 year old at the date of capture.

All bats were habituated to the presence of humans, but nevertheless, every observation session was preceded by a short initial habituation period (10 min during which the observer was already present, but no data was collected) to minimize disturbance effects. Eighteen males (10 harem males and 8 nonharem males) were observed for 1–2 h on at least 10 different days with similar weather conditions, which resulted in a minimum of 10 h of observation per male (mean = 13 h, range = 10–20). Multiple males per colony were observed simultaneously whenever feasible. The distribution of observation sessions was balanced equally for every male over the entire day. Two observers (M.K. and A.G.F.) collected data at all colonies. During each observation session, we counted the number and measured the duration of all hover displays with a handheld stopwatch (to 0.1 s accuracy) and noted which male was hovering and how many females he had in his territory. Nonharem males were only monitored when they had at least one female in their territory during the complete observation session (which they only had sporadically when females decided to switch roosting positions temporarily). In addition, we counted the total number of harem and nonharem males in the colony. The number of females being courted was calculated per male, whereas the number of competing males was calculated per colony to avoid pseudoreplication. Because we wanted to know how long males can hover when uninterrupted, we considered only hover displays that were terminated by the hovering male (and not by the female flying away or behaving aggressively towards the male, i.e., attempting to hit him with a folded wing).

We calculated the mean hover display duration for every

male across all observation sessions. The frequency of hover displays was calculated per hour for every male across all observation sessions, as the amount of observation time differed for every male. Our data were normally distributed, thus allowing us to use parametric statistics. However, because of the relatively small sample size, we used nonparametric alternatives whenever possible and calculated exact instead of asymptotic P values (after Mundry and Fischer 1998). Values are reported as means ± 1 SD unless stated otherwise and the statistical level of significance was set at $\alpha = 0.05$. Statistical tests were conducted using SPSS version 11.5 (SPSS Inc., Chicago, Illinois, USA) and G*Power version 3.0.10 (Franz Faul, University Kiel, Kiel, Germany; Faul et al. 2007).

Results

Male social status was influenced by male age and the number of females being courted (binary logistic regression with social status as dependent variable and either male age or number of females as independent variable; male age: Wald statistic = 3.254, $P = 0.071$; number of females: Wald statistic = 4.906, $P = 0.027$). Harem males were older than nonharem males (harem males: median = 1.5 years, range = 0.5–3.5 years; nonharem males: median = 1 years, range = 0.5–1.5 years; Mann–Whitney U test: $U = 16$, $N_1 = 9$, $N_2 = 8$, exact $P = 0.046$) and had more females than nonharem males (harem males: median = 4, range = 1–8; nonharem males: median = 2, range = 1–3; Mann–Whitney U test: $U = 10.5$, $N_1 = 10$, $N_2 = 8$, exact $P = 0.005$).

To test for differences in hover display performance between harem and nonharem males, the effects of male age and the number of females being courted were removed before comparing the frequency and duration of hover displays for harem and nonharem males. For both the duration and frequency of hover displays, we conducted a separate multiple regression with male age and the number of females being courted as independent variables and used the result-

Fig. 2. In harem males of the greater sac-winged bat (*Saccopteryx bilineata*), the hover display duration (mean ± 1 SD) was significantly influenced by male age. The older a harem male, the longer his mean hover display duration.
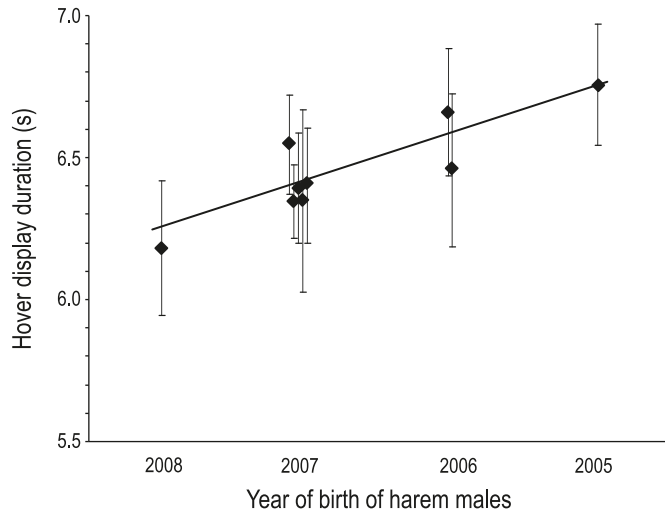
ing residuals in subsequent analyses. We observed a total of 639 hover displays (35.5 ± 14.1 hover displays per male; range = 21–77 hover displays; 18 males). The frequency of hover displays per hour did not differ significantly between harem and nonharem males (Mann–Whitney U test with residuals: $U = 16$, $N_1 = 9$, $N_2 = 8$, exact $P = 0.059$), even though there was a slight tendency for harem males to hover more often than nonharem males (median hover display frequency per hour; harem males = 3.4; nonharem males = 2.3). The duration of hover displays differed significantly between harem and nonharem males (Mann–Whitney U test with residuals: $U = 5$, $N_1 = 9$, $N_2 = 8$, exact $P = 0.002$), with harem males hovering almost 2 s longer than nonharem males (median hover display duration; harem males = 6.4 s; nonharem males = 4.7 s; see also Fig. 1).

