



Male courtship displays and vocal communication in the polygynous bat *Carollia perspicillata*

Mirjam Knörnschild^{a,b,*}, Marion Feifel^a and Elisabeth K.V. Kalko^{a,b}

^a Institute of Experimental Ecology, Faculty of Natural Sciences,
University of Ulm, Germany

^b Smithsonian Tropical Research Institute, Balboa, Panama

* Corresponding author's e-mail address: mirjam.knoernschild@uni-ulm.de

Accepted 26 December 2013; published online 4 February 2014

Abstract

Male courtship behaviour towards choosy females often comprises elaborate displays that address multiple sensory channels. In bats, detailed quantitative descriptions of multimodal courtship displays are still fairly scarce, despite the taxon's speciose nature. We studied male courtship behaviour in a polygynous Neotropical bat, Seba's short-tailed fruit bat *Carollia perspicillata*, by monitoring harem males in a captive colony. Courting male *C. perspicillata* performed stereotypic tactile, visual and acoustic displays. A courtship sequence, directed at one female at a time, lasted up to 120 s. During courtship, males approached females by brachiating or flying, hovered in front of them, pursued them on the wing, sniffed them and repeatedly poked the females with one or both folded wings; the latter behaviour was the most conspicuous male courtship display. Immediately before copulation, males wrapped their wings around the females and bit their necks. As acoustic display, courting male *C. perspicillata* produced highly variable, monosyllabic courtship trills. The species' vocal repertoire consisted of ten different social vocalisation types, three for benign interactions (courtship trills, wobbles, isolation calls), four for aggressive encounters (aggressive trills, down-sweeps, warbles, distress calls) and the remaining three for unknown behavioural contexts (V-shaped calls, flat down-sweeps, hooks). Courtship trills and aggressive trills were exclusively produced by males. We measured 245 courtship trills of five males and found statistical evidence for a strong individual signature which has the potential to facilitate female choice, mate recognition or neighbour-stranger recognition among male competitors.

Keywords

vocalisation types, individuality, courtship display, acoustic display, trills.

1. Introduction

Male courtship displays serve different purposes, most importantly species identification, intra-sexual competition and mate attraction. When females are choosy, male courtship displays are often elaborate and represent one of the most complex aspects of social communication (reviewed in Bradbury & Vehrencamp, 1998). Male traits (i.e., secondary sexual characters) that are crucial for courtship displays are sexually selected and several non-exclusive models of intersexual selection have been proposed to explain the evolution of trait characteristics, namely the Fisherian runaway selection model (Fisher, 1930), the good genes indicator model (e.g., Zahavi, 1975; Maynard Smith, 1976, 1985; Andersson, 1986) and the direct benefits indicator model (e.g., Hoelzer, 1989; Price et al., 1993). Males of monogamous species often display only a single trait (e.g., songs of male gibbons; Marshall & Marshall, 1976), whereas males of lekking or polygynous species normally display multiple traits (e.g., body size, antlers and roars of male red deer; Reby & McComb, 2003). Displays of male traits can be unimodal or multimodal, thus incorporating different sensory channels (Møller & Pomiankowski, 1993).

Individually distinct courtship displays frequently occur in polygynous or lekking species (frogs: e.g., Pettitt et al., 2013; birds: e.g., Fusani et al., 2007; Fitzsimmons et al., 2008; mammals: Behr & von Helversen, 2004; Jahelková et al., 2008; Hoffmann et al., 2013), probably because it is advantageous that male competitors or attracted females can discriminate between different courting males based on individually distinct display characteristics (Jennions & Petrie, 1997). Whenever males are displaying in the vicinity of one another and females associate with males for extended periods of time, individually distinct courtship signals may facilitate female choice of mating partners (Behr & von Helversen, 2004; Jahelková et al., 2008).

In bats, male courtship displays may comprise tactile, visual, olfactory or acoustic components. A typical tactile courtship display is allogrooming (e.g., *Pteropus alecto*: Markus, 2002). Erectile crests (e.g., *Chaerophon chapini*: Fenton & Eger, 2002), wing flicking (e.g., *Macrotus californicus*: Berry & Brown, 1995) or hover flights (e.g., *Glossophaga soricina*: Knörnschild et al., 2010) are examples of visual courtship displays but may have the additional function of displaying odour to conspecifics (reviewed in Altringham & Fenton, 2003). Olfactory signals play an important role in the courtship displays of many bat species (e.g., *Leptonycteris curasoae*:

