

Calling-song function in male haglids (Orthoptera: Haglidae, *Cyphoderris*)

Glenn K. Morris, Paul A. DeLuca, Matthew Norton, and Andrew C. Mason

Abstract: We studied the response of males to the singing of nearby male conspecifics in two species of the orthopteran genus *Cyphoderris*, primitive relatives of crickets and katydids. Lone male *Cyphoderris buckelli* stridulating in a large cage made a phonotactic approach to a nearby speaker broadcasting conspecific calling song. But in field experiments no phonotaxis to song broadcasts occurred; rather, a significant number of male *C. buckelli* increased their chirp duty cycle and pulse rate. There was no change in their carrier frequency. Calling male *Cyphoderris monstrosa* were exposed in the field to (i) playback of a synthetic calling song at a typical conspecific pulse rate, (ii) relayed broadcast of their own call, and (iii) low-frequency audio noise. Call duty cycle decreased significantly in response to the noise, while the pooled song models fell just short of significance. Singing *C. buckelli* were marked individually and their perches flagged over successive nights. We observed low site fidelity and extensive male displacement. Such behaviour is inconsistent with defense of topographically fixed singing territories and concurs with the absence of fighting in this species. Chirp duty cycle was increased significantly in *C. buckelli* in response to the singing of nearby conspecifics, but unlike in *C. monstrosa*, this change in duty cycle plays no role in overt aggression, though it may maintain a male's relative attractiveness to females.

Résumé : Nous avons étudié la réaction de mâles à l'écoute de chants d'autres mâles voisins de la même espèce chez deux orthoptères du genre *Cyphoderris*, des parents primitifs des grillons et des sauterelles. Des mâles solitaires de *Cyphoderris buckelli*, stridulant dans une grande cage, se sont déplacés par phonotaxie vers un voisin émettant le chant d'appel de l'espèce. Lors d'expériences en nature, il n'y avait pas de comportement de phonotaxie; au contraire, un nombre significatif de mâles de *C. buckelli* ont augmenté leur cycle actif de stridulation et leur taux d'impulsions, sans modifier leur fréquence porteuse. Des mâles stridulants de *Cyphoderris monstrosa* en nature ont été exposés à (i) l'écoute d'enregistrements d'un chant d'appel synthétique de taux d'impulsion typique du chant de leur espèce, (ii) la retransmission par relais de leur propre chant et (iii) un bruit audio-acoustique de basse fréquence. Ils ont réduit leur cycle actif de stridulation en réponse au bruit, mais leur réaction aux modèles de chant (données regroupées) était juste sous les limites du seuil de signification. Des *C. buckelli* stridulateurs ont été marqués individuellement et leurs perchoirs localisés au cours de nuits successives. Il y avait une faible fidélité au site et les mâles se déplaçaient beaucoup. Un tel comportement n'est pas compatible avec la défense de territoires de chants topographiquement définis, mais il l'est avec l'absence de combats chez cette espèce. Le cycle actif de stridulation augmente de façon significative chez *C. buckelli* en réaction à la présence de stridulateurs actifs de même espèce dans les environs, mais, contrairement à *C. monstrosa*, cette modification du cycle actif ne joue pas de rôle d'agression évidente, mais elle peut servir à maintenir l'attrait relatif du mâle chez les femelles.

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Introduction

Phonotaxis by females to the calling signal of male conspecifics has been demonstrated for many species of male ensiferan Orthoptera (Ewing 1989). On this basis, calls of males in the suborder are said to function in female attraction. More recent studies (e.g., Latimer and Sippel 1987;

Brown et al. 1996; Simmons and Ritchie 1996) show that such attraction can involve fine discrimination by females, as they respond to song features reflecting differences in a male's quality as a potential mate.

Because it is a broadcast, a male's calling signal is heard not just by female conspecifics but also by conspecific males. The responses evoked in male listeners vary. In some species the call initiates phonotaxis, one male approaching another and often entering into a fight (Morris 1972; Brush et al. 1985; Mason 1996). In other species there is no approach and no overt aggression (Simmons and Bailey 1993; Sakaluk et al. 1995), but the singing of one male affects the singing of his neighbour, creating chorusing and phasing (Greenfield 1994). Yet another male response to an encroaching calling neighbour is passive withdrawal (Dadour and Bailey 1985). And still another is "active attraction," a phonotactic response oriented to the collective acoustic output of a group rather than to individuals (Ewing 1989, p. 157). By means of active attraction an isolated insect may reach and remain within a group of conspecifics (Morris and Fullard 1983)

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and so improve its access to suitable habitat, food, or potential mates.

Here we address responses to conspecific calling song in males of two species, *Cyphoderris monstrosa* and *Cyphoderris buckelli*. As relict Ensifera they are closely related to crickets and katydids, but are placed in their own family, the Haglidae (Gwynne 1995). The two species live in lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) forests in the mountains of northwestern North America. We studied them in the Canadian Rockies in southern Alberta and British Columbia. A related species, *Cyphoderris strepitans* (Morris and Gwynne 1978), occurs in Colorado and Wyoming.

Just after sunset in May and June, males of *Cyphoderris* spp. walk up from the ground to perch and call through the early hours of the night. Male *C. monstrosa* station themselves high up, 2 m to many metres above the ground, on the trunks of relatively mature trees. Calling *C. buckelli* remain within a metre of the forest floor, calling from understory shrubs. The two species can occur syntopically (Buckell 1924) (G.K.M. and A.C.M., unpublished observation at Paul Lake, B.C.), but this is apparently uncommon.

The calling songs of *Cyphoderris* spp. are very similar in physical structure. Both species make a succession of chirps, each chirp an evenly spaced series of sound pulses (Morris and Gwynne 1978). The pulses are cricket-like in their musicality, having a narrow, relatively high-Q spectral peak and a correspondingly sinusoidal waveform (Figs. 1, 2). But *Cyphoderris* spp. carriers, at 12–15 kHz, are higher than those of cricket calling signals, which are all <10 kHz (Otte 1992). *Cyphoderris monstrosa* also exhibits an unusual ear-tuning mismatch (Mason et al. 1999): the frequency of maximum auditory sensitivity is near 2 kHz in both sexes and does not correspond to the calling-song carrier.

These species are unusual in being acoustically active at very low temperatures (Morris and Gwynne 1978). Also, the pulse rates of both species are slow enough at 6–14°C to allow the pulses to be resolved by human listeners as chirp infrastructure. The pulse rate distinguishes the songs of the two species and is strongly affected by temperature. For a given temperature the pulse period of *C. buckelli* is always longer than that of *C. monstrosa* (Fig. 6 in Morris and Gwynne 1978). There is also a modest distinction in carrier: the average carrier frequency for *C. monstrosa* is 12 kHz, while that of *C. buckelli*, higher in a smaller animal, is 15 kHz (Mason 1996).

In a series of laboratory encounters in which singers interacted on a vertical log, the calling signal of *C. monstrosa* was found to elicit fighting between males (Mason 1996). The increasingly sustained calling song of this species (increased chirp duty cycle; see below) correlated with aggressive dominance (Mason 1996). This song change predicted fight outcomes. Muted males, winners of previous fights, continued to win their aggressive encounters but experienced more sustained escalation from their opponents, which shows that rivals make use of song information during encounters (Mason 1996).

In the studies reported here, both *Cyphoderris* species were examined in the wild for the effect upon a male singer of broadcasting the calls of a conspecific male in close proximity. For *C. monstrosa* we also examined the effect of broadcast low-frequency audio noise. And in *C. buckelli* we

investigated site fidelity by marking and then recapturing free-living singers over successive nights. Our goal was to gain insight into the contrasting roles of song-mediated male behaviours in these two species.

Materials and methods

Cyphoderris monstrosa

Study population

Recording and playback using this species were conducted in 1991 (by A.C.M.) in forest adjacent to the Kananaskis Field Station of the University of Calgary near Canmore, Alberta. Male *C. monstrosa* emerge here from leaf litter at dusk in a subalpine mixed coniferous forest dominated by lodgepole pine. They climb and sing several metres above the ground, from the trunks of relatively mature western white spruce (*Picea glauca*) trees.

Song structure and recording

Field recordings of calling songs were obtained for 16 male *C. monstrosa* singing from natural perches. This occurred at least 2 h after the first singer of the evening was heard, when singing in the population had become general and sustained. Each male's singing was sampled three times in succession at intervals of 5 min. Two alternative recording systems were used: (1) a Racal Store 4D instrumentation tape recorder receiving the output of a Bruel and Kjaer 2204 sound-level meter, fitted with a 1/2" condenser microphone (Larsen-Davis, model 2540); (2) a Sony Walkman Professional audio tape recorder with an ECM 909 microphone. The first system has a uniform frequency response up to 40 kHz, the second is limited to the audio range. Three playback models were then constructed with a view to testing the response of singers to chirp duty cycle. (Chirp duty cycle is the proportion of a multichirp time sample that is spent producing a chirp; in our studies we always calculated this over an interval of 2 min.)

Broadcast signals

The possibility that solitary singing males would alter their singing, especially chirp duty cycle, in response to the broadcast of conspecific calling song was examined in a series of field playback experiments. Males were exposed to one of three acoustic stimuli. Two of these were calling-song models intended to represent output from nearby "rivals" (synthetic, or a rebroadcast of the subject male's calls) and the third consisted of continuous low-frequency noise without amplitude-modulation structure.

