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# Function of male song in the greater white-lined bat, *Saccopteryx bilineata*

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The use of vocalizations by males to attract mates and defend territories is widespread in birds but uncommon in mammals. In the greater white-lined bat, males defend small territories in tree buttresses and produce complex audible vocalizations. During the day, females roost within these territories, and males with females in their territories have higher reproductive success than males without females. To determine call function, we recorded male vocalizations on the island of Trinidad and made behavioural observations of the focal male and nearby bats at the time the calls were given. Noisy broadband calls were directed mainly at other males whereas tonal calls were used primarily in interactions with females. Two other types of calls were given independently of any observable context and may be involved in territorial defence or conspecific notification. Poisson regression showed that males with song repertoires that contained more unique types of composite syllables had more females in their territories. In addition, several acoustic features of one common call type significantly correlated with the number of females on a territory. Male vocalizations may, therefore, transfer information to colony members about male quality or fighting ability.

Many male animals have evolved vocalizations that are used in territorial defence, mate attraction, or both; any of these uses of vocalization can strongly affect reproductive success (Bradbury & Vehrencamp 1998). Male vocal displays are well documented in orthopterans (reviewed in Zuk & Simmons 1997), anurans (e.g. Ryan 1980; Arak 1983) and songbirds (reviewed in Catchpole & Slater 1995). Male vocal displays are also found in some marine mammals, such as humpback whales, *Megaptera novaeangliae* (Payne & McVay 1971), and several types of seals (Bartholomew & Collias 1962; Stirling & Siniff 1979; Thomas & Stirling 1983; Bartsh et al. 1992; Terhune 1994; Van Parijs et al. 1997).

In terrestrial mammals, however, vocal displays are uncommon, and many species rely on olfactory or visual displays for mate attraction and territorial defence (Bradbury & Vehrencamp 1998). Primates are one group of terrestrial mammals in which males produce vocal displays for these functions. Male mouse lemurs, *Microcebus murinus*, use trill calls to attract females (Zimmermann & Lerch 1993), and male gibbons, *Hylobates* spp., use song in territorial and mate defence (Mitani 1988; Cowlishaw 1992). Male orang-utans, *Pongo pygmaeus* (Mitani 1985), and howler monkeys, *Alouatta* spp. (Carpenter 1935), use vocal displays to maintain spacing between groups.

Bats are the other group of male terrestrial mammals in which vocal displays have been documented. Male epomophorine bats commonly use vocal displays (Wickler & Seibt 1976); male hammer-headed bats, *Hypsignathus monstrosus*, call to attract females to a lek (Bradbury 1977a). Male *Nyctalus noctula* also produce vocalizations that are thought to attract females (Sluiter & van Heerdt 1966). *Pipistrellus pipistrellus* males advertise the location of day roosts to females with song-flight displays (Lundberg & Gerell 1986) and use social calls for territorial defence (Barlow & Jones 1997). In the megadermatids, *Megaderma lyra* produce song-flight displays aimed at females in their groups (Leippert 1994) and *Cardioderma cor* use song to delineate feeding territories (McWilliam 1987).

Complex vocal displays have also been reported in the greater white-lined bat (Bradbury & Emmons 1974; Davidson & Wilkinson 2002). At dawn, males return to defend roost territories and produce complex audible vocalizations consisting mainly of short repeated tones for a period lasting 10–15 min (Bradbury 1977b). Although mating occurs in December or January, males vocalize and defend territories year-round (Bradbury & Emmons 1974; Tannenbaum 1975). Up to eight females can roost within the territory of a male, while other peripheral males

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hold territories without roosting females (Bradbury & Vehrencamp 1976). In this species, males with females roosting within their territories have higher reproductive success than males without females (Heckel et al. 1999). Also, females are more mobile than males; most juvenile females disperse from their natal colonies, and adult females readily move within and between colonies (Tannenbaum 1975).

