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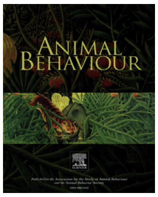

Intraspecific sexual mimicry for finding females in a cicada: males produce ‘female sounds’ to gain reproductive benefit

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In insects various ways to produce sounds have evolved for communication both within and between species. Cicada males are particularly known for their loud and diverse songs which are produced by tymbal organs. Females of some cicada species can produce sounds by wing flicking in response to male calls. The cicada species *Subpsaltria yangi* is unusual in that, besides the tymbal organs of males, it has well-developed stridulatory organs that are found in both sexes. Here, we investigated sound production and mating behaviour of this cicada species. We show that, in the context of pair formation, females produced sound signals by stridulation in response to advertisement signals produced by males with tymbal organs. We also found that the sounds produced by male cicadas with stridulatory organs were extremely similar in acoustic structure to those of females, which indicates that males mimic the signals produced by females during pair formation. Acoustic playback experiments suggested that, by producing female-like sound signals, a male could deceive a receptive female into treating him as a rival female, which makes the male more effective in eliciting acoustic responses from the receptive female. Therefore, the males could gain reproductive benefit by mimicking female sound signals, since they rely primarily on females' acoustic responses to find females. Our study provides the first experimental evidence for sound production by a stridulatory mechanism in cicadas, and a novel case of intraspecific sexual mimicry based on acoustic similarity.

Intraspecific sexual mimicry or transvestism, whereby individuals of one sex take on the appearance (e.g. behaviour, pheromone and colour) of the opposite sex, is a common form of deception (Cremer, Sledge, & Heinze, 2002; Thornhill, 1979). Intraspecific sexual mimicry has evolved independently in a diverse range of taxa including birds (Jukema & Piersma, 2006; Rohwer, Fretwell, & Niles, 1980; Slagsvold & Saetre, 1991), fishes (Dominey, 1980; Gross & Charnov, 1980; Kodric-Brown, 1986), reptiles (Mason & Crews, 1985; Whiting, Webb, & Keogh, 2009), amphibians (Howard, Moorman, & Whiteman, 1997; Massey, 1988), cephalopods (Brown, Garwood, & Williamson, 2012; Norman, Finn, & Tregenza, 1999), mammals (Le Boeuf, 1974; Muller & Wrangham, 2002) and insects (Field & Keller, 1993; Forsyth & Alcock, 1990; Gosden & Svensson, 2009; Scott, 1986). To our knowledge, almost all examples of intraspecific sexual mimicry are based on visual or chemical similarities. Here, we provide evidence of a new type of intraspecific sexual mimicry which occurs in association with acoustic behaviour.

Acoustic behaviour is a mode of communication used by many species of animals (Alexander, 1967), particularly in vertebrates and arthropods. In insects, a variety of species communicate with sound which may be produced by different structures and methods (Alexander, 1967; Gerhardt & Huber, 2002). Among acoustic insects, cicada males are particularly known for their loud and diverse sounds (Claridge, 1985). In cicadas, sound communication plays a crucial role in reproduction, in which acoustic advertisement is generally the province of males. Females of some cicada species can produce sounds by wing flicking in response to male calls, and the sounds of these female cicadas function as signals to communicate their availability for reproduction (Cooley & Marshall, 2001; Sanborn & Phillips, 1999).

The sounds of male cicadas are generally produced by a pair of tymbal organs, situated dorsolaterally on either side of the first abdominal segment (Pringle, 1957). Despite the predominance of the tymbal mechanism among cicadas, a relatively small number of cicada species also possess a stridulatory mechanism which is composed of a scraper (usually a part of one of the tegminal veins)

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and a file (a specialized part of either the mesonotum, the pronotum or the hind wing) (Duffels, 1993; Moulds, 2005). To our knowledge, almost all previous studies have just focused on the morphological features of the stridulatory organs and used them as characters in the taxonomy of cicadas. The acoustic communication and associated behaviours in these species have been little investigated (Boulard, 2006; Dugdale & Fleming, 1969). What remains a puzzle is the communicative significance of the sounds generated by the stridulatory organs in these cicadas.