The synthetic chirp stimulus was fashioned from a train of sound pulses, each 10 ms in duration (full intensity) with 0.5 ms linear rise/fall times, delivered at a rate of 33/s. These were generated by modulating a 12-kHz tone from a signal generator (Exact 126) using a Colbourn Envelope Shaper. Pulse trains (chirps) with a duration of 2 s, separated by 1-s intervals of silence, were generated by gating the output of the signal generator with a programmable voltage source (Grass SD-9). This created an artificial song with a duty cycle of 0.67 (2-s bursts of song and 1-s pauses). This signal was amplified (Pioneer GM-43A) and broadcast via a loudspeaker (Realistic Piezo-tweeter) placed pointing upward at

the base of the tree in which the male was singing. Playback intensity was calibrated with a sound-level meter (B and K Type 2204, Larsen–Davis 2540 microphone) and set to 100 dB sound-pressure level (SPL) (re 20 μ Pa) at 10 cm. This intensity is comparable to that of a singing *C. monstrosa* at the source.

For delayed rebroadcast of the subject male's song, males were recorded using the Racal Store 4D recorder and the recording was simultaneously amplified and broadcast as described above. The record and playback heads of this recorder are separated by several centimetres of tape-travel distance, so playback was delayed relative to the original signal by the time taken for tape to move between the two heads. At a tape speed of 7.5 in./s (1 in. = 25.4 mm) this delay was approximately 2 s. Males in this treatment were therefore subjected to an acoustic stimulus based upon their own output but lagging it by about 2 s.

Feedback from the speaker was controlled by mounting the microphone in a parabolic reflector. This made the microphone directional enough to selectively record the singing male, but was only possible for males singing from sufficiently high perches, and even then the speaker gain had to be reduced. Playback levels for these trials were below 100 dB at 10 cm to a variable and unknown extent, determined by the feedback limit. However, this variation was not systematically biased by the males' perch heights. When males were on lower perches, less separation of the speaker and microphone was allowed, and consequently playback intensities were lower than when males perched at greater heights. But these males were also closer to the speaker and so received a less attenuated stimulus. The recording protocol for the rebroadcast treatment was as described below, except that recording was continuous during the 15-min playback interval (since generation of the playback stimulus required that the male be recorded).

The purpose of the noise trials was to control for the possibility that any changes in male acoustic output during song playbacks were not specific responses to the detection of rival song. The protocol in these experiments was identical with the synthetic song playbacks except that the acoustic stimulus was continuous, band-limited noise broadcast at 100 dB SPL. The output of a random noise generator (General Radio Type 1390-8) was band-pass filtered (Krohn-Hite 3202, 2–8 kHz pass-band) to produce a noise signal biased to low audio frequencies and with little energy at the species' song frequency (Fig. 2B).

Analysis

For all treatments, male singing was recorded both before and during playback. For noise and rebroadcast treatments, three samples of song were recorded in each condition. Males were recorded for approximately 1.5 min at intervals of 5 min. In synthetic song trials only single samples of singing prior to playback were taken. Multiple recordings of singing in the absence of playback stimuli were made to obtain measures of the consistency of individual males in the song parameters that were compared between solitary singing and playback conditions. Playback was continued for 15 min.

The acoustic output of 9 males exposed to rebroadcast of their own singing was recorded in the field; 9 males were re-

corded during playback of synthetic song and 8 males were recorded in the presence of broadcast noise.

For analysis, multiple measurements of a single male in the same condition were pooled (i.e., all pre-playback measurements from the same male were pooled) to give single measures for the two conditions (solitary singing, singing with playback) in each treatment. The difference in these two measures (playback vs. solitary) represented a male's response to playback. Statistical tests were carried out using SYSTAT software (Wilkinson et al. 1992).

Cyphoderris buckelli

Playback experiment with caged males

In 1977 (16–22 June), 9 male *C. buckelli* were exposed indoors to playback of conspecific song. (This study was not previously published, but is referred to by Sakaluk et al. 1995.) The males used were collected as adults in early May at Paul Lake Provincial Park near Kamloops, British Columbia, Canada.

Their behaviour was tested in a wood-frame cage (1.8 \times 0.75 \times 0.6 m) with a plywood floor; its roof, sides, and ends were screened and internal access was via a large top-hinged door in one side. Two speakers (Philips De Forest 4-in. dome tweeter, AD0160/T8), each mounted flush in one side of a wooden box (~20 \times ~20 cm), were placed one at each end of the longest dimension of the cage. The speakers faced each other at a distance of 140 cm. The centre of each speaker was raised to 16 cm above the cage floor by resting it on four cardboard recording-tape boxes. The cage floor was covered uniformly with a layer of dry leaves (pine, oak, and maple). Midway between the speakers, a bark-covered log section about 10 cm in diameter and 0.5 m long was set on end.

The playback tape recording was of a virgin male recorded in 1976 singing indoors at 21.9°C in a wire-mesh cage; a Sennheiser (MK4) directional microphone was positioned dorsally. This male was collected from Rutland, B.C., only 5 days before it was recorded (May 8). A Uher 4000 Report L tape recorder was used at 7½ in./s both to record and to play back this signal. A 2204 B and K sound-level meter with a ½-in. microphone (4133) rested on the cage floor 60 cm from the speaker, while the recorder was adjusted to deliver 82 dB (re 20 μ Pa). The experiment took place under red light from four 25-W bulbs in the ceiling, positioned symmetrically to the cage corners. The temperature was 21–23°C.

Each male underwent four repetitions of a two-part 20-min trial. He was released alone in the cage and after exploratory walking he climbed the central log. From there he (invariably) began steady stridulation. The trial was started after the male had been stationary and calling on the log for at least 30 s.

One speaker was randomly selected in advance as a goal speaker. The male's response during each of the first and second 10-min intervals was scored in relation to locomotion toward or away from this goal speaker. An approach to within 20 cm of the goal speaker, i.e., travelling >50 cm of the 70-cm distance between the cage centre (where the log base was) and the speaker, was scored as +1. Walking in the opposite direction, to within 20 cm of the non-goal speaker,

was scored as -1. Remaining on the log and singing was scored as 0.

After 10 min, if the male remained on the log (in fact this was always the case), calling song was broadcast from the goal speaker. The response of the male within this second 10-min interval was scored in the same fashion. After all 9 males had been tested once, the experiment was replicated 3 more times with the same 9 males. No insects ever approached the silent speaker; in all 36 trials, males continued singing from the log during the 10 min of silence when both speakers were quiet. Six of the 9 males made at least one approach to the broadcast sound during the second 10-min interval.

Field playback experiments

Study populations

In 1994 and 1995 two populations of this species were studied (by G.K.M. and P.A.D.) in southern British Columbia. The study area is north of the western arm of Kootenay Lake and south of Kokanee Glacier Park in the Kokanee Creek drainage. Singing by males begins here in early May at elevations of 500–700 m and lasts for several weeks. Calling activity at higher elevations, up to 1400 m, begins progressively later in the season.

Southern access to Gibson Lake in Kokanee Glacier Park was via a Forest Service Road (FSR) from B.C. Highway 3A. About 1 km (direct distance) from Highway 3A, at an elevation of 740 m, a second FSR branches off the first and runs northeast to Busk Creek. One study population (herein the “forks” population) was located at this junction. As is characteristic of this species, singers perched low (<2 m) on vegetation; the site is a south-facing slope and insects were usually within 20 m of the road. The forest here is characterized by western hemlock (*Tsuga heterophylla*) and western red-cedar (*Thuja plicata*) with a few very mature ponderosa pine: “Columbia Forest” grading into “Dry Forest” (Cowan and Guiguet 1965). The males never perched to sing on the several very large trees (Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine) that were present.

The second population occupied a larger area and was dispersed less regularly and at lower density within the campsite area of Kokanee Creek Provincial Park (herein the “park” population) north of and adjoining Highway 3A, almost at the elevation of Kootenay Lake (549 m). Singers were recorded in both 1994 and 1995 at the forks; marking and recapture studies here during 1995 assessed male movement. Playback trials were carried out in the Park population in 1995.

Song structure

In both 1994 and 1995, singing male *C. buckelli* ($n = 51$) were tape-recorded at the forks study site using a Sony (D6C) cassette recorder with a Sony (ECM 909) microphone and parabola (PBR 330). Each male was recorded while he was at least 1 m from any singing neighbours, though within earshot of several other singers. Each was approached where he happened to perch in the field, was usually (unavoidably) briefly disturbed into silence, but was then recorded for several minutes after he resumed steady singing. Eighteen recordings made at the forks site in 1995 (as part of the marked-male study; see below) were combined with 5 obtained at

the same site in 1994. The complete 51-male analysis cohort was achieved by incorporating the pre-playback recordings of 28 of the males involved in the broadcast study (see below). Temperatures were noted at the time of recording with a thermistor (Omega™ HH23) placed within a few metres of and at the same height as the singer. Most of the marked forks specimens were ultimately captured and preserved in 70% alcohol; all of the playback males were retained in this way.

A sample of at least 10 consecutive pulses was digitized from each field recording. With a software analysis program (DADISP®) we determined the pulse period (measured between pulse onsets), the fast Fourier transform (FFT) spectrum, and peak principal carrier frequency for each of the 10 pulses. For each male we determined a mean value (from 10 measures per male) of the main acoustic parameters: pulse period and peak carrier. We then tested statistically for any temperature effects upon these parameters and for any possible predictive value regarding size (pronotal length) or body mass.