Throughout the day, males periodically produce short vocalizations that contain some of the same elements as calls produced at dawn (Bradbury & Emmons 1974; Davidson & Wilkinson 2002). These vocalizations appear to be produced in response to the actions or calls of other bats, or are given spontaneously with no obvious visual or auditory stimulus. Because of their fidelity to a single day roost and diurnal activity patterns, male *S. bilineata* are ideal subjects for investigating the function of such complex vocal displays. To infer the function of calls produced by male *S. bilineata*, we observed the behaviour of males at several roost sites. Although evidence of differences in male song that impact reproductive success are well documented in other animals (reviewed in Searcy & Andersson 1986), evidence for selection on male vocal displays in mammals is absent, except for roaring rate in red deer, *Cervus elaphus*, produced during male–male contests (Clutton-Brock & Albon 1979). If male *S. bilineata* use vocal displays for female attraction or territorial defence, males with territories containing more females should produce different acoustic cues in their displays than males without females. Accordingly, we measured several acoustic features from the vocal repertoire of *S. bilineata* to determine whether any characteristics of male vocal displays predict the number of females roosting within the territory of a male.

## METHODS

### Field Methods

We captured, measured and individually marked bats at four colonies of *S. bilineata* (Guanapo, Biche 1, Biche 2 and La Victoria) on the island of Trinidad, West Indies, in July 1998 (Davidson & Wilkinson 2002). To record the vocalizations and associated behaviours, we used an Audio-technica 18-inch (45.7-cm) shotgun microphone (model AT4071A) with an AKG Acoustics line amplifier (Model B-18) fed into a Sony TR-81 HI8 video camera. By focusing on a group of banded males and associated females at a colony, we were able to monitor the song and associated behaviours of three to five males at each colony. We videotaped for several hours at a time between the hours of 0600 and 1030 from 26 July to 11 August 1998 (Davidson & Wilkinson 2002). At this time of the year, first light appears at 0530 hours.

Each day we videotaped, we mapped the spacing and location of all bats at the colony and updated male locations if movements occurred during the course of recording. We determined a male's territory from observations of his roosting locations and from any boundary disputes with neighbouring males. We associated a female with a particular male if she roosted within his territory more than 50% of the time that he was observed. We were able to assign females to 15 males by this method. One additional male at the La Victoria colony had a long, narrow territory that contained two females. He displayed to females within his territory and defended these females against approaches from other males, but during the majority of the time that he was taped, the females were hidden from view.

### Sound Analysis

We used a Kay DSP 5500 sonagraph to digitize vocalizations at 81.92 kHz with 12 bits, which provided a maximum frequency of 32 kHz and a dynamic range of 72 dB. A vocalization was attributed to a particular bat if the pattern of mouth movements on the tape corresponded to the pattern of sounds appearing on the real-time spectrogram of the sonagraph. To measure calls, we used Signal (version 3.0, Engineering Design, Belmont, Massachusetts, U.S.A. 02178) to produce spectrograms of each vocalization with a 512-point fast Fourier transformation (FFT) and Hamming window, which provided a time resolution of 6.3 ms and a frequency resolution of 160 Hz. Following Kanwal et al. (1994), we defined a call as a single bout of vocalizing surrounded by at least 500 ms of silence and syllables as units separated by at least 10 ms of silence within a call (Davidson & Wilkinson 2002). A simple syllable is a sound element produced singly (Fig. 1). Syllables that contain more than one element were defined as composite syllables (i.e. two or more simple syllables combined with no silence).

To determine whether production of different types of song elements differed between males, we examined 311 calls produced by 19 males from the four colonies. For each bat, we determined the number of syllable types, $n_{\mathrm{max}}$, as the sum of the number of types of simple and composite syllables. Then, using a method based on Wildenthal (1965), we estimated repertoire size as the asymptotic number of syllable types, $N_{\mathrm{TOT}}$, in the repertoire of each male (Davidson & Wilkinson 2002). For each male, we also tabulated the frequency with which 21 song elements were produced (Fig. 1). In this analysis, a simple syllable counted as one element, whereas composite syllables were broken down into their simple syllable elements. For example, a single composite syllable that contained three simple syllables was counted in three element categories. Although each of the 21 simple syllables was produced by at least two males, some of the elements were more commonly observed than others. Whereas some males produced most of the 21 simple syllables, others produced fewer of them (Davidson & Wilkinson 2002). To enable categorical analysis, we combined the 21 simple syllable elements into six categories, based upon similar acoustic characteristics. We combined syllables A–C into a 20-kHz category, syllables D–F into a screech category, syllables G–H into a whine category, syllables I–K and M–Q into a short-FM-tone category and syllables R–U into a long-tone category (Fig. 1). For the sixth category, the inverted-V, only