Subpsaltria yangi Chen (Cicadidae: Tettigadinae) is an endemic, Chinese cicada species (Chen, 1943; Chou, Lei, Li, Lu, & Yao, 1997). This species is unusual in that, besides the tymbal organs, the males also possess a well-developed stridulatory mechanism, i.e. a striated area (file) situated on each side of the mesonotum and a projecting scraper formed by the base of each tegmen (Chen, 1943; Chou et al., 1997). As usual, the females do not have tymbal organs, but possess the same stridulatory organs as males (Chou et al., 1997). Previously known from just a few museum specimens collected from Shaanxi Province, China, this cicada species had not been seen in the field since 1989 and was thought to be extinct. A survey of the insect fauna of Helan Mountains (located at the border of Ningxia and Inner Mongolia Nationality Autonomous Regions of northern China) led to the discovery of two populations of *S. yangi* in June 2011. This rediscovery of *S. yangi* provides a unique opportunity for further investigation of this little-known cicada species.

Here, we aimed to clarify the mechanism of stridulation in *S. yangi* males and females, and to determine what functions are served by the stridulatory sound production in the communication system of this cicada species. To address these questions, morphological characteristics of the stridulatory organs of males and females were examined, and scraper ablation experiments were conducted to determine whether the stridulatory organs were involved in sound production. Acoustic analysis was conducted for both sexes. The function of the sounds produced was investigated by observing the mating behaviour, and conducting acoustic playback experiments in the field. Our goal was to analyse how a complex acoustic system functions and in particular to understand the role of acoustic signals produced by the stridulatory organs.

METHODS

The Study Site and Species

The study site, Chunshugou valley (38°33.699′N, 105°55.217′E), is located in the Helanshan National Nature Reserve, Ningxia Hui Nationality Autonomous Region, China. A natural population of *S. yangi* was found on the slopes at elevations between 1400 m and 1600 m. Investigations were performed during the summer emergence of this cicada (May–June) in 2011, 2012 and 2013. Adults feed mainly on *Ephedra lepidosperma* (Ephedraceae), a medicinal plant used in traditional Chinese medicine.

This study was carried out in full compliance with the laws of the People's Republic of China. No specific permits were required for our field investigation. The study species is not included in the ‘List of Protected Animals in China’.

Behavioural Observations and Acoustic Analysis

Vegetation in the dry habitat of *S. yangi* consists primarily of drought-tolerant dwarf shrubs and herbaceous plants, generally not exceeding 1 m in height, allowing easy observation of the cicadas' behaviour. Cicadas were observed under both natural conditions and in cages. Behaviour was video-recorded using a Nikon Coolpix P100 digital camera (Nikon Corporation, Indonesia). Effort was made to minimize the disturbance to the cicadas during behavioural observation by avoiding any noise and sudden movements by the observer.

All acoustic recordings were made using a linear PCM recorder with stereo microphones (PCM-D50, Sony, China; frequency range 20–20 000 Hz and a 44.1 kHz/16 bit sampling resolution). The sounds were recorded in WAV file format, and stereo recordings were converted to mono at a sampling rate of 44.1 kHz and resolution of 16 bits. Acoustic analysis was conducted using Raven Pro 1.4 (The Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) and Seewave (Sueur, Aubin, & Simonis, 2008), a custom-made library of the R software platform (R Development Core Team, 2011). Terminology for the description of acoustic signals followed that of Alexander (1967).

Morphology of the Stridulatory Organ

The morphological structure of the stridulatory organ was analysed for both sexes. Micrographs were captured with a Retiga 2000R digital camera (QImaging, Canada) mounted on a Nikon SMZ1500 stereoscopic zoom microscope (Nikon Corporation, Tokyo, Japan), and then 80 sequential shots at different focal depths were processed using the Auto-Montage Pro software to generate a single composite image. The morphology of the stridulatory organ was also examined using a scanning electron microscope (S-3400N, Hitachi, Tokyo, Japan) to show the ridges of the stridulatory file.

Scraper Ablation Experiments

We conducted scraper ablation experiments to assess the role of stridulatory organs in sound production of males. Individual males of *S. yangi* were collected in the field. A male was kept in a cage (0.6 × 0.6 × 0.6 m) with freshly cut twigs, and its sound signals were recorded. The scrapers of both forewings of the male were then carefully removed with surgical scissors, and the sounds produced by the male were recorded a second time. Finally, the sounds recorded before and after ablation of the paired scrapers were analysed and compared in detail.

We ran this scraper ablation experiment with a total of 10 individuals. All experiments were carried out between 0900 and 1500 hours, a period corresponding to the peak singing activity of this cicada. During the experiments, the ambient temperature ranged from 29 to 34 °C.