For each of 47 *C. buckelli* field singers calling at various temperatures (range 7.2–14.6°C) we measured chirp durations during a 2-min sample. Chirps vary greatly, lasting from a fraction of a second to >50 s. (Some of the males responding to playback produced successive chirps lasting 25–28 s.) We calculated the duty cycle for each of these males and performed a regression of duty cycle on temperature. To deal with this variable, which is a proportion, we applied an arcsine transformation.

Construction of playback signals

We tested whether a *C. buckelli* field singer would alter his calling song in response to the singing of a nearby male conspecific. Three song parameters were regarded as possibly changing: chirp duty cycle, peak carrier frequency, and pulse rate.

A number of playback tapes of *C. buckelli* songs were created, one for each even-numbered temperature between 6 and 22°C. The most appropriate tape was then utilized for whichever field temperature we encountered. For most trials the temperature was either 10 or 12°C. These sound models were all based upon a single pulse taken from a male field-recorded on 17 May 1994 at the forks (Figs. 1A, 1B). The original recording was made at 10.9°C using a Sony tape recorder and microphone. This male had a peak carrier frequency of 15.2 kHz and a pulse period of 20.1 ms. The duration of each pulse was about 3.1 ms.

The pulse digitized from his recorded call was captured at a sampling rate of 200 kHz into a computer using a Keithley (DAS50) analog > digital board, low-pass filtered at 20 kHz. The call of this male was shorter than the average pulse duration we had estimated for the species, so DADISP software was used to extract and duplicate midpulse waves and then to reinsert these in midpulse to lengthen the pulse to 5.3 ms (Fig. 1D; decay was included in measuring pulse duration).

Decisions about the parameters to be utilized in the 1995 playback songs (chirp, pulse duration, pulse period, carrier) were of necessity made prior to obtaining the more definitive values (including 1995 recordings) reported in the present paper. To decide upon the playback pulse rates we utilized

previously published pulse rates (Morris and Gwynne 1978; $n = 12$), augmented ($n = 10$) from song recordings made in 1994 at Nelson, B.C.

For each temperature we created a different pulse period. From a sample of 10 males obtained at the forks in 1994 and recorded at temperatures of 6–13°C, we determined a mean chirp duration of 4530 ms and an average between-chirp silent interval of 1096 ms. We therefore constructed playback songs for the different temperatures, making chirps of 4.5 s duration repeated at 1-s intervals. A custom software program (prepared by Mr. Peter Wall) controlled a digital > analog board (Keithley AWFG) to generate a preset repetition of the prepared pulse for each temperature.

As noted above, chirp duty cycle is the proportion of a multichirp time sample spent producing a chirp. (Duty cycle can of course also be considered at the resolution level of the pulse, e.g., pulse duty cycle.) Chirp duty cycle was calculated here as the sum of the durations of uninterrupted pulse trains per 2 min. A sample of 10 males singing in the field (1994) at temperatures between 6 and 13°C, the temperatures likely to be encountered in our field experiment, produced, on average, a chirp lasting 4.5 s with an interval of about 1 s between chirps. This was therefore taken as the basis of our playback chirp durations, creating a playback duty cycle of about 0.75.

The pulse ultimately broadcast had a slightly altered amplitude envelope, caused not by the playback tape recorder, speaker, and amplifier but by some unknown factor in the creation of the cassette tapes: a few waves at the beginning and a few at the end had a very slightly higher amplitude (Fig. 1E). This is reflected in a slight departure from the original in the form of the spectrum (Fig. 1F).

Broadcasts and analysis

A Pioneer stereo car radio amplifier (GM-42A) powered by a 12-V car battery drove a Technics leaf tweeter connected to one channel. Playback levels were set to give 88–90 dB at 20 cm (re 20 μ Pa) measured with a 2204 sound-level meter (on “fast” meter response) fitted with a ¼-in. B and K microphone. Based on half the distance to the receiver, this would make the speaker signal 96 dB at 10 cm. This represents a conservative sound level for most males. (For example, the male involved in playback 1, captured after that event and singing from a screen cage the following night, had a sound level of 101 dB 10 cm dorsal (12°C).)

For each of 29 trials a singer was located and kept in view by an observer using red light. We avoided choosing males that were near (<1 m) another singer. The speaker, clamped to a very low tripod, was placed on the ground 0.6–1 m away and directed toward the singer. The speaker–insect distance was determined initially by eye (to minimize disturbance), then measured afterward as a straight-line distance, disregarding the singer’s height. (The leaf tweeter is narrowly directional and so careful attention was paid to its alignment with the insect and this was adjusted slightly during playback if the test male moved.) We were extremely careful to minimize our disturbance of each singer in finding him and placing the speaker, and we aborted any potential trials in which the found male seemed to change from his initially encountered singing activity. To start the trial, about 3 min of the male’s singing was recorded by a second person

onto a Sony Walkman tape recorder using a microphone with a parabola. The recording was made from behind the speaker so that its directionality would combine with that conferred by the parabola to make the test male’s signal distinguishable from the speaker signal (on the basis of higher amplitude) during later analysis. Recording of the tested male continued while playback was initiated by a third observer. Recording was interrupted after 3 min and resumed again at 6 min post playback onset, continuing then for at least another 2 min.

The analog magnetic tape records were digitized with band-pass filtering (5–20 kHz) using an AP2 data processor (Tucker Davis Technologies) in a PC computer, sampling at 40 kHz. Subsequent measures were accomplished from data files in DSP (see above). For duty-cycle calculations we used the software CSRE (Computerized Speech Research Environment, AVAAZ). Duty cycle was calculated as the proportion of time spent engaged in chirp output, summed across a time sample of 2 min.

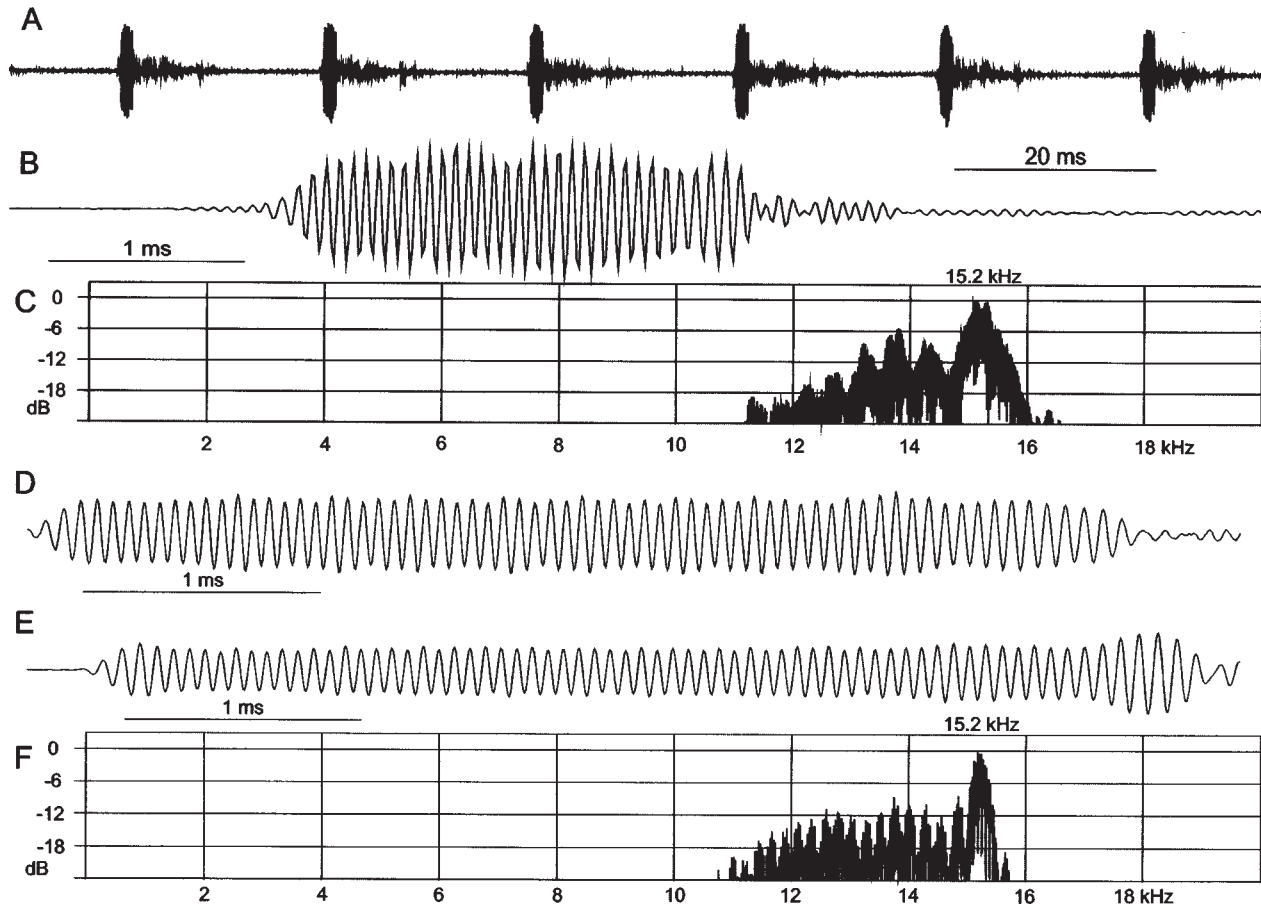
Marking and recapture

We first collected male singers at the forks on May 3, a cold night during which the temperature dropped to 7°C before 10 p.m. On this date the population was just starting breeding activity (all 5 males examined that night had intact underwings, i.e., were virgins). (During mating, females feed upon the male’s metathoracic wings, which are modified for this purpose; thus the state of his wings is a gauge of his sexual history (Morris 1979).) The population was monitored for just over 2 weeks, beginning on the night of 4 May and ending on the night of 16 May. Daytime rain and very cold nights on May 11 and 12 limited singing activity. No census was taken on May 5 or 15, though these were nights of calling activity. On the other 8 nights during the interval, calling males were very active and a census was conducted. This involved two searchers who moved through the population systematically back and forth within the area where singers were heard, between about 10 p.m. and midnight. Males were located, usually by their song, and captured, and a coloured number was affixed to their pronotum with cyanoacrylate glue. An attempt was made to travel into all areas from which singing was heard.