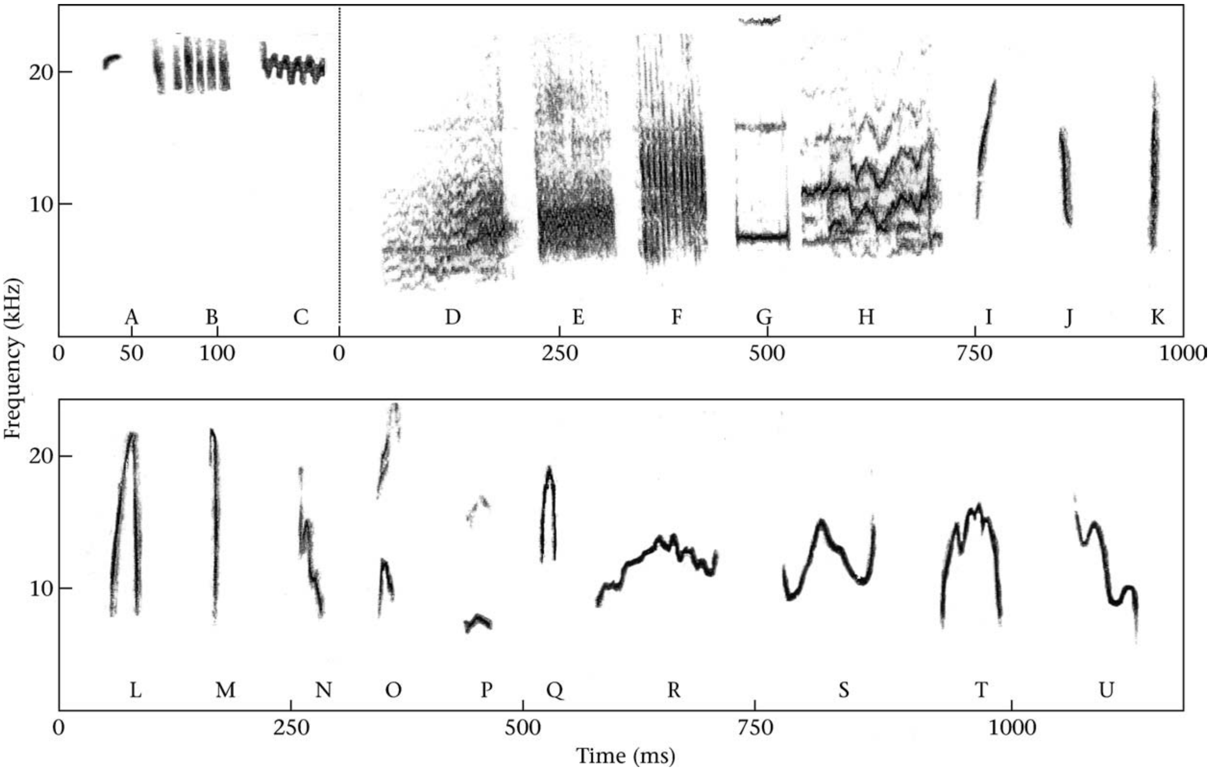

**Figure 1.** Spectrograms representing song elements in the male repertoire. The 21 element types are amalgamated into six categories: 20 kHz (A—C), screech (D—F), whine (G—H), short FM tone (I—K; M—Q), inverted-V (L) and long tone (R—U).

syllable L was used because of its extremely stereotyped composition.

## Context Classification and Call Association

To determine the context in which each call was given, we observed a male for 1—2 s before and after a call was given. Males often accompanied a call with the wave of a closed wing; we attributed a call as being directed at a particular bat if the focal male waved his wing and turned his head towards a nearby bat while calling. We recorded the identity and behaviour of any nearby bats involved in interactions with the calling male. Three categories of behavioural context were scored. When a nearby bat crawled along the tree towards the focal male or flew into or near his territory, we scored these behaviours as Approach. If the focal male responded with a vocalization to a call of a nearby bat, we scored this as Call Response. The third category of behaviour (Other) included three separate behaviours, each with small sample sizes: nearby bats retreating away from the male, nondirectional moving (rocking or shifting position) and flying passes without landing nearby.