Acoustic Playback Experiments

Although results obtained from the scraper ablation experiments and behavioural observations demonstrated that males of *S. yangi* used their stridulatory organs to produce acoustic signals in the context of pair formation (see Results), there was not enough information to determine the functional significance of male stridulatory sound production. To clarify this function, playback experiments were performed to test the behavioural responses of both males and females to various acoustic stimuli.

We created four types of acoustic stimuli: (1) natural male sounds, which consisted of alternating tymbal and stridulatory sounds (Fig. 1a); (2) male tymbal sounds, which were created by replacing the stridulatory sounds found in natural male sounds with silence (Fig. 1b); (3) male stridulatory sounds, which were created by replacing the tymbal sounds found in natural male sounds with silence (Fig. 1c); and (4) female stridulatory sounds (Fig. 1d). These acoustic stimuli can enable us to compare the efficiency of different sound signals (female stridulatory sounds alone, male stridulatory sounds alone, male tymbal sounds alone, and

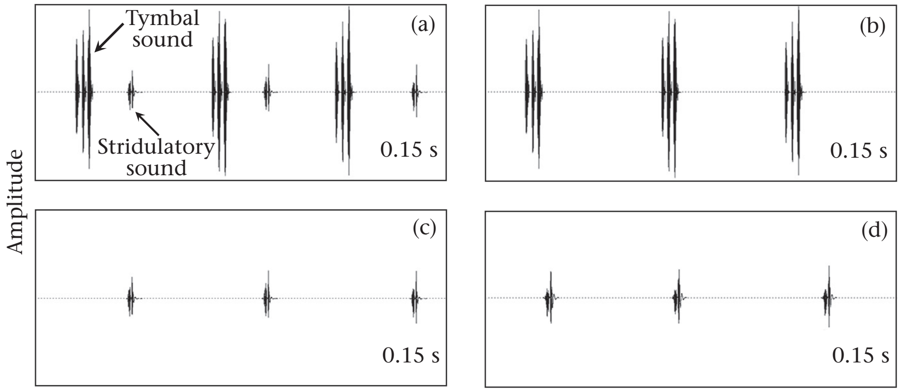

Figure 1. Oscillograms of the four types of acoustic stimuli used in playback experiments. (a) Natural male sounds. (b) Male tymbal sounds. (c) Male stridulatory sounds. (d) Female stridulatory sounds.

male tymbal + stridulatory sounds) in eliciting phonotactic responses from males and acoustic responses from females. These acoustic stimuli were generated at a sample rate of 44.1 kHz and 16-bit resolution with the R package Seewave. Playbacks were conducted using a Sony PCM-D50 Linear PCM Recorder and a Mogic Q2 loudspeaker (frequency response, 150–20 000 Hz). A digital sound level meter (Benetech GM1357; fast response, A weighting) was used to measure sound pressure levels. The stridulatory sounds produced by males and females are similar in acoustic level. Prior to playback experiments, the male tymbal sounds and the male and female stridulatory sounds were adjusted to the natural levels, 85 dB SPL and 60 dB SPL, respectively, measured at 50 cm from the loudspeaker. All playbacks were conducted between 0900 and 1500 hours.

We examined the efficiency of the four types of stimuli in eliciting acoustic responses from females. Females were collected before playback experiments were conducted. Previous work on periodical cicadas found that immature and mated females were sexually unreceptive and did not respond to advertising males (Cooley & Marshall, 2001). Therefore, only females that were responding acoustically to a calling male in the natural habitat, and were therefore sexually receptive, were captured ($N = 20$). They were kept on their host plants covered with gauze netting until testing. Females were tested individually, as follows. A single female was placed in a cage (0.4 × 0.3 × 0.3 m) and allowed to adapt to the ambient conditions for 3 min. The four types of acoustic stimuli were then played in random order from a loudspeaker placed approximately 1 m from the female. Each sound stimulus was presented for 5 min. During the playback of each sound stimulus, we recorded the number of sounds produced by the female in response to the playback.

The efficiency of the four types of acoustic stimuli in eliciting phonotactic responses from males (i.e. attracting advertising males) was tested. For each type of sound stimulus, 20 males were tested. Altogether, 80 playback experiments were carried out with 80 different males. For each playback test, an undisturbed, actively signalling male was initially located in its natural habitat. One of the four acoustic stimuli was broadcast from the loudspeaker which was placed on the ground and approximately 3 m from the signalling male. During the playback, we recorded whether the male responded phonotactically to the acoustic stimulus. A phonotactic response was defined as the male flying towards and landing within 50 cm of the loudspeaker. Any males flying away or remaining still after 3 min of the playback were considered to have made no positive phonotactic response. After each test, we moved to another site and conducted a new playback experiment with a different signalling male.