The midline length of the pronotum of each male from the forks (1995) was measured in the field at the time of his first capture and marking. This was done using electronic calipers (Fowler Ultra-cal III) while observing him under a clamped magnifying glass. Pronotal lengths of the other males (those used in the playback experiments) were measured from the preserved specimens in the laboratory using the ocular micrometer of a microscope. Also noted was the state of a male’s metathoracic wings.

On each night the capture site of a singer was flagged with a date-labelled piece of coloured survey tape or a survey flag. During the day following a night’s census, we used a tape rule to measure direct-line distances between flagged male locations. We made a large map of the site (May 13). Every male relocation was entered on this map, which had an approximate scale of 1 cm : 1 m. Major landmarks were noted on the basis of tape-rule-measured distances, e.g., a single large ponderosa pine (diameter at breast height 1.9 m), road-edge signs, “twin-trunk fir,” stump etc. The locations of

Fig. 1. Song structure and signals broadcast to *Cyphoderris buckelli*. (A) Six pulses from a field recording (made at 10.9°C) of the male whose pulse was the basis of playback sound models. (B) One of the pulses shown in A at a higher resolution, showing its sinusoidal waveform. (C) FFT power spectrum of several unmodified pulses: principal peak at 15.2 kHz, 11.5–15.5 kHz bandwidth 18 dB down. (D) Pulse used in all playback models with waves inserted midpulse. (E) The same lengthened pulse as it appeared after broadcast. (F) FFT spectrum of several broadcast pulses (from the 10°C sound model): principal peak at 15.2 kHz, 11.4–15.4 kHz bandwidth 18 dB down.



flags were then estimated by eye and compass, careful attention being paid to the location of individuals relative to that of neighbours, i.e., one can be confident that the direction from any plotted male to a neighbour was within one of the eight primary points of the compass.

Randomization models of movement

To assess the sedentariness of *C. buckelli* singers over successive nights, two different Monte Carlo randomization models were constructed (Good 1994; Manly 1991). With both we tested the hypothesis that males exhibit site fidelity; specifically we tested whether the mark–recapture data provided evidence of centrally directed movement. Both models simulate a random walk by shifting individuals on a nightly basis in randomly selected directions.

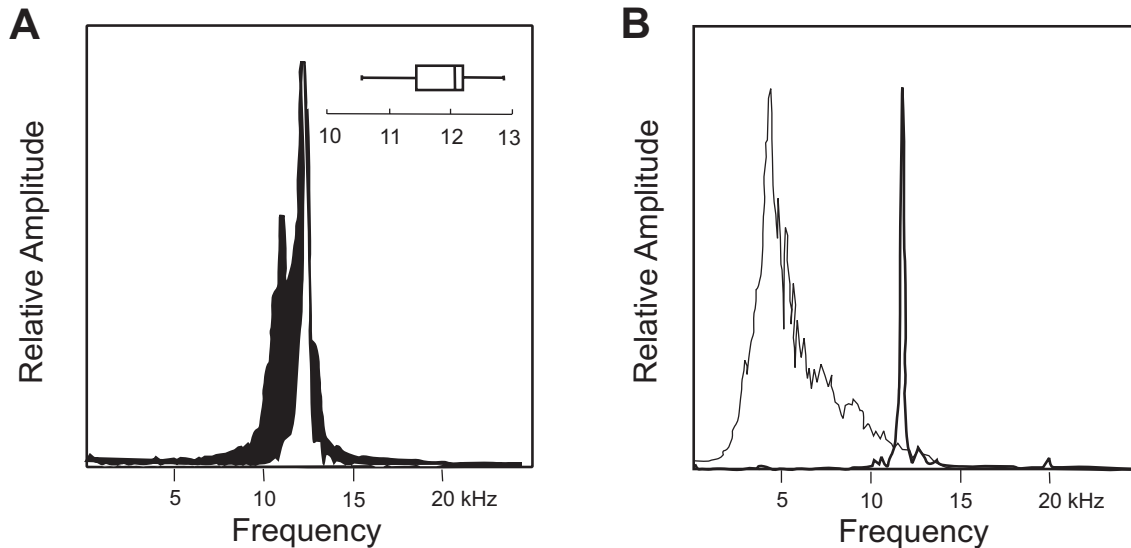
The first model used randomly generated nightly displacements and directions. The second combined the observed nightly displacements of recaptured animals with randomly generated angles. Details of both models are presented below. All randomly generated angles were restricted to one of the eight primary compass directions.

The first model required calculation of the mean displacement (D) per night (D/night) of the marked males. D/night

values were not normally distributed, so a log-transformation of the data was carried out. The log-transformed D/night value was 1.53 ± 0.1158 m (mean \pm 1 SE). The model then generated log-transformed daily displacements from this normal frequency distribution. After a D/night value was generated (untransforming the randomly determined distance), each animal was allowed to move randomly for between 5 and 100 nights (model duration). Each night, a random angle was generated and new coordinates (x , y) were calculated. At the end of the model duration, the total distance moved from the origin (original capture site) was calculated. The model was iterated 1000 times for each model duration. The mean distance moved for the 1000 animals was determined and compared with that observed in the actual mark–recapture data.

The second model used the mark–recapture data as the source of daily displacements. Each recaptured animal (48 individuals) was allowed to move in a random direction on each night of recapture. After all recaptures were exhausted, the distance from the origin (the point at which the animal was originally marked) was calculated. Each of the 48 animals was allowed to move randomly in this fashion, and its net displacement was then calculated. The randomized (cal-

Fig. 2. Spectra of *Cyphoderris monstrosa* calling song and playback treatments; the relative amplitude scale is linear. (A) Average spectrum of 15 males (solid black); the breadth reflects inter-individual variation in peak frequency; the spectrum of one male is shown (white); most males are about 12 kHz. Inset: Median and 50 and 75% ranges of song frequencies for this sample of males. (B) Frequency spectra for the two artificial acoustic stimuli used in playback experiments. Synthetic song (right) was composed of pure-tone 12-kHz pulses; the noise stimulus (left) was low-frequency random noise with maximum energy at the most sensitive region of the insect's ear, but little at the frequency of *C. monstrosa* song.



culated) distance from the origin was then subtracted from the observed distance from the origin (calculated from the mark-recapture map)

$$D_{\text{arg}} = \sum (D_{\text{obs}} - D_{\text{rand}} / \text{no. of specimens})$$

for each animal, and the mean of this difference was calculated. This entire procedure was performed 1000 times, and the grand mean difference was calculated as the test statistic.

This model, using all recaptured animals, may have led to biased results, given that some specimens were recaptured only once. Since only 1 day's movement was recorded for these individuals, the observed distance from the origin must be equal to that calculated by randomly generating angles. Thus, the mean difference calculated from all 48 recaptured individuals was biased towards zero. To determine the effect of this bias, the same model was run with only those animals captured 2 or more times (25 individuals). Both models were written by one of the authors (M.N.) and are available upon request.

Results

Cyphoderris monstrosa

The pulse rate of *C. monstrosa* varies linearly with temperature (Morris and Gwynne 1978). The song frequency is near 12 kHz, with some inter-individual variation in this physical parameter (11.9 ± 0.66 kHz (mean \pm 1 SE), $n = 17$; Fig. 2A, inset). Variability in song temporal pattern is evident both within and between individuals. But on a given evening, within-male variation in call temporal parameters is lower than between-male variation (Fig. 3, Table 1).

Analysis of variance of the differences (playback vs. solitary) in male duty cycles showed a significant overall effect of treatment ($F = 6.915$, $p = 0.004$; playback in Table 2). Pairwise comparisons (Tukey's HSD) showed that the noise

treatment was significantly different from both rebroadcast ($p = 0.029$) and synthetic song ($p = 0.005$), but the two song treatments did not differ from each other ($p = 0.688$).

For further analyses these two treatments (synthetic song, rebroadcast song) were pooled. Comparisons of playback with solitary duty cycles within treatments indicated a significant decrease during noise playback (Wilcoxon's test, $p = 0.025$) but no significant change during song playback (Wilcoxon's test, $p = 0.33$). In other words, there was no significant change in duty cycle for males exposed to synthetic song or to rebroadcast of their own song, whereas males reduced their acoustic output in the presence of noise. However, there was a nonsignificant tendency for males in the song treatments to increase their duty cycles during playback. This trend was marginally significant when two outside values (Wilkinson et al. 1992) were removed from the analysis (Wilcoxon's test, $p = 0.044$).