Using syllable similarity, we divided 294 calls from 19 bats into five categories of calls. Calls were classified by whether they contained primarily: (1) broadband noise or screech elements (Fig. 2a), (2) both screech and FM whine components (Fig. 2a), (3) the screech-inverted-V syllable (Fig. 2b), (4) short, repeated FM tones (Fig. 2c) and (5) longer, tonal syllables with few harmonics (Fig. 2d). Individual bats were not equally represented in the sample and produced from one to 59 calls. We combined the screech and screech—whine categories because we found no significant difference in the distribution of behaviours of nearby bats in response to these two call categories ($\chi^2_2 = 6.44$, $P = 0.17$) or the sex of those bats ($\chi^2_1 = 1.16$, $P = 0.55$). We then performed chi-square contingency tests to determine whether any of the four categories of calls (Fig. 2) were given in particular contexts (Approach, Call Response, or Other), or in response to a particular sex (male or female). We also performed a chi-square contingency test on one behavioural category, Approach, to determine whether the calling male produced different call types when bats of either sex approached. Of the 71 Approach calls, 31% could not be included in this analysis because the sex of the interacting bat was not known. The contingency tables for the remaining categories of behaviour, Call Response and Other, of nearby bats could not be calculated because in both cases more than 50% of the cells were empty.

## Repertoire and Call Variation and Female Number

To determine how vocal variation relates to the number of females found within the territory of a male, we examined male song repertoire at three levels: (1) repertoire diversity and syllable production, (2) production of elements that make up the syllables, and (3) acoustic characteristics of the first syllable of the most