Muñoz-Romo & Kunz, 2009; *Saccopteryx bilineata*: Voigt & von Helversen, 1999). Acoustic signals constitute the best studied component of male bats' courtship displays (reviewed in Fenton, 1985; Altringham & Fenton, 2003). Such advertisement calls or courtship songs can either be produced from roosting males (e.g., *Hypsignathus monstrosus*: Bradbury, 1977; *Nyctalus noctula*: Weid, 1994; Pfalzer & Kusch, 2003) or from males on the wing, a behaviour that is termed songflight (e.g., *Pipistrellus pipistrellus* and *P. pygmaeus*: Barlow & Jones, 1997; *Megaderma lyra*: Leippert, 1994; *Vespertilio murinus*: Zagmajster, 2003). In other bat species, courting males vocalise both during flight and while roosting (e.g., *Pipistrellus nathusii*: Jahelková et al., 2008; *Nyctalus leisleri*: von Helversen & von Helversen, 1994; *Neoromicia nana*: O'Shea, 1980). Courtship displays of male bats can also be multimodal and comprise visual, olfactory and acoustic components at once (e.g., *Tadarida brasiliensis*: Bohn et al., 2008, 2009; *Saccopteryx bilineata*: Voigt et al., 2008; *Erophylla sezekorni*: Murray & Fleming, 2008).

Seba's short-tailed fruit bat *Carollia perspicillata* is a common and widely distributed Neotropical frugivore (Cloutier & Thomas, 1992). This highly gregarious species exhibits resource-defence polygyny (Williams, 1986; Fleming, 1988). In the day-roost, males vigorously defend roosting territories and the females therein against male competitors (Porter, 1979a; Williams, 1986). Male harems can contain up to eighteen females and their current offspring (Williams, 1986). Several harem territories, bachelor groups, solitary bachelors and mixed-sex subadult groups can occur in the same day-roost (Porter, 1978, 1979a; Williams, 1986). Harem males are not larger but older and heavier than bachelor males (Williams, 1986). A male abandons his territory only after being displaced or when taking over a superior territory from a competitor (Porter, 1979a; Williams, 1986). Male–male disputes appear to be ritualized and contain two highly stereotypic behaviours, nosing and boxing (Porter, 1978). Nosing males confront each other roosting face to face for up to 10 min and show no movements other than tongue flicking (Porter, 1978). If nosing does not resolve the conflict, male opponents engage in boxing bouts during which they hit each other with folded wings (Porter, 1978); nevertheless, opponents are rarely injured (Porter, 1979a). Male tenure as harem holders in the day-roost can last up to two years (Williams, 1986). Harem males often return to the day-roost at night, probably to defend their harem territories against intruders (Williams,

1986). Females and bachelor males generally do not return, suggesting that harem groups do not forage together at night (Williams, 1986).

The species' vocal repertoire has been partially characterized before (Porter, 1979b; Straub & Esser, 2000; Knörnschild et al., 2013), qualitatively describing nine different vocalisation types (Porter, 1979b). However, the potential existence of vocal signatures could not be elucidated (Porter, 1979b), except for pup isolation calls (Knörnschild et al., 2013). In the wild, females choose harem territories mainly based on roosting site characteristics and harem males were never observed to actively recruit females into their territories (Williams, 1986; Fleming, 1988). However, captive evidence indicates that harem males sometimes recruit females with hover flights and vocalisations (Porter, 1979a). When females are oestrous, harem males engage in courtship activities. Prior to copulations, harem males sniff roosting females and poke them with their folded wings (Porter, 1979a). During copulations, males wrap their wings around the females and bite their necks (Porter, 1979a). It was noted before that courtship activities were accompanied by vocalisations but they were not analysed (Porter, 1979a).

In our study, we aimed to describe the complete vocal repertoire of *C. perspicillata* in its behavioural context, with special emphasis on male courtship vocalisations, and to describe the associated courtship behaviour of males. Specifically, we hypothesised that male courtship vocalisations encoded an individual signature presumably because individual recognition helps to mediate mate choice by selective females or competition for access to females among males. If a reliable individual signature existed, we predicted that males could be statistically distinguished based on the acoustic parameters of their courtship vocalisations.

2. Material and methods

2.1. Study animals

Our captive group of *C. perspicillata* originated from a breeding colony of the Zoological Garden in Frankfurt, Germany, and was housed in an indoor flight cage at the University of Ulm, Germany, from 2009–2011. During data acquisition in 2011, our study colony consisted of 35 bats (5 harem males, 9 bachelor males, 11 females, 10 pups) which occupied a $4.2 \times 3 \times 2$ m wooden flight cage. The five harem males were born in the large breeding colony of the Zoological Garden in Frankfurt, Germany; therefore, it

is unlikely that they were close relatives (e.g., brothers, or fathers and sons). Bats were kept at 25°C ambient temperature and 70% humidity. They were provided with an *ad libitum* diet consisting of fresh fruit (banana, melon, cucumber, apple, grapes), vitamin enriched mash (semolina and fruit), honey and water. We maintained a reversed 12 h day and night cycle to facilitate behavioural observations and sound recordings (day: 02:00–14:00; night: 14:00–02:00). All bats were caught once with mist-nets (Ecotone Nylon Mist Nets 716; Ecotone, Gdynia, Poland) and banded with coloured split plastic rings (size X3; A.C. Hughes, Hampton Hill, UK) on their forearm, which made it possible to distinguish individuals from a distance. Bats were habituated to human observers sitting quietly on the floor of the flight cage.