For the field playbacks reported here several males, 2 in response to synthetic song and 2 to rebroadcast, descended from their singing perches and approached the speaker. One other male was observed to descend from his perch during noise broadcast and move to a neighbouring tree, where he resumed singing.

Cyphoderris buckelli

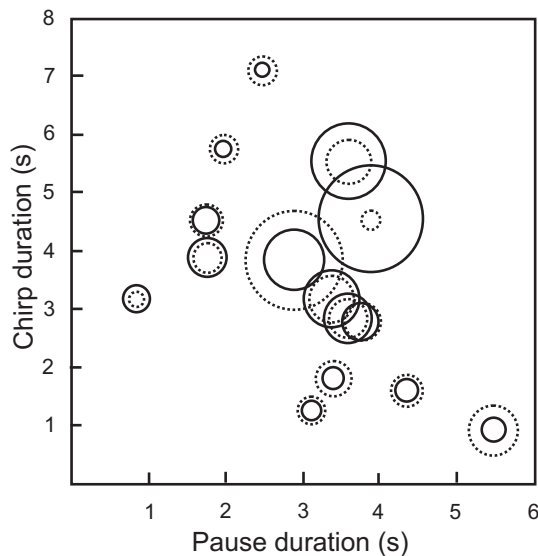
Song-structure regressions

The song of *C. buckelli* has its mean principal peak at 14.7 kHz (range 11.7–16.3 kHz, $s = 0.86$, $n = 51$). Figure 4 shows how the pulse period shortens dramatically with increasing temperature: 85% of pulse-rate variation is explained by the regression on temperature ($F = 287.17$, $p < 0.01$). The principal peak of the carrier frequency is not significantly affected by temperature (Fig. 5) ($F = 0.77$, $p = 0.39$), but chirp duty cycle is (Fig. 6): it increases with higher temperature

Table 1. Variability in three temporal measures of *Cyphoderris monstrosa* song.

(A) Mean and coefficient of variation (CV).					
Measure	Chirp duration (s)	Pause duration (s)	Duty cycle		
Mean \pm SD	4.1 \pm 1.2	2.5 \pm 1.3	0.61 \pm 0.16		
CV	0.30	0.50	0.26		
(B) ANOVA.					
Within subjects	Sum of squares	df	Mean square	<i>F</i>	<i>P</i>
Time	1.319	2	0.660	1.024	0.364
Time \times measure	1.037	4	0.259	0.402	0.806
Error	55.412	86	0.644		

Fig. 3. Temporal variability in *C. monstrosa* song. Within- and between-male variation in two song temporal parameters (chirp and pause duration). The graph shows mean chirp duration plotted against mean pause duration for individual males ($n = 15$). Plotted points are the centres of the circles, and those at the upper left represent males with long chirp durations and short pauses, while points at the lower right represent males with short chirps and long pauses. Areas of the circles are proportional to the standard deviation of the corresponding mean (solid circles denote chirps; broken circles denote pauses). The range of variation is greater between than within males.



($F = 17.06$, $p < 0.01$). About 27% of chirp duty cycle variance was explained by temperature change.

Since carrier frequency in this species is unaffected by temperature, we disregarded temperature differences in making a determination of carrier repeatability (Lessells and Boag 1987; Boake 1989). We measured high repeatability for the principal carrier, 0.88, an indication that this song parameter shows substantially less within-male than among-male variation. Carrier is thus a consistent characteristic of individual singers and so is a possible basis for discriminating between individuals. And there is much variation in carrier frequency within the singing population (Fig. 5).

Pronotum length predicts a male's mass ($F = 4.25$, $p = 0.048$, $n = 33$). Thus, 12% of the variation observed in mass was explained by a male's size. But there was no significant

Table 2. ANOVA of duty-cycle changes in *C. monstrosa* song during playback.

	Sum of squares	df	Mean square	<i>F</i>	<i>p</i>
Playback	0.356	2	0.178	6.915	0.004
Error	0.592	23	0.026		

predictive value of size (midline pronotal length) for principal carrier ($F = 2.44$, $p = 0.12$, $n = 51$).

Playback experiment with caged males

Table 3 gives the pooled scores from the 36 trials and indicates the consistency of individual males. We determined (pooled) signed difference scores, d_i , between the first and second 10-min intervals for each male. Under a null hypothesis (H_0) that the median difference between the first (silent) 10 min and the second (broadcast song) 10 min is zero, the difference scores in this design can be considered to be drawn from a symmetrical population, i.e., the mean is an accurate representation of central tendency and is equal to the median. This satisfies the assumption required for use of the non-parametric Walsh test (Siegel 1956). The H_0 is that the population mean of these differences is 0. Since we expected attraction to the sound, a one-tailed test is appropriate and the H_a is that the population mean is >0 . We reject the H_0 at a significance level of 0.05 and conclude that the difference scores are significantly higher than zero. Broadcast of calling song had a significant attractive effect on the 9 calling males in this indoor experiment.

Field playback experiments

An acoustic response to playback, obvious in some males, was an increase in chirp duty cycle. Such a change is illustrated for one of the tested males in Fig. 7. Before playback his chirp duty cycle was 0.29 (Fig. 7A); during the fourth 2-min interval after playback started it became 0.77 (Fig. 7C).

Figure 8 shows the distributions of chirp duty cycle for all tested males. The mean chirp duty cycle for the 2-min interval just before playback began was 0.33 ($n = 25$). For the 2-min interval immediately after broadcast began, this became 0.44 ($n = 25$), and during the fourth 2-min interval of playback, average chirp duty cycle increased to 0.52 ($n = 18$).

We tested differences in chirp duty cycle before and after playback using a one-sample *t* test (duty cycle was arcsine-transformed). During both the first and fourth 2-min intervals following playback onset there was a significant increase

Fig. 4. Regression of pulse period on temperature for a 51-male cohort of *C. buckelli* at Nelson in 1995.

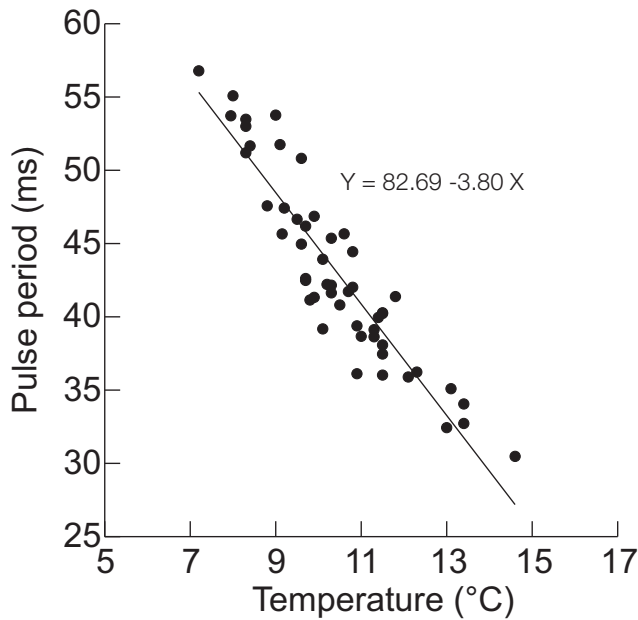
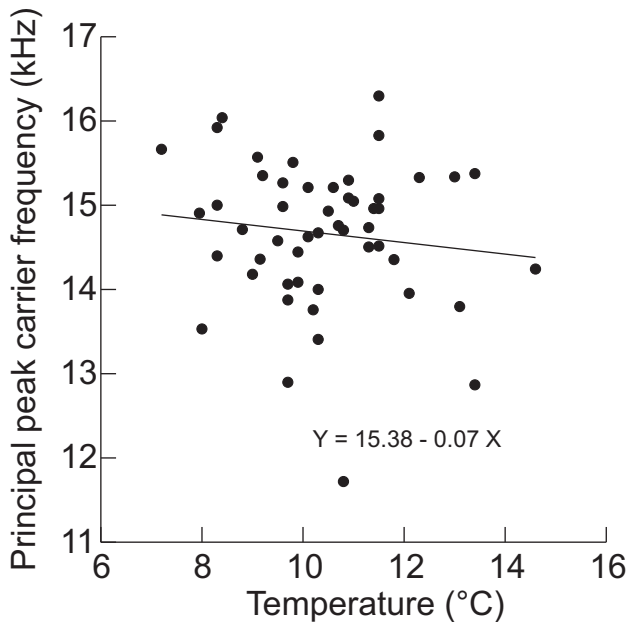


Fig. 5. Regression of principal carrier frequency on temperature for the 51-male cohort of *C. buckelli* at Nelson in 1995.



in chirp duty cycle over that obtaining in the last 2 min immediately preceding playback (first interval: $n = 25$; $t = 3.074$, $p = 0.005$; fourth interval: $n = 18$, $t = 3.822$, $p = 0.001$).

There is a lack of symmetry in the distribution of duty cycles in the fourth 2-min interval after playback began: this is manifest in the unequal lengths of the two whiskers of the fourth 2-min interval (Fig. 8) and reflects the fact that for a few males, chirp duty cycle significantly lagged late in the playback.