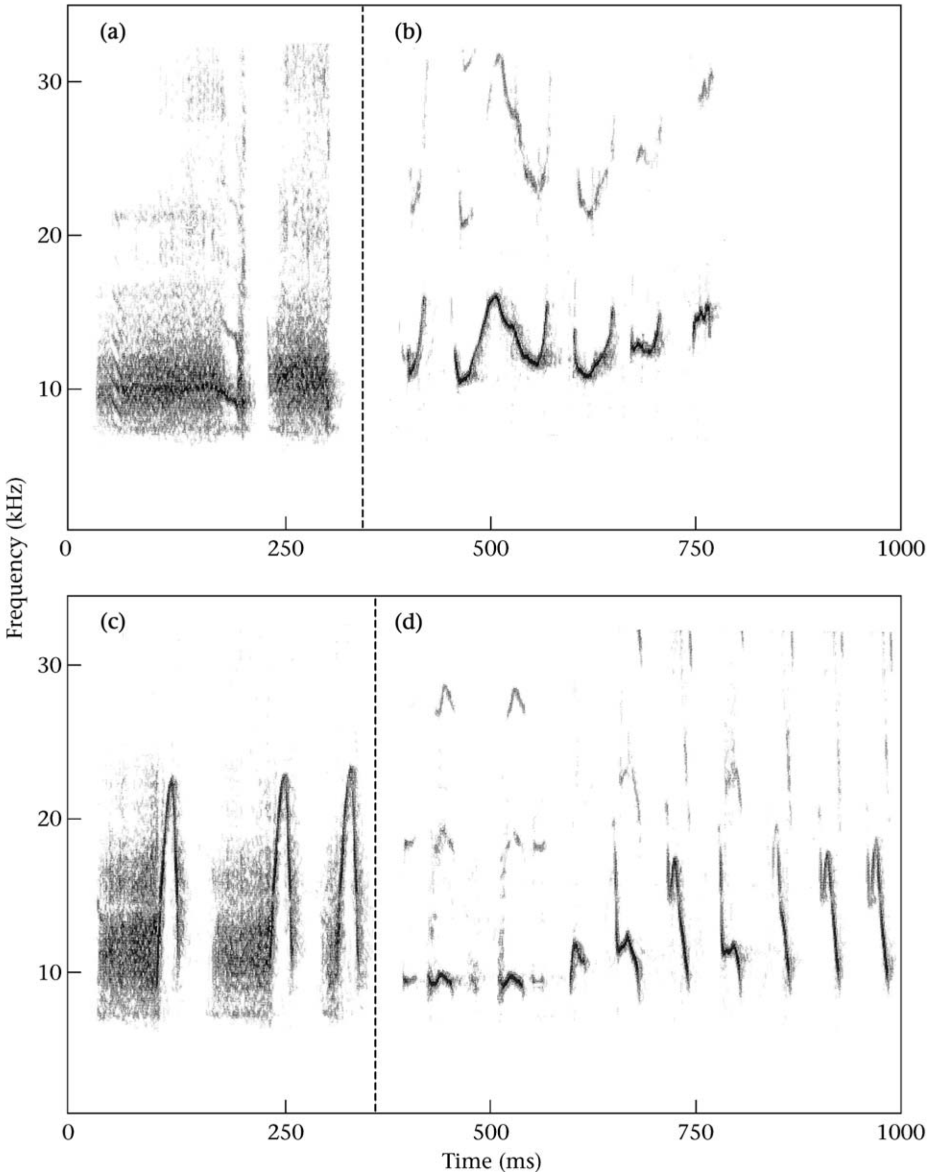

**Figure 2.** Examples of screech (screech–whine) call type (a), long tonal call type (b), screech-inverted-V call type (c) and short tonal call type (d).

common call type, the screech-inverted-V call. To measure repertoire diversity, we calculated a Shannon–Wiener index for each bat using the 21 element categories (Margalef 1958). To determine how syllable production and repertoire diversity related to the number of females within the territory of a male, we created a regression model using the GLIMMIX macro (SAS Institute 1997) using 16 males recorded at four colonies. We excluded three of the 19 original males from this analysis because each had only one call recorded (Davidson & Wilkinson 2002). Although the total number and diversity of vocal elements produced by a male tend to increase asymptotically with time, individual males differ in the rate at which they produce new distinct composite syllables, ranging from 1.6/h to 6.3/h (Davidson & Wilkinson 2002). Therefore, to compare males on a common scale, we regressed the total number of syllables produced ($n_{\mathrm{max}}$), the number of different composite syllables produced, the Shannon–Wiener index and the estimated number of syllable types ($N_{\mathrm{TOT}}$) for each male on the time that each male was observed to obtain residuals for each of the variables. We then used these residuals in a stepwise Poisson regression model to determine whether any of these variables predicted the number of females within a male's territory. We selected a stepwise model because it uses only those variables with information that predicts or combines to predict the number of females in a male's territory (Kleinbaum et al. 1998). The significance level to enter all models was set at 0.10, and the significance level to exit was set at 0.051, thereby allowing a marginally significant variable to enter into the model because factors already in the model may have synergistic effect on its predictive power.

To determine how production of elements related to territory occupancy by females, we counted how many times each male produced each of the six syllable categories (screech, whine, short tone, inverted-V, long tone and 20 kHz) that are displayed in Fig. 1. Again, to account for differences in the time that each male was observed, we regressed each of the six element categories on the time each male was observed to obtain residuals. We then used these residuals in a stepwise Poisson regression model to determine whether the rate at which these elements were produced predicted the number of females within a male's territory.

To determine how acoustic variation in a common call type related to the number of females within a male's territory, we measured six acoustic features from screech-inverted-V calls. This call type accounted for 38.1% of daytime calls. We used 96 calls from 16 males for this analysis. The first syllable of this call contains two distinct parts: an introductory broadband noise (screech) portion and a stereotyped frequency-modulated (FM) portion (inverted-V). Duration and peak frequency of the power spectrum were measured from the screech; duration, first peak of the power spectrum, maximum frequency and the bandwidth of the power spectrum 10 dB below the peak were measured from the inverted-V (Davidson & Wilkinson 2002). We also counted the number of inverted-V elements in each call. We then performed a stepwise repeated measures Poisson regression to determine whether any of these seven traits predicted the number of females roosting in a male's territory. To determine whether size of males had an influence on their call frequency, we used a weighted regression model to predict mean maximum frequency from the forearm length of males.

We used SAS (version 6.12) for all statistical procedures (SAS Institute 1997).

## RESULTS

### Call Context Associations

The frequency of call types produced by males (screech, screech-inverted-V, short tones, or long tones) was found to be contingent on two factors: the behaviour of a nearby bat ($\chi^2_6 = 16.0$, $P = 0.014$; Table 1) and the sex of the interacting bat ($\chi^2_3 = 28.9$, $P < 0.001$; Table 2). Screech calls were produced in response to calls of other bats more than expected, and they were given less frequently than expected in response to approaches. Additionally, interactions with males produced more screech calls, whereas interactions with females produced more long, tonal calls. The latter result is primarily influenced by the Approach category. When other bats approached the focal male, the call that was produced was dependent on the sex of the bat, with approaching females receiving more calls containing long tones and fewer calls containing screech elements ($\chi^2_3 = 15.3$, $P = 0.0016$; Table 3).