2.2. Behavioural observations

Video recordings of male courtship behaviour (obtained with a Sony Handycam DCR-SR32 with night-shot function and two infrared lights (Sony HVL-IRM)) were subjected to detailed behavioural analyses (focal animal sampling *sensu* Altmann, 1974). All observations were made during the synchronised postpartum oestrus of females which we expected to occur 3–10 days after parturition (following Badwaik & Rasweiler, 2000); thus, we assured that all females were equally receptive to male courtship attempts. We noted how males interacted with females during seven courtship sequences per male which were selected mainly based on video recording quality. For each male, our selection included at least one courtship sequence directed at each of the harem females. Additionally, selected courtship sequences were stemming from at least 5 different days during the females' postpartum oestrus.

We quantified how often and how long harem males engaged in the following courtship and mating display types: approaching (brachiating or flying towards the female), hovering (hovering in mid-air directly in front of the female), sniffing (sniffing the female with body arched forward, sometimes accompanied by rapid wing beats), repeated wing poking (poking the female with one or both folded wings), wing wrapping (embracing the female with both partially opened wings), and copulating (pelvic thrusts, sometimes accompanied by neck biting). Additionally, we noted the total duration of each courtship sequence, since displays belonging to the same courtship sequence were sometimes intercepted by several seconds of inactivity.

2.3. Sound recordings and acoustic analyses of male courtship trills

Sound recordings were made with a high-quality ultrasonic recording setup (300 kHz sampling rate and 16 bit depth resolution) consisting of an ultrasonic microphone (Avisoft USG 116Hme with condenser microphone CM16; frequency range 1–200 kHz) connected to a laptop computer (JVC, MP-XP741DE) running the software Avisoft-Recorder v4.2 (R. Specht, Avisoft Bioacoustics, Berlin, Germany). To assess the behavioural context of each vocalisation type in the vocal repertoire, we conducted simultaneous behavioural observations directly with a night vision scope (Litton Monocular M911) or remotely with a digital video camera with night-shot function (Sony Handycam DCR-SR32) and infra-red lights (Sony HVL-IRM).

Vocalisation types were defined visually based on their appearance in spectrograms (Hamming window with 1024-point fast Fourier transform and 93.75% overlap). Gradations between different vocalisation types were not observed; therefore, we considered it valid to define vocalisation types in a purely qualitative way. In total, we inspected 4062 vocalisations (excluding the ubiquitous echolocation calls; see Table 1 for details).

We used Avisoft-SASLab Pro (v5.2, R. Specht, Berlin, Germany) for acoustic analyses. Courting male *C. perspicillata* produced monosyllabic courtship trills in series (Figure 1F). However, since we selected trills from as many different series as possible (to reduce temporal dependence among calls), the acoustic parameter 'interval' was not used in further analyses. We analysed 245 courtship trills from five harem males (94, 76, 38, 20 and 17 trills per male, respectively). The disproportionate amount of trills per male was caused by the difference in vocal activity between males; the two males with the smallest harems (each containing one female) were less vocal than the three other males that defended larger harems (containing two, three and four females, respectively). Only trills with excellent signal-to-noise ratio were selected for acoustic measurements. We determined the start and end of trills automatically (–25 dB relative to the peak frequency of the signal). Trills were multiharmonic but we used only the fundamental frequency for measurements because it normally contained most of the sound energy. Measurements were taken from spectrograms using a Hamming window with 1024-point fast Fourier transform and 93.75% overlap, which resulted in a frequency resolution of 293 Hz and a time resolution of 0.2133 ms. We measured five spectral parameters (peak frequency, minimum and maximum frequency, bandwidth, entropy) at twenty different locations distributed

Table 1. Characteristics of vocalisation types from the vocal repertoire of *C. perspicillata*.