We also tested before–after playback for other song parameters, using one-sample t tests for chirp duty cycle

Fig. 6. Regression of chirp duty cycle on temperature for a 47-male cohort of *C. buckelli* at Nelson in 1995.

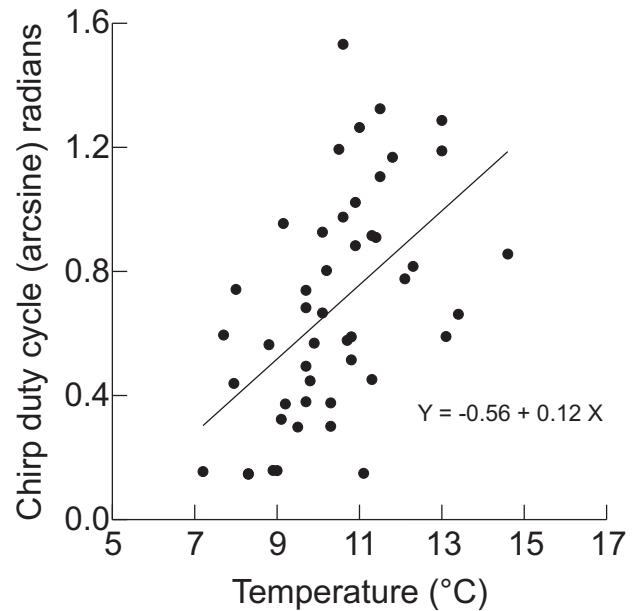


Table 3. Scoring of male *Cyphoderris buckelli* in an indoor phonotaxis experiment.

Specimen No.	Score in first 10 min	Score in second 10 min
1	0	0
2	0	+2
3	0	+4
4	0	+3
5	0	0
6	0	0
7	0	+1
8	0	+1
9	0	+1

(difference between before playback and the fourth 2-min interval), pulse rate, and carrier frequency and applying a sequential Bonferroni technique (Rice 1989).

The calculated t value for chirp duty cycle was significant as given above ($p = 0.001$). Similarly for pulse rate, measured as the difference in time required to complete 10 phonotomes (a phonotome is all the sound generated during one movement cycle of the forewing generator (Leroy 1966)): the drop in pulse period taken during the second 2-min interval after playback onset was significant ($n = 28$, 27 df, mean = -10.879 , $t = -2.640$, $p = 0.014$, Bonferroni-adjusted $p = 0.04$). The change in carrier frequency ($n = 28$, 27 df, mean 0.095 , $t = 0.774$, $p = 0.14$, Bonferroni-adjusted $p = 1$) was not significant. The mean duration of 10 consecutive phonotomes, sampled before playback, was 445.3 ms; taken in the second 2-min interval after playback had begun, 10 phonotomes were completed in 434.4 ms. These values correspond to 22.5 and 23.0 pulses/s, respectively.

The behaviour of males of other acoustic Orthoptera (e.g., Morris 1972; Brush et al. 1985), together with the response observed in the caged trials (see above), led us to expect approaches to the broadcast speaker. But this did not happen.

Fig. 7. One of the males (22) involved in the *C. buckelli* playback experiment (9°C). (A) Chirps and chirp intervals during the final minute before playback; chirps are well spaced and of variable duration and interval. (B) The same male's singing during the 3rd minute of playback; the broadcast signal is evident as low-amplitude regular traces in the background. (C) The same male in the 8th minute, singing with a much increased duty cycle.

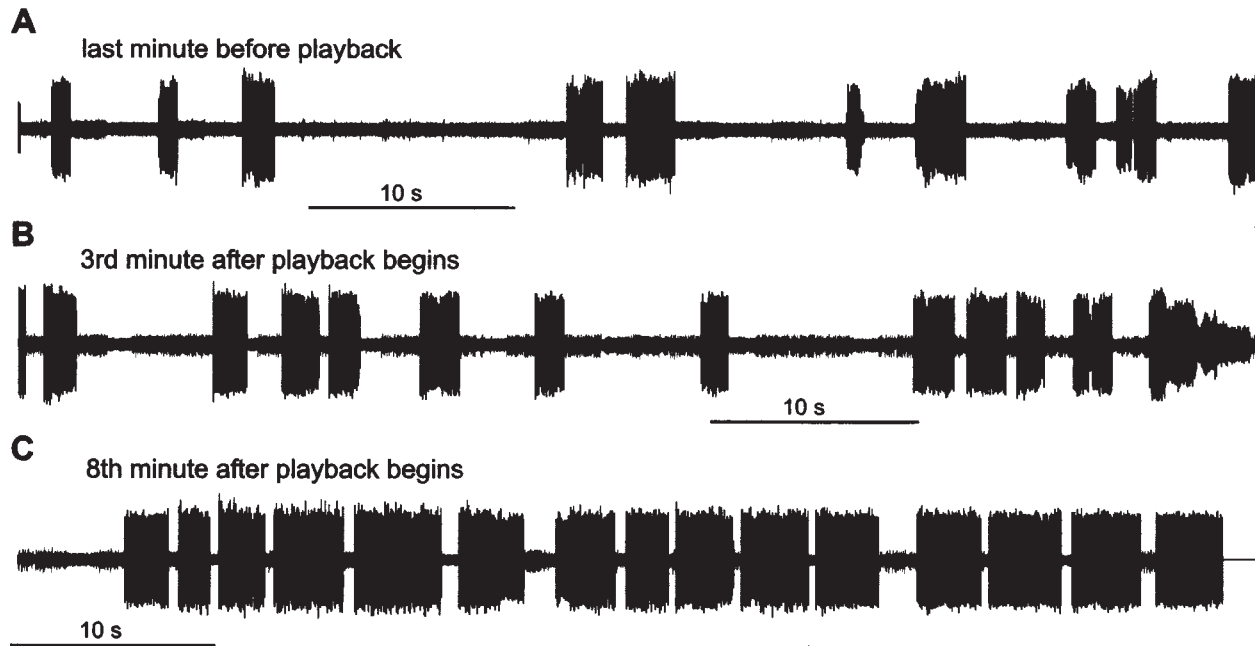
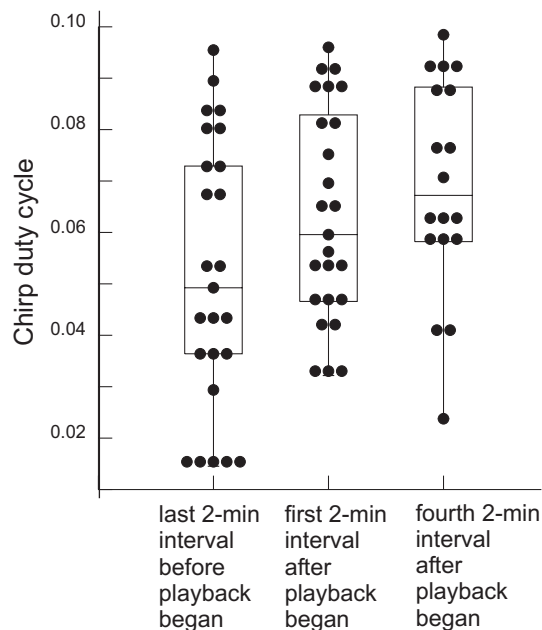


Fig. 8. Duty cycles of *C. buckelli* (arcsine-transformed) calculated for the 2 min just before speaker playback began, then for the first and fourth 2-min intervals during the 10 min of playback.



One male (with an extremely high pre-playback duty cycle: >0.95) walked downward ~ 35 cm on his perch almost immediately upon playback onset; this male continued to sing, though his duty cycle diminished, as he then walked, turning, pausing, and singing, across the forest floor for about 60 cm. But he moved transversely to the broadcast field of the speaker. This was the only substantial net displacement vaguely in the direction of the speaker observed in the 29

trials; other tested males showed modest locomotion distance (20–50 cm) down their perch plant or no locomotion. Two males walked off their perch plant and withdrew ~ 20 cm on the ground. In all 29 trials we observed no positive phonotactic response.

The cohort of males involved in these playback trials included 8 virgins and 21 non-virgins.

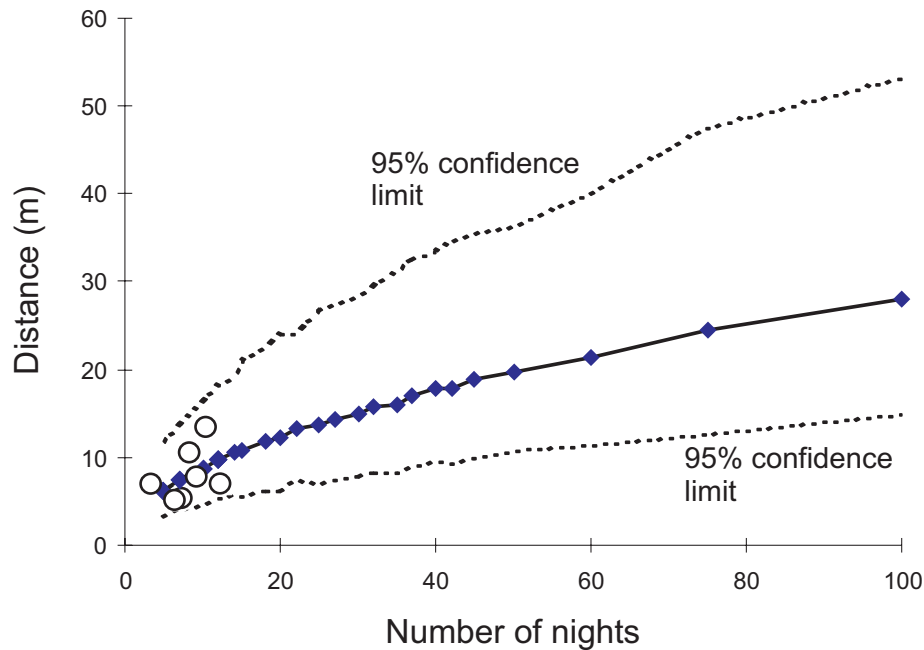
Marking and recapture

We marked a total of 93 insects during the study interval. About half the insects marked were retaken on at least one subsequent night (the proportion recovered at least once was 0.52), but 45 were never recaptured. The mean net displacement from their original capture site for 48 different males (recovered 1–7 times) was 11.7 m; the median was 9.7 m. The largest net displacement of a male was 44.4 m.