Potential additional influences on the duration of hover displays were subsequently analysed separately for harem and nonharem males. In nonharem males, neither male age nor the number of females being courted nor the number of competing males had a significant effect on hover display duration (multiple regression; $F_{[3,7]} = 1.406$, $P = 0.364$, power = 0.312; age: $t = 0.674$, $P = 0.537$; number of females: $t = 1.739$, $P = 0.157$; number of males: $t = –0.189$, $P = 0.859$). In harem males, male age significantly influenced the duration of hover displays (Fig. 2), whereas the number of females being courted or the number of competing males had no significant influence on hover display duration (multiple regression; $F_{[3,8]} = 8.975$, $P = 0.019$, power = 0.994; age: $t = –4.601$, $P = 0.006$; number of females: $t = 0.392$, $P = 0.711$; number of males: $t = 1.235$, $P = 0.272$).

Discussion

Even though the durations of hover displays measured in our study were in the same range as reported by an earlier study (up to 14 s; Voigt and von Helversen 1999), we found, on average, much longer hover displays (median = 1.9 s, $N = 481$ in Voigt and von Helversen (1999) vs. median =

5.9 s, $N = 639$ in our study). This discrepancy is probably caused by the difference in colony sizes (one very large colony in Voigt and von Helversen (1999) vs. several small to medium-sized colonies in our study). In a very large colony, male hover displays are often terminated early by other intruding males (C.C. Voigt, personal communication), whereas we never observed such interruptions in our medium-sized and small colonies.

Hover displays precede copulations (Tannenbaum 1975; Caspers et al. 2009) and could function as multimodal signals containing information on male quality. Not only the energetic costs of hover displays but also associated behaviours like odour fanning and vocalizing probably constitute criteria for female choice (Voigt et al. 2008). The presentation of odour and its potential role for female choice has been described in impressive detail (Voigt and von Helversen 1999; Voigt et al. 2001; Voigt 2002; Caspers et al. 2008, 2009), whereas the vocalizations emitted by hovering males have received less attention in the past (Behr and von Helversen 2004). The energetic demands for producing loud and long whistles probably increase the energetic costs of hover flights, especially when odour is presented simultaneously with specialized wing strokes that negatively affect buoyancy (Voigt and von Helversen 1999), and hence, make the hover displays even more costly (Voigt et al. 2008).

Our results demonstrate that the mean duration of hover displays differed between harem and nonharem males when effects of male age and the number of females being courted were removed. This finding corresponds to studies on other species which report that the duration of male courtship constitutes a useful signal to females (Seymour and Sozou 2009) and that variation in male courtship displays is indicative of variation in male quality (Knapp and Kovach 1991; Stapley 2008). If male social status is linked to male quality, harem males might be better able to pay the severe energetic costs that are probably associated with hover displays (Norberg et al. 1993; Winter 1998; Winter et al. 1998; Voigt and Winter 1999). Thus, the duration of hover displays could be used by females to evaluate the quality of courting males. Reproductive success of harem males is positively correlated with harem size (Heckel and von Helversen 2003) and long hover displays might be important to convince females to roost in a certain territory. The energy expenditure of courting males (i.e., mass-specific field metabolic rate) increases with harem size (Voigt et al. 2001) and the latter correlates with the frequency of hover displays (Voigt and von Helversen 1999). This indicates that metabolic rate is related to display rate in *S. bilineata* (Voigt et al. 2008), as has been shown for several bird species (Vehrencamp et al. 1989; Höglund et al. 1992; but see Dearborn et al. 2005). Nevertheless, the field metabolic rate could not be used as an indicator of male social status in *S. bilineata*, as there were no significant differences between harem and nonharem males (Voigt et al. 2001). This is probably owing to the measured energy budgets corresponding to all activities and not specifically to hover displays; the noncourtship-related activity of nonharem males probably lead to a high metabolic field rate, thus masking the differences between harem and nonharem males (Voigt et al. 2001).

Our study demonstrates that the social status of male bats

is directly linked to the mean duration of their hover displays, which suggests that male courtship performance is used by females to assess male quality. We could not determine lifetime reproductive success for the males in our analyses, but previous studies showed that harem males have a higher reproductive success than nonharem males (Heckel et al. 1999; Heckel and von Helversen 2002). Thus, the social status of a male can influence his reproductive success, potentially because the duration of hover displays is linked to male quality and therefore might be important for female choice. Especially in species with extensive female mate choice, investment in courtship performance might be as beneficial for male reproductive success as investment in male–male competition (Sih et al. 2004).

Acknowledgements

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