Vocalisation type	Production mode	Syllable type	Behavioural context	Frequency of occurrence	Sex and age of vocalising bat
Down-sweeps	Mainly in series	Monosyllabic	Aggressive interactions	Very common (41.8%)	Adults of both sexes
Warbles	Singly or in series	Multisyllabic	Aggressive interactions	Common (2.5%)	Adults of both sexes
Aggressive trills	Singly or in series	Monosyllabic ^a	Aggressive interactions	Very common (11.1%)	Adult males
Distress calls	Singly or in series	Multisyllabic	Aggressive interactions	Common (6.2%)	Adults of both sexes
Wobbles	Mainly singly	Monosyllabic	Benign interactions	Rare (0.3%)	Adults of both sexes
Courtship trills	In series	Monosyllabic	Benign interactions	Very common (12.3%)	Adult males
Isolation calls	In series	Monosyllabic	Benign interactions	Very common (24.6%)	Pups of both sexes
Echolocation calls	In series	Monosyllabic	No discernible interactions	Ubiquitous	All bats
V-Shaped Calls	Singly or in series	Multisyllabic	No discernible interactions	Rare (0.6%)	Unknown
Flat down-sweeps	Mainly Singly	Monosyllabic	No discernible interactions	Rare (0.2%)	Unknown
Hooks	Singly or in series	Monosyllabic	No discernible interactions	Rare (0.4%)	Unknown

Vocalisation nomenclature in comparison to an earlier study (Porter, 1979b): aggressive warbles and distress calls correspond to ‘screeches’, courtship trills to ‘whines, warbles, trills and FM glides’, isolation calls to ‘infant backchecks, half-trills and trills’, and echolocation calls to ‘FM pulses’ as described in Porter (1979b). Percentages refer to the total number of inspected calls (4062 calls). Echolocation calls were excluded from the calculation of percentages due to their ubiquitous nature.

^a Aggressive trills were often combined with down-sweeps.

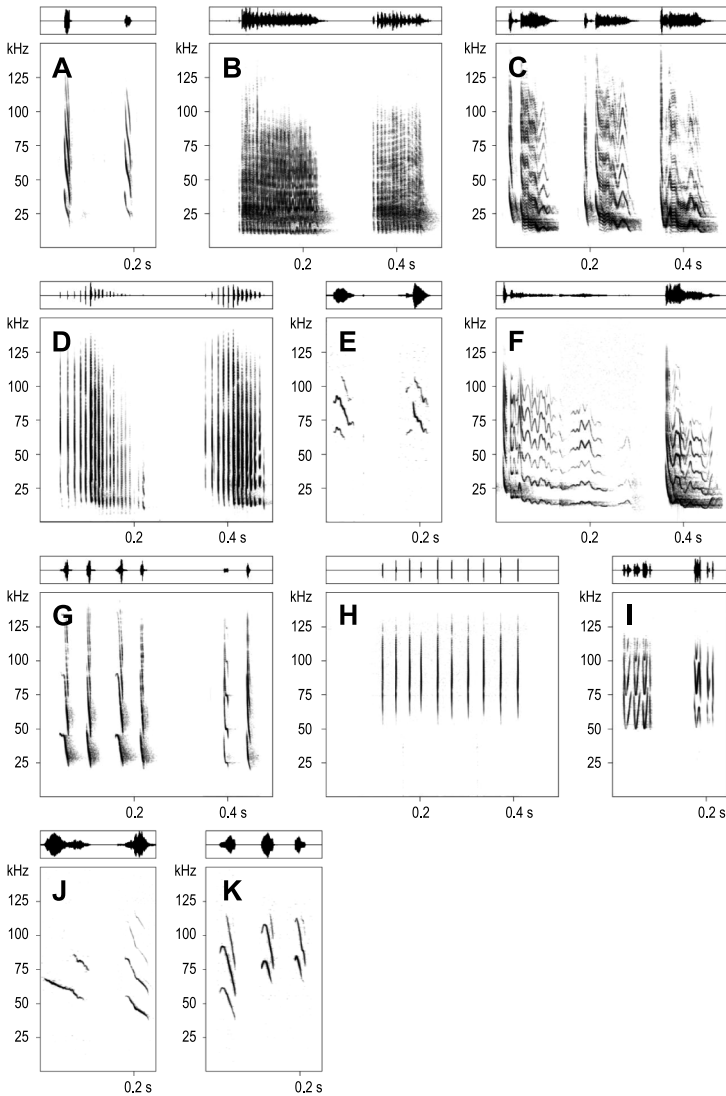


Figure 1. Vocal repertoire of captive *C. perspicillata* consisting of 10 social vocalisation types in addition to echolocation calls: aggressive down-sweeps (A), aggressive warbles (B), male aggressive trills (C), distress calls (D), benign wobbles (E), male courtship trills (F), pup isolation calls (G), echolocation calls (H), V-shaped calls (I), flat down-sweeps (J) and hooks (K). The spectrograms depict frequency as a function of time and were generated using a 1024-point fast Fourier transform, a frame size of 100% and a Hamming window with 75% overlap. These settings resulted in a frequency resolution of 293 Hz and a temporal resolution of 0.8533 ms for files with 300 kHz sampling frequency and 16 bit depth.

equally over the call (resulting in 100 spectral parameters describing call curvature) as well as averaged over the entire call. Moreover, we measured two temporal parameters (duration, time to maximum amplitude) and one waveform parameter (energy). In total, we obtained 108 acoustic parameters per trill.