Statistical Analysis

Statistical analysis was undertaken with SPSS 17.0 software (IBM, Armonk, NY, U.S.A.). Prior to conducting parametric tests, we used Kolmogorov–Smirnov tests to determine whether data were distributed normally and Levene's tests to test data for homogeneity of variances. All statistical tests were two tailed, and $P < 0.05$ was considered significant.

RESULTS

Morphology of Stridulatory Organ

The morphology of the paired stridulatory organs is similar in both sexes. The well-developed file is a modification of an area on the anterior angle of the mesonotum (Fig. 2a, b). Each file consists of a row of parallel ridges which are highly sclerotized and oriented longitudinally (Fig. 2c, d). The ridges situated in the central part of the file are longer than peripheral ridges of the file. The number of ridges varied from 16 to 21 in males (mean ± SD = 19 ± 1.8, $N = 10$) and from 16 to 23 in females (mean ± SD = 20 ± 2.1, $N = 10$). No significant difference was found in the number of ridges between males and females (Mann–Whitney U test: $z = -0.078$, $N_1 = N_2 = 10$, $P = 0.938$). The base of the inner margin of the forewing, functioning as the scraper, is slightly curved outwards and contacts the surface of the file (Fig. 2e).

Tymbal and Stridulatory Sound Production in Males

Males of *S. yangi* produced two types of sounds to signal for mates. Sound type I was generated by tymbal action which was accompanied by obvious vertical movements of the male abdomen (Supplementary Video S1). Production of sound type II was always associated with quick, up-and-down movement of the forewings (Supplementary Video S1). Oscillograms of the sounds recorded from an individual male with intact forewings showed clearly that the tymbal and forewing movement sounds were produced alternately (Fig. 3a). Each tymbal sound was made up of three or four chirps (Fig. 3a, c). The sound produced during a single up-and-down movement of the forewings could be divided into three parts (Fig. 3e). The first part (A) was separated by a silent interval from the following two parts, B and C (Fig. 3e). The average durations of parts A, B and C were 12.53 ± 1.07 ms (mean ± SD, $N = 30$), 4.13 ± 0.73 ms ($N = 30$) and 12.90 ± 0.66 ms ($N = 30$), respectively. The interval between parts A and B was 3.83 ± 0.75 ms (mean ± SD, $N = 30$).