The first Monte Carlo model, using randomly generated daily movements (D/day) and angles, reveals no evidence of calling-site fidelity (sedentariness). There was no significant centrally directed movement. Figure 9 shows the mean distances from the origin (each male's original capture location) generated by the model and the observed data. All observed data points fall well within the 95% confidence limits of the randomized data. At the $\alpha = 0.05$ level, therefore, there is no statistically significant difference between the mean observed displacement from a male's original site and the data generated by the model.

The second model produces the same conclusion. The grand mean difference between a recapture site's distance from the original capture location, determined by randomly selecting angles (model), and that actually observed in the field was 0.116 m. The distribution of these differences is normal and centred around zero. The significance of the hypothesis that the observed distance from the origin is less

Fig. 9. Per-night average distances (○) from their original capture sites of male *C. buckelli* marked and recaptured in the field compared with distances generated by the random-walk model (◆).



than that generated by random walking is $p = 0.60$. Thus, there is no significant difference between the observed behaviour of the animals and that produced by random walking.

Eliminating those animals that were recaptured only once (to eliminate the possibility of bias) did not change the conclusion. When only those animals recaptured 2 or more times were used in the model (25 individuals), the grand mean difference in distance moved from the origin was 0.253 m. Again the distribution of these differences was normal and centred around zero.

Courtship stridulation?

One of the males tape recorded in the field at the forks early on the night of May 7 (11.8°C) exhibited an unusual song-pulse structure (Fig. 10), which continued over the several minutes of the record. Identical pulse envelopes recurred in alternate pulses and alternate pulse periods differed consistently in duration. Four numbered consecutive pulses are shown in Fig. 10. Close examination of the changing amplitude of the waveform in even-numbered pulses reveals strong similarity; this amplitude modulation is likewise distinctive and identical for the odd-numbered pulses. The pulse periods for odd-numbered pulses are shorter than those for even-numbered pulses; the graph below the trace in Fig. 10A makes this time difference more apparent.

Discussion

Chirp duty cycle

Mean chirp duty cycle for male *C. buckelli* increased significantly in response to the song of a conspecific male broadcast nearby. Males of this species engage in acoustic rivalry, with increased chirp durations and increased singing rates (the pulse rate also increased significantly). But for *C. buckelli*, rivalry does not extend to approaching another

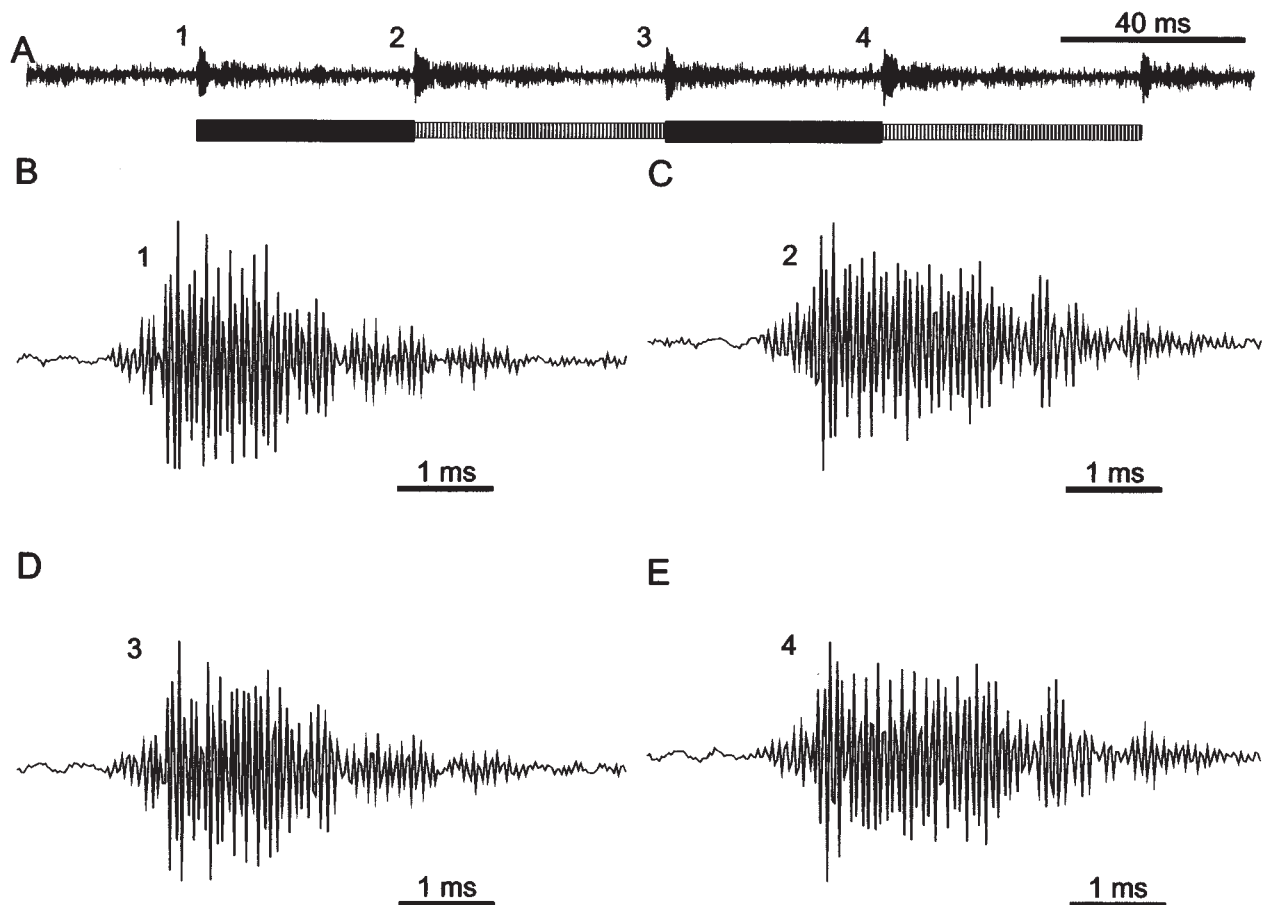
male and engaging him in a fight. We observed no phonotaxis by the tested male in any of the 29 trials. And in >100 h of field observation we have never observed male *C. buckelli* approaching each other and making physical contact (fighting). (The only exception is an anecdotal field observation by G.K.M. reported in Sakaluk et al. (1987).) Overt aggression comparable to that of *C. monstrosa* is non-existent in *C. buckelli*.

Male *C. monstrosa* responded to the song of a conspecific male broadcast nearby with only a non-significant increase in chirp duty cycle. But the trend in these data was toward increasing duty cycle and this became significant on the exclusion of two outliers.

Based on the results of other studies of *C. monstrosa*, chirp duty cycle is known to be an effective song parameter. Agonistic interactions were staged indoors, with males encountering each other on a vertical log arena (Mason 1996). In 23 of 25 male pairings that escalated to fights, the winner (and ultimately undisplaced) male "had a higher duty cycle" than the displaced male. And for 13 males, their duty cycle was significantly higher when they won than when they lost. The relative duty cycles of competing male *C. monstrosa* successfully predict the outcome of fights, and duty cycle was shown to be a "true indicator of aggressive ability" and to convey information used by the insects (Mason 1996).

All available evidence indicates that like male *C. buckelli*, male *C. monstrosa* engage in acoustic rivalry by increasing chirp durations. But unlike *C. buckelli*, rivalry in this species does extend to approaching another male (4 of the 18 males in our *C. monstrosa* field trials walked toward the broadcast speaker) and engaging in overt aggression. And in *C. monstrosa*, changing duty cycles mediate the fight's progress. Chirp duty cycle is implicated in the agonistic signalling of both haglid species, but the end result of this rivalry is different: one species escalates to vigorous fighting and the other does not.

Fig. 10. Example of switch-wing stridulation in *C. buckelli*. One male (95-12) exhibited two alternately identical pulse periods (A). Pulse amplitude modulation differs in accordance with period: odd (1, 3) and even (2, 4) pulses show a strong similarity of pulse envelope.



Ecological considerations

The marking and recapture studies of *C. buckelli* reveal an almost complete absence of site fidelity in this species. Most males move to different singing locations on successive nights in a fashion consistent with choosing random bearings and travelling random distances. This high degree of displacement is in accordance with the absence of overt aggression in this species; no appreciable part of the population of singers remains in place to defend a singing location.