We performed a principal component analysis with varimax rotation on the 100 parameters describing call curvature and extracted 18 principal components (with eigenvalues > 1) which explained 84.8% of the total variance. We ascertained the appropriateness of our data set for a principal component analysis by performing Bartlett's test and by calculating the KMO index which measures sampling adequacy. The principal component analysis fulfilled Kaiser-Meyer-Olkin (KMO) and Bartlett's test criteria (KMO index: 0.873, Bartlett: $\chi^2_{4950} = 58\,526.892$, $p < 0.0001$). We performed a stepwise discriminant function analysis (DFA) on the 18 principal components describing call curvature and the remaining eight original parameters (mean peak frequency, mean minimum and maximum frequency, mean bandwidth, mean entropy, duration, time to maximum amplitude, energy) to test for an individual signature in courtship trills. The DFA used a leave-one-out-cross-validation procedure that classified each trill based on discriminant functions established with all trills except the one being classified. The significance of the classification success obtained by the DFA was estimated by using one-tailed binomial tests (following Mundry & Sommer, 2007). Statistical tests were conducted using SPSS v20.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Courtship displays and mating

All five harem males were observed to perform the courtship displays brachiating or flying towards the female, hovering directly in front of the female, sniffing the female, poking the female with one or both folded wings, and pursuing the female on the wing (see Table A1 and Video 1 in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>). However, not all above mentioned display types were necessarily performed in every courtship sequence of every male. Only three of five males displayed wing wrapping by embracing the female with both partially opened wings, and only two of them

preceded from wing wrapping to neck biting and, ultimately, copulating (Table A1). Copulations lasted between 17 and 31 s. Afterwards, both sexes began autogrooming. All harem males produced courtship trills when courting females.

3.2. Vocal repertoire

Carollia perspicillata produced 10 different social vocalisation types in addition to echolocation calls (Figure 1) and, for most vocalisation types, we were able to elucidate the behavioural context in which they were uttered. Four vocalisation types were produced during aggressive encounters, namely down-sweeps, warbles, trills and distress calls (Figure 1A–D). During mild aggressive interactions, bats produced mainly down-sweeps; when aggressive interactions escalated in physical conflicts, bats switched to producing warbles and, if they were the inferior part, distress calls. Aggressive down-sweeps, warbles and distress calls were produced by both sexes, whereas aggressive trills were exclusively produced by males roosting in their respective territories and often preceded aggressive male–male interactions. Three vocalisation types were uttered during benign interactions, namely wobbles, courtship trills and isolation calls (Figure 1E–G). Wobbles were produced by both sexes when bats were roosting close together and appeared to be relaxed. Courtship trills were exclusively produced by males when courting females. Isolation calls were produced by dependant pups of both sexes to solicit maternal care. Echolocation calls (Figure 1H) were uttered during flight and while roosting alertly. The behavioural context for the remaining three vocalisation types, namely V-shaped calls, flat down-sweeps and hooks (Figure 1I–K), could not be determined. Table 1 gives details on the production mode, syllable characteristics, and the frequency of occurrence of all vocalisation types; moreover, it associates the described vocalisation types with the terms used in a previous study on the social communication of *C. perspicillata* (Porter, 1979b).

3.3. Statistical evidence for an individual signature in male courtship trills

Males produced courtship trills in series while courting females in their territory. The mean interval between trills in series was 0.79 s (range 0.33–2.56 s), the mean duration was 0.08 s (range 0.04–0.20 s) and the mean peak frequency was 13 749 Hz (range 8433–26 010 Hz). Courtship trills were monosyllabic but could be preceded by one or two down-sweeps (which

were normally used during mild aggressive interactions), especially when males appeared agitated and females tried to elude their courtship attempts. Thus, the production of down-sweeps in addition to courtship trills probably encoded the extent of male agitation. Harem males could be individually distinguished based on their courtship trills (Figure 1F). A stepwise DFA with 245 courtship trills of 5 harem males classified 86.1% of trills to the correct harem male (Figure 2, Tables 2 and 3), which was significantly higher than expected by chance (20%; binomial test: $p < 0.001$). The acoustic pa-