**Table 1.** Frequencies of call types produced by males in response to other bats

| Call type | Behaviour of nearby bat | | |
|---|---|---|---|
| | Approach | Call | Other* |
| Screech | 36 (41.5)† | 21 (12.8) | 23 (26.1) |
| Screech-inverted-V | 17 (14.4) | 1 (4.5) | 10 (9.1) |
| Short tones | 11 (10.3) | 0 (3.2) | 9 (6.5) |
| Long tones | 7 (5.2) | 0 (1.6) | 3 (3.3) |

*Includes flying by, moving and retreating.
†Expected values under independence are in parentheses.

**Table 2.** Frequencies of call types produced by males to bats of each sex

| Call type | Sex of interacting bat | |
|---|---|---|
| | Male | Female |
| Screech | 44 (32.1)* | 13 (24.9) |
| Screech-inverted-V | 9 (9.6) | 8 (7.4) |
| Short tones | 3 (6.2) | 8 (4.8) |
| Long tones | 2 (10.1) | 16 (7.9) |

*Expected values under independence are in parentheses.

### Repertoire and Call Variation and Female Number

Stepwise Poisson regression analysis of the four measures of repertoire complexity and syllable production revealed that only the residual number of different composite syllables produced by a male predicted the number of females in a male's territory ($F_{1,14} = 6.31$, $P = 0.025$; Fig. 3). The Shannon–Wiener index, total number of syllables and the estimated number of syllable types did not enter the model and were not significant predictors individually (Table 4). Although the number of different composite syllable types was positively correlated with the number of females, this result did not influence the production of song elements. None of the residuals from the six song element categories (screech, whine, short tone, inverted-V, long tone and 20 kHz) significantly predicted territory occupancy by females (Table 4).

Acoustic variation in the screech-inverted-V call also was important in predicting the number of females within a male's territory. Four of six acoustic features were included in the stepwise model: maximum frequency of the inverted-V, duration of the inverted-V, duration of the screech and number of inverted-V elements in each call (Table 5). The relationship between the mean number of

**Table 3.** Frequencies of call types produced by males to approaching bats of each sex

| Call type | Sex of approaching bat | |
|---|---|---|
| | Male | Female |
| Screech | 19 (13.2)* | 5 (10.8) |
| Screech-inverted-V | 5 (5.5) | 4 (4.5) |
| Repeated tones | 3 (4.4) | 5 (3.6) |
| Long tones | 0 (3.9) | 7 (3.1) |

*Expected values under independence are in parentheses.

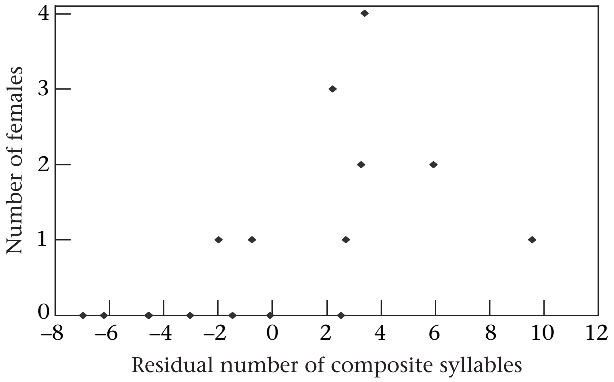

**Figure 3.** Plot of the number of females roosting within the territory of a male in relation to the residual number of composite syllables produced (accounting for time observed) by the male.

inverted-V elements produced by a male to the number of females in his territory is shown in Fig. 4. The number of inverted-V elements and the duration of the inverted-V had a synergistic effect on the significance of the maximum frequency of the inverted-V. The first peak of the power spectrum of the inverted-V was not retained in the final model because it negatively correlated with the number of inverted-V elements ($r_P = -0.30$, $N = 95$, $P = 0.004$). A weighted regression of mean maximum frequency values for each bat revealed that maximum frequency did not depend on forearm length ($R^2 = 0.11$, $F_{1,10} = 1.24$, $P = 0.29$), which is a standard measure of bat body size.