In *C. strepitans*, the species that occurs in Wyoming and Colorado, there is also no indication of overt aggression. And in explaining its absence, Mason (1996) noted that because *C. strepitans* sings from sagebrush, comprised of "low bushes with many tangled branches," whereas "*C. monstrosa* sing from the trunks of spruce trees at considerable heights, with few or no branches below them," escalation is more cost-effective for *C. monstrosa* than for *C. strepitans*. For *C. monstrosa* the cost of ejecting a rival is relatively low and the cost of searching for the limited (tree trunk) resource is high. The benefit of holding the resource in terms of access to females is perhaps also high. Contests in such situations are expected to be settled with escalation (Maynard Smith and Parker 1976). The argument can be applied equally well to *C. buckelli*.

The use of habitat by *C. monstrosa* and *C. buckelli* differs. The perches where fighting by *C. monstrosa* occurs are topographically limited: a male is restricted to the surface of a

mature tree trunk. Because females, which emerge each night from the leaf litter, apparently use this trunk as a highway into the canopy to feed, the presence of a female there during the evening is predictable: she may walk by on this narrow surface within a narrow time interval. Because the trunk is an elevated vertical surface, gravity can increase the cost of losing fights: a dislodged male will usually fall a long distance and must then expend energy just to re-engage with his opponent. The substrate occupied by *C. monstrosa* lends itself to the monopolization of females in space and time (Emlen and Oring 1977).

By contrast, for *C. buckelli*, perch substrates consist of a network of thin leaves and dead or living branches in the understory. A dislodged male will not fall far and can readily renew an attack. There is almost unlimited availability of singing perches because the substrate is so extensive. Nor are females moving through the vegetation in any consistent direction. Males can move so easily within the understory that energy invested in excluding one rival would soon require reinvestment to deal with another. Height, female habit, the extent and nature of the substrate, and mobility of rivals combine to make escalation of aggression advantageous in one species but not in the other.

But though they do not escalate to fighting and so do not need chirp duty cycle in this context, male *C. buckelli* can still benefit by reacting to the duty cycle of a rival. In the earliest evolved acoustic pairing system, wherever males

sang within earshot of each other and were selected by their differential ability to attract females, they were inevitably acoustic competitors. This acoustic rivalry would be driven by the need to monopolize female perception: whichever male's song was perceived, that would be the source approached. Ensiferan perception mechanisms (Pollack 1988; Romer and Krusch 2000) will suppress response to the (only slightly) weaker of two or more sound inputs, and on the basis of a long inhibition-time constant, will favour high duty cycles. By virtue of such mechanisms a female will actually hear only the slightly louder and (or) more sustained of two competing singers. So if one male singing near another fails to match or exceed a rival's sound level and duty cycle, he is much less likely to be approached by a female. In such circumstances males could benefit from responding beforehand to a neighbour's singing activity. If a neighbour is a better singer in terms of level and duty cycle, withdrawal will improve a male's chances of attracting a mate. This may be why male *C. buckelli* have evolved to respond to the duty cycles of nearby singers even though they never use encoded information in subsequent fights. To avoid "suffering by comparison" a male must match his neighbour's duty cycle or move on.

"Match or move" predicts that males that are unable to compete successfully with the calling activity of a neighbouring rival will ultimately cease singing and withdraw. And we did observe some males that appeared to reduce their duty cycle slightly toward the end of the test interval: the asymmetry in the "whiskers" in Fig. 8 indicates somewhat lowered duty cycles in certain males. And there was a very slight indication of locomotory withdrawal within the 10-min playback interval of our trials. One supposes that substantial withdrawals would ultimately occur if the acoustic stimulus was continued for a longer time, a prediction that should be tested.

Chirp duty cycle is an important acoustic parameter in male interactions for both these species and encodes information about the capacities of rivals. It is reasonable to expect that it could be similarly employed by females of *Cyphoderris* spp. But there is no experimental evidence that females of these species respond phonotactically to male calls. When and if such evidence is obtained, it seems likely that females of the two species might discriminate chirp duty cycle in different ways. In the nonterritorial species, *C. buckelli*, this parameter may serve for active discrimination of a male's quality as a prospective mate and females evince preferences for males with higher chirp duty cycles. But in the strongly territorial *C. monstrosa*, discrimination between duty cycles by females may be superfluous, so females show no discrimination: a female *C. monstrosa* need not choose a potential mate by his singing, but only accept as a better mate any male who successfully occupies a tree trunk.

Noise response in *C. monstrosa*

Cyphoderris monstrosa exhibit a frequency mismatch: they have low auditory sensitivity at the calling-song carrier and high sensitivity near 2 kHz (Mason et al. 1999). The noise playback was created as a control for specificity of song response, to be readily perceptible to the insect while lacking any species-characteristic amplitude modulation. That the insects responded (unexpectedly) to this sound by significantly

reducing their singing may be explained as being predator-related (Mason 1991).

The most intense frequencies of the continuous noise playback coincide with maximal ear sensitivity while containing little energy at the frequencies of the calling song (Fig. 2B). So the noise could compromise the insect's ability to hear predator-related sounds in the low-frequency audio range. The observed reduction of singing obtained here in response to continuous low-frequency audio noise is consistent with this hypothesis. A male experiencing input in this low-frequency band may be inhibited from continuing to make his location conspicuous to possible eavesdropping predators.

Active aggregation

On the face of it, the approach of male *C. buckelli* to speaker broadcasts indoors is inconsistent with the absence of approach to the (nominally) identical stimulus in the field experiments. But one may explain these two different responses on the basis of different behavioural contexts: in one case the males are isolated, in the other they are not.

The males in the indoor experiment were caged singly, within earshot of a few other males, but in relative isolation. That they were singing and stationary on the log as the experiments began indicates a level of normalcy in their behaviour, i.e., they were not restless and exploring their environment, though that environment was very different from their typical habitat. However, the 10-min interval before the speaker broadcast began is the equivalent for a male of singing all by himself in the forest. A singer in such a situation might be selected to respond phonotactically to distant singers. This response is consistent with an active aggregation response, oriented to the sound of a distant singer and having nothing to do with rivalry.

Male *C. buckelli* singing at the forks site formed a coherent deme on the mountainside, with well-defined limits to the singing population. Moving 20 m deeper into the forest, away from the road edge, one passed abruptly beyond any singing. Yet it was not apparent that the habitat at this transition differed suddenly in any way from the habitat farther within. The break in the forest canopy caused by the presence of the road admits sunlight, and together with the southern exposure of this study site, may partly explain the distribution of these singers. This area was free of snow at a much earlier date than were immediately adjacent areas; the situation was repeated farther up the Busk road branch and on another mountainside nearby. However, the singing group is more cohesive than can be accounted for by the broad effects of southern exposure and open canopy. Singing may well play some role in maintaining these singers as an aggregation.

Active acoustic aggregation (Ewing 1989) occurs when a relatively isolated insect reacts to collective distant song output with positive phonotaxis. The function of the response is to bring and keep an individual within an aggregation. So the absence of taxis in the outdoor experiments could be viewed as resulting from those trials taking place entirely within a deme of singers in normal habitat; one would expect no active aggregation here. Indoors, on the other hand, active aggregation is a reasonable response to observe in an isolated individual in unsatisfactory surroundings; he is

attracted by a cue predictive of food, shelter, and the potential for mates.

A role for phonotaxis in the maintenance and formation of a singing population is a possibility in a number of chorusing insects, e.g., periodical cicadas (Alexander 1975), *Conocephalus* katydids (Morris and Fullard 1983), and midges (Downes 1969). An expectation in such cases is that males, sexually unreceptive females, and immatures should exhibit attraction to the chorus; in mole crickets, males are attracted to acoustic traps (Ulagaraj and Walker 1973) as are already-mated females with stored sperm.

Adaptiveness of switch-wing stridulation

The recurrence of identical alternating pulse envelopes with distinctive alternating pulse periods is the first evidence of switch-wing singing in *C. buckelli*. This song pattern results from reversing wing overlap at each sound pulse and was first reported by Spooner (1973) for *C. monstrosa*. The tegmina of males of all *Cyphoderris* species are bilaterally symmetrical with a functional file and scraper on both forewings; likewise for their haglid relative *Prophalangopsis obscura* (see plate LIV in Zeuner 1939). And other acoustic Ensifera also show forewing bilateral symmetry (Morris et al. 1975; Masaki et al. 1987; Morris and Mason 1995). In *C. monstrosa* both tegminal overlaps are commonly observed in field-caught males, with some individuals changing their overlap at longer intervals (hours or days) (Morris and Gwynne 1978). And the same is true of *C. buckelli* and *C. strepitans* (G.K.M., unpublished data).

Spooner (1973) supposed that switch-wing singing was the typical method of calling in *C. monstrosa*, but this is not the case. It has only been observed in this species on one other occasion, when a male's singing was recorded while he interacted in antennal-contact range of a female (Morris and Gwynne 1978). Its absence as a response to playback in the trials with *C. buckelli* shows that it has no role in male rivalry. But whether this form of the song can serve in courtship is still an open question. As such it would be a way to convey acoustically a male's fluctuating asymmetry to a listening female (Watson and Thornhill 1994; Faure and Hoy 2000). As a courting signal the rarity of its detection in the field is not hard to understand, in that most recorded and observed field males are not in the company of females; courtship (as distinct from copulation) is perhaps a brief process in these species.

Acknowledgements

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