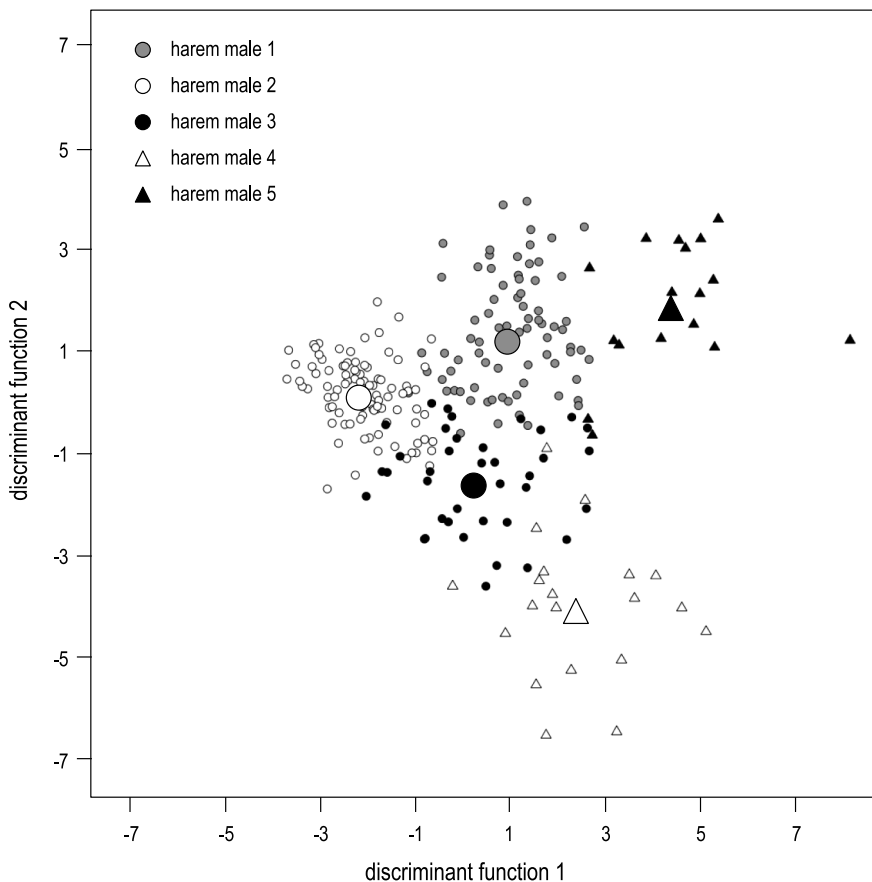


Figure 2. Individual signature in courtship trills of male *C. perspicillata*. The first two functions of a discriminant function analysis define a signal space in which the location of each male (large symbols) and every trill (small symbols) is depicted. Please note that there is only little overlap between males, indicating a pronounced individual vocal signature.

Table 2.

Statistical evidence for an individual signature in courtship trills of *C. perspicillata* (245 trills from 5 males) by means of assessment of model fit.

Assessment of model fit ^a	DF1	DF2	DF3	DF4
Eigenvalue	3.906	2.584	0.718	0.370
Percentage of variation	51.5	34.1	9.5	4.9

^a Stepwise discriminant function analysis with cross-validation.

rameters most important for individual discrimination were mean maximum frequency, mean entropy, mean bandwidth and duration. The remaining ten acoustic parameters included in the DFA (Table 4) were mean minimum frequency and nine principal components that encoded information on call curvature.

4. Discussion

Our vocal repertoire description of *C. perspicillata* is in concordance with earlier work. Differences in vocalisation nomenclature occur since we lumped several of the previously described vocalisation types (Porter, 1979b). Nevertheless, we described more vocalisation types than the earlier study (Porter, 1979b), thus adding to the species' vocal repertoire description. The vocal repertoire of *C. perspicillata* is one of the few vocal repertoires described for phyllostomid bats (e.g., *Glossophaga soricina* and *G. commissarisi*: Knörnschild et al., 2010) despite the family's speciose nature. Most studies on phyllostomid bats focus on a few selected vocalisation types from the species' repertoire such as isolation calls (e.g., *Phyllostomus discolor*: Esser & Schmidt, 1989; *P. hastatus*: Bohn et al., 2007) or contact calls (e.g., *P. hastatus*: Boughman, 1997; *Diaemus youngi*: Carter et al., 2008). In general, phyllostomids seem to have structurally less complex

Table 3.

Statistical evidence for an individual signature in courtship trills of *C. perspicillata* (245 trills from 5 males) by means of test of functions.

Test of function	DF1–DF4	DF2–DF4	DF3–DF4	DF4
Wilk's Lambda	0.024	0.119	0.425	0.730
Chi-square (all $p < 0.0001$)	872.954	499.998	200.662	73.777

Table 4.