# DISCUSSION

## Call Context Associations

Different categories of male call types were produced in response to the behaviour of nearby colony members. The largest deviations from expected values involved the screech category; males gave more screech calls than expected in response to calls by other bats and gave fewer screech calls to approaches by other bats. Both male and female *S. bilineata* often perform screech calls while waving a closed wing at a bat roosting nearby (personal observations). The higher than expected number of screech calls in response to other calls is likely to be related to the tendency of males to respond to a screech call with a screech call. Other types of calls produced by *S. bilineata* are less likely to produce a call as a response. Males also directed significantly more screech calls towards male bats and more tonal calls towards female bats. This difference was largely due to the Approach category; approaches by males elicited more screech calls and approaches by females elicited more tonal calls.

**Table 4.** Poisson regressions of the number of females per male on measures of song repertoire complexity and frequencies of song elements produced

| Type | Variable | $F_{1,14}$ | $P$ |
|---|---|---|---|
| Repertoire complexity and diversity | Distinct composite syllables | 6.31 | 0.025 |
| | Estimated syllable types ($N_{TOT}$) | 2.16 | 0.164 |
| | Number of syllables produced | 2.09 | 0.170 |
| | Shannon–Wiener index | 1.21 | 0.289 |
| Frequency of element categories | Short tone | 1.83 | 0.198 |
| | Whine | 1.40 | 0.257 |
| | Long tone | 1.36 | 0.263 |
| | Screech | 1.30 | 0.273 |
| | Inverted-V | 0.21 | 0.652 |
| | 20 kHz | 0 | 0.956 |

**Table 5.** Poisson regressions of the number of females per male on four acoustic features of screech-inverted-V calls

| | Stepwise | | Individual | |
|---|---|---|---|---|
| Variable | $F_{1,76}$ | $P$ | $F_{1,79}$ | $P$ |
| Number of inverted-V elements in call | 11.32 | 0.0012 | 13.30 | 0.0005 |
| Duration of inverted-V | 10.98 | 0.0014 | 9.28 | 0.0031 |
| Maximum frequency of inverted-V | 8.11 | 0.0057 | 3.30 | 0.0730 |
| Duration of screech | 4.21 | 0.0435 | 5.58 | 0.0206 |

The use of broadband calls for interactions with males and tonal calls for interactions with females is consistent with the motivation-structure (MS) hypothesis (Morton 1977), which states that broadband calls are primarily aggressive in nature, and tonal calls are given in fear or appeasement. Owings & Morton (1998) suggested that low-frequency, broadband calls are associated with aggression because larger animals can produce lower frequencies, and tonal calls are associated with appeasement because they are most similar to the tonal calls of infants. The screech call produced by male *S. bilineata* appears to function in territorial defence or individual spacing on the tree and can be directed at females that approach too closely. Calls with long tones appear to function as appeasement or mate attraction calls. These results are consistent with findings in other mammals (see meta-analysis in August & Anderson 1987).

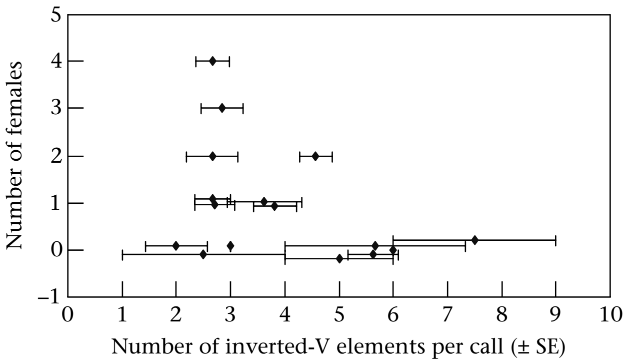

**Figure 4.** Plot of the number of females roosting within the territory of a male in relation to the mean number of inverted-V elements per call (±SE).