Structure matrix showing the canonical loading of the discriminant functions for the 14 acoustic parameters included in the stepwise discriminant function analysis (sorted by their relevance for discrimination).

Acoustic parameter	DF1	DF2	DF3	DF4
Maximum frequency (mean)	0.366	−0.496	0.392	−0.251
Entropy (mean)	0.495	0.314	−0.171	−0.032
Bandwidth (mean)	0.385	0.100	0.415	−0.278
Duration	0.210	0.151	−0.300	−0.113
PC 8 (call curvature)	−0.075	0.057	0.064	−0.117
PC 7 (call curvature)	0.008	−0.203	−0.053	0.624
PC 2 (call curvature)	0.050	−0.042	0.295	0.203
PC 16 (call curvature)	−0.029	0.040	−0.082	0.312
Minimum frequency (mean)	0.102	−0.566	0.013	0.255
PC 9 (call curvature)	0.180	0.050	−0.049	−0.105
PC 10 (call curvature)	0.023	0.015	0.274	0.158
PC 14 (call curvature)	0.104	0.043	0.273	0.142
PC 12 (call curvature)	0.064	0.122	0.099	0.220
PC 3 (call curvature)	0.311	0.200	−0.204	0.122

vocal repertoires than other speciose bat families such as molossids (e.g., *Tadarida brasiliensis*: Bohn et al., 2008, 2009), emballonurids (e.g., *Saccopteryx bilineata*: Behr & von Helversen, 2004; Knörnschild et al., 2006; Knörnschild & von Helversen, 2008), vespertilionids (e.g., *Myotis lucifugus*: Barclay et al., 1979; Mendelez et al., 2006), mormoopids (e.g., *Pteronotus parnellii*: Kanwal et al., 1994; Clement & Kanwal, 2012) or rhinolophids (e.g., *Rhinolophus ferrumequinum*: Andrews & Andrews, 2003, 2006).

Courtship displays of male *C. perspicillata* comprise visual, tactile and acoustic components, thus incorporating different sensory channels. Courting males regularly sniffed females; however, it is unclear whether females assess the odour of courting males as well. Vocal displays of courting male *C. perspicillata* consisted of monosyllabic trill series. Trills were not produced on the wing but when males roosted in their respective territories and courted females there. The relative stationary position of vocalising *C. perspicillata* males contrasts with the ‘songflight’ behaviour known from other bat species (e.g., *Pipistrellus pipistrellus* and *P. pygmaeus*: Barlow & Jones, 1997; *Vespertilio murinus*: Zagmajster, 2003) but seems to be the typical behaviour for species in which courting males defend roosting territories (e.g., *Nyctalus noctula*: Weid, 1994; *Saccopteryx bilineata*: Voigt et al., 2008). In the bat

species studied to date, males produce courtship vocalisations with differing degrees of structural complexity, ranging from simple calls (e.g., *Neoromicia nana*: O'Shea, 1980) and basic motives (e.g., *Pipistrellus nathusii*: Jahelková et al., 2008) repeated in series to complex and intertwined combinations of motives (e.g., *Tadarida brasiliensis*: Bohn et al., 2009; *Saccopteryx bilineata*: Behr & von Helversen, 2004). In this regard, bat courtship song is comparable to bird courtship song in which structural complexity similarly ranges from simple to complex motives (Bohn et al., 2013). The courtship trills of male *C. perspicillata* showed comparatively low structural complexity but nevertheless encoded an individual vocal signature. Such individual signatures in courtship vocalisations have been shown for several other bat species and are hypothesized to facilitate individual recognition (e.g., *Pipistrellus nathusii*: Jahelková et al., 2008; *Tadarida brasiliensis*: Bohn et al., 2009; *Saccopteryx bilineata*: Behr & von Helversen, 2004).

In conclusion, our study demonstrates that the vocal repertoire of the bat *C. perspicillata* is more comprehensive than previously described and that male courtship trills have the potential to facilitate the discrimination of individual males via a pronounced individual vocal signature. Future work is needed to elucidate whether the individual signature in male courtship trills is actually used by conspecifics, e.g., in the context of female choice, mate recognition or neighbour–stranger recognition (as reviewed in Tibbetts & Dale, 2007).

Acknowledgements

Valuable comments by M. Metz and M. Nagy substantially improved the manuscript. We are indebted to Stefanie Aichele and Simone Pechman for their help in data acquisition. We are especially grateful to the Bat Center GmbH Noctalis, Bad Segeberg, Germany (<http://www.noctalis.de/>), for taking care of all *C. perspicillata* after the completion of our study. This work was supported by a start-up grant from the University of Ulm, Germany (M.K.).

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Supplementary material

Video 1. Courtship sequence except of male *C. perspicillata*. The courting male displays wing poking, sniffing and brachiating towards the female. The harem male is banded on his right forearm, the female on her left forearm. The female is carrying her 7-day-old pup. Video footage was taken from directly under the night-roost with a digital video camera with night-shot function (Sony Handycam DCR-SR32) and additional infra-red lights (Sony HVL-IRM).

Appendix: Supplementary material
Table A1.
 Quantitative characteristics of courtship displays of male *C. perspicillata*.

Male No.	Hover flight	Brachiating	Flying	Sniffing	Wing poking	Pursuing female	Wing wrapping	Neck biting/copulating	All behaviours	Duration of courtship sequences (s)
Cumulative performance time (s) of different courtship displays during seven courtship sequences										
1	2.3 ± 1.2 (0-8)	6.4 ± 2.5 (1-21)	0.1 ± 0.1 (0-1)	5.3 ± 2.1 (0-15)	24.4 ± 12.3 (0-82)	2.0 ± 0.9 (0-7)	3.3 ± 1.8 (0-13)	0.1 ± 0.1 (0-1)	44.0 ± 13.5 (11-97)	51.3 ± 12.5 (11-97)
2	1.4 ± 0.8 (0-6)	3.1 ± 0.9 (0-7)	0.3 ± 0.3 (0-2)	4.3 ± 1.0 (0-8)	4.3 ± 2.5 (0-18)	3.4 ± 2.2 (0-16)	0.4 ± 0.5 (0-3)	6.9 ± 4.7 (0-31)	24.1 ± 6.5 (9-55)	48.0 ± 10.0 (13-94)
3	3.9 ± 1.6 (0-13)	2.0 ± 1.5 (0-11)	not observed	4.1 ± 1.3 (0-10)	2.1 ± 1.2 (0-7)	3.1 ± 2.5 (0-18)	0.1 ± 0.1 (0-1)	not observed	15.4 ± 3.8 (8-35)	62.0 ± 13.8 (11-124)
4	1.7 ± 0.4 (0-3)	0.1 ± 0.1 (0-1)	0.1 ± 0.1 (0-1)	0.3 ± 0.2 (0-1)	0.4 ± 0.3 (0-2)	0.4 ± 0.3 (0-2)	not observed	not observed	3.1 ± 0.4 (2-5)	22.3 ± 13.8 (2-104)
5	1.4 ± 0.4 (0-3)	0.4 ± 0.4 (0-3)	0.4 ± 0.3 (0-2)	0.3 ± 0.2 (0-2)	1.3 ± 0.5 (0-3)	0.4 ± 0.4 (0-3)	not observed	not observed	4.3 ± 0.7 (2-7)	23.4 ± 16.3 (2-120)
Frequency of occurrence of different courtship displays per courtship sequence										
1	0.9 ± 0.5 (0-3)	1.6 ± 0.4 (1-4)	0.1 ± 0.1 (0-1)	1.3 ± 0.4 (0-3)	3.1 ± 1.4 (0-10)	0.7 ± 0.2 (0-1)	1.1 ± 0.6 (0-4)	0.1 ± 0.1 (0-1)	9.0 ± 2.5 (3-21)	
2	0.7 ± 0.4 (0-2)	1.0 ± 0.2 (0-2)	0.1 ± 0.1 (0-1)	1.0 ± 0.2 (0-2)	0.9 ± 0.3 (0-2)	0.6 ± 0.2 (0-1)	0.1 ± 0.1 (0-1)	0.3 ± 0.2 (0-1)	4.7 ± 0.6 (3-8)	
3	2.7 ± 1.1 (0-9)	0.6 ± 0.2 (0-1)	not observed	1.0 ± 0.2 (0-2)	0.6 ± 0.3 (0-2)	1.4 ± 1.1 (0-8)	0.1 ± 0.1 (0-1)	not observed	6.4 ± 2.0 (2-18)	
4	1.3 ± 0.3 (0-2)	0.1 ± 0.1 (0-1)	0.1 ± 0.1 (0-1)	0.3 ± 0.2 (0-1)	0.3 ± 0.2 (0-1)	0.3 ± 0.2 (0-1)	not observed	not observed	2.4 ± 0.4 (1-4)	
5	1.0 ± 0.4 (0-3)	0.1 ± 0.1 (0-1)	0.3 ± 0.2 (0-1)	0.1 ± 0.1 (0-1)	0.6 ± 0.2 (0-1)	0.1 ± 0.1 (0-1)	not observed	not observed	2.3 ± 0.4 (1-4)	

Male courtship intensity was assessed by the cumulative time each male performed courtship behaviours during the seven courtship sequences analysed per male. Mean ± SE are given. The range is reported in parentheses.