No significant contextual association was indicated for either screech-inverted-V or short, repeated, tonal calls. Neither was found to be dependent on the behaviour of bats interacting with the focal male. For the screech-inverted-V call, 74% of calls were not associated with the behaviour of a nearby bat. Many of the screech-inverted-V calls were not produced in response to obvious visual or auditory cues. According to the MS rules, a chevron-shaped call (bark), such as the inverted-V, is neither aggressive nor appeasing; in many animals, it is given in a neutral situation, such as notification of conspecific competitors or predators (Owings & Morton 1998). Acoustic features of inverted-V calls produced by *S. bilineata* show individual-level variation (Davidson & Wilkinson 2002), which makes recognition of individuals in a colony possible. Individual variation has been suggested to be an important factor in the evolution of territorial defence calls (Bradbury & Vehrencamp 1998), and neighbour recognition is important in territorial defence by some male songbirds (Stoddard 1996). With the more aggressive introductory screech element attached, the spontaneously produced screech-inverted-V call could function as a territorial defence or conspecific notification call.

Fifty-seven per cent of the calls containing short, repeated tones were found to have no obvious context. These calls most resemble the longer morning song produced by males at dawn before the return of the females. The pattern of dawn calling found in *S. bilineata* has been reported in several species of birds (Stacier et al. 1996) where it has been associated with intraspecific competition. Similar to *S. bilineata*, golden-winged warblers, *Vermivora chrysoptera*, sing one song type at dawn, then intermittently produce this song type throughout the day (Highsmith 1989). The lack of consistent context for short-tone call types in *S. bilineata* and the temporal similarity to the pattern of song produced by some birds suggest that this call type also may function in territorial defence. Thus, different call types may have different functions in *S. bilineata*, and the complex male display may have more similarities to those found in songbirds than those found in most other types of mammals.

## Repertoire and Call Variation and Female Number

Males that produced more types of composite syllables tended to have more females roosting in their territories. In contrast, in no case did the production of song element types correlate with female occupancy. These results suggest that even though all males appear to use the same types of song elements, males with more females on their territories combine those elements into a greater variety of composite syllables. Repertoire complexity may, therefore, function in a manner similar to that observed in songbirds, where males with larger repertoires attract more females (Catchpole 1980) and have higher reproductive success (Hiebert et al. 1989).

In addition, four acoustic features measured from the most common call type, the screech-inverted-V call, significantly predicted the number of females within the territory of a male. Males that produced calls with fewer inverted-V elements had more females within their territory. These results contrast with those for crickets and frogs where more song elements within a call are typically preferred by females (Ryan 1983; Simmons 1988). Males with lower maximum frequencies of the inverted-V also tended to have more females on their territories. In toads, larger males produce lower tones that advertise their size to competing males and assessing females (Davies & Halliday 1978). In *S. bilineata*, we did not find a correlation between call frequency and size. In mammals, call frequency rarely correlates with size (see McComb 1991). Using playbacks, McComb (1991) found that female red deer preferred higher roaring rate, rather than pitch, of male calls. The rate differences displayed during contests between male red deer appear to be honest displays of fighting ability (Clutton-Brock & Albon 1979). Male *S. bilineata* that had inverted-V and screech components of longer duration also had more females on their territories. The maximum frequency and duration of the inverted-V vary significantly between individuals, and maximum frequency varies between colonies (Davidson & Wilkinson 2002). Thus, these acoustic features could be used for recognition of individual males or patrilines by both males and females and are not likely to reflect motivational differences.

Recently Heckel et al. (1999) used microsatellite markers to determine that male *S. bilineata* in Costa Rica that had one to seven females within their territories had higher average reproductive success than males with no females, although males did not always sire the offspring of females within their territories. These results are consistent with those of Tannenbaum (1975), who found that some females within the territories of experimentally sterilized males in Panama produced pups while others did not. It appears that female *S. bilineata* actively select their roosting location and are highly mobile; some females shift roosting territories during the course of a day and some disperse to other colonies as adults. Thus, the roosting preferences of females seem likely to influence whether or not a territorial male sires their offspring. Our results suggest either that females use vocal displays to choose mates or that males that successfully defend roost sites preferred by females produce complex songs. In the latter case, male song may contain honest information about fighting ability or condition (Kodric-Brown & Brown 1984). Other than roaring rate in red deer (Clutton-Brock & Albon 1979; McComb 1991), acoustic variation in male vocal display has not been found to correlate with reproductive success in any mammal. Playback experiments are needed to determine how sexual selection influences the acoustic differences that appear to be so strikingly correlated with reproductive success in *S. bilineata*.

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