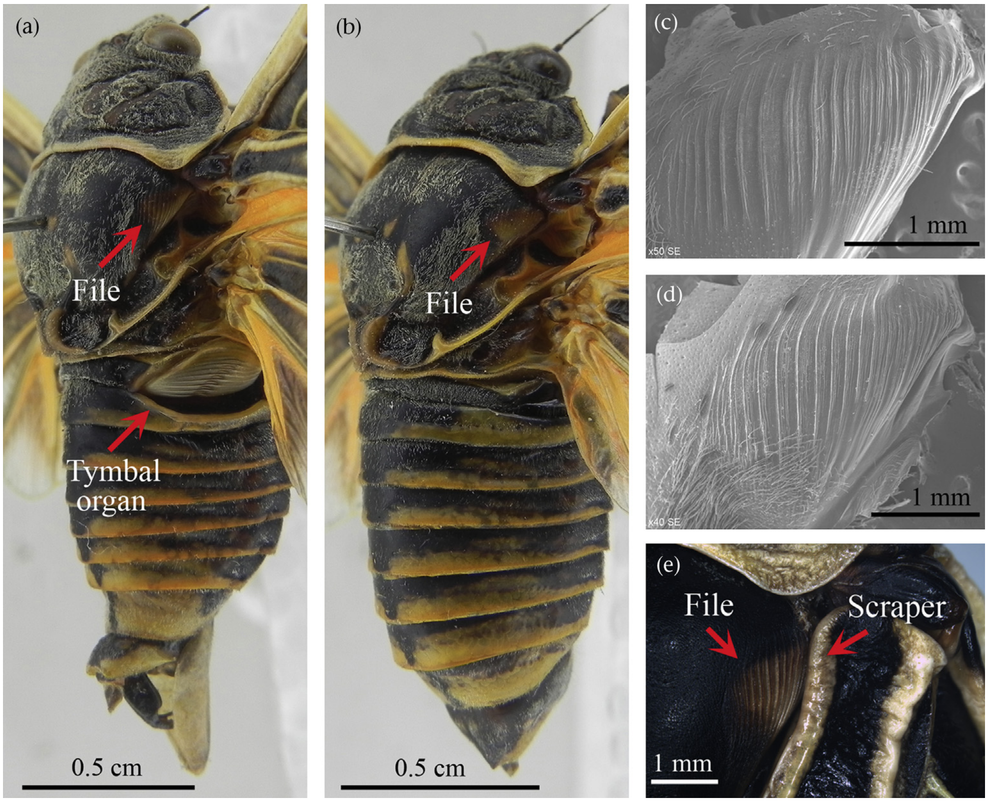

Figure 2. Sound production structures of *S. yangi*. (a) Location of the tymbal organ (lower red arrow) and stridulatory file (upper red arrow) of a male. (b) Location of the stridulatory file of a female (red arrow). (c) Scanning electron micrograph of the stridulatory file of a male. (d) Scanning electron micrograph of the stridulatory file of a female. (e) Image showing that the scraper contacts the surface of the file.

When the paired scrapers were removed, the male cicada produced sounds normally associated with the tymbal organs (Fig. 3b, d). Ablation of the scrapers did not interfere with the movements of the forewings, and some sound was still produced over the course of the movements. However, there was a remarkable difference between the sounds produced by forewing movement recorded from males before and after the ablation. After ablation, these sounds consisted of only one part, C (Fig. 3f), and parts A and B

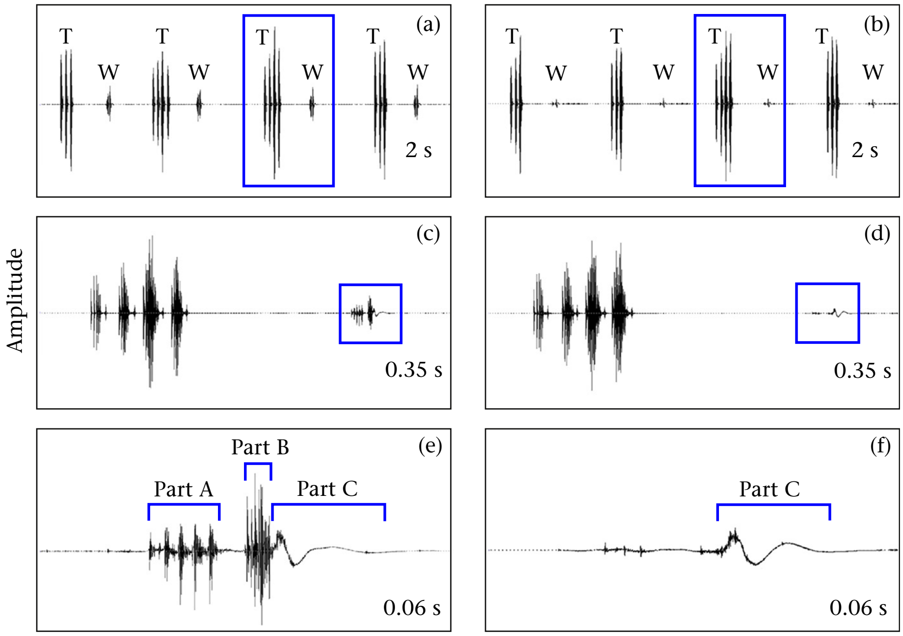

Figure 3. Comparison of sounds recorded from a male before and after removal of the paired scrapers. (a) Oscillogram of sounds produced by the male with intact forewings. Sounds produced by tymbal organs are marked with 'T', and sounds generated during movements of the forewings are marked with 'W'. (b) Oscillogram of sounds produced by the male after ablation of the paired scrapers. The tymbal sounds and the sounds generated during the forewings' quick movements are also marked with 'T' and 'W', respectively. (c) Detail of oscillogram marked by the box in (a). (d) Detail of oscillogram marked by the box in (b). (e) Detail of oscillogram marked by the box in (c). (f) Detail of oscillogram marked by the box in (d).

disappeared completely (Fig. 3f). These results showed that the stridulatory organs were responsible for the sound production of parts A and B. In all 10 scraper ablation experiments, we obtained consistent results, which provided solid evidence that the males of this species generate sounds using their stridulatory organs.

The results obtained from behavioural observations and scraper ablation experiments indicate that the pattern of stridulatory sound production of male *S. yangi* involves a single up-and-down movement of the two forewings. An upward motion of the forewings causes the scrapers to rub against the ridged files, producing an upward chirp (part A). Similarly, when the forewings move downwards, the scrapers are pushed along the files again, and a downward chirp (part B) is generated. When the forewings move down to their resting position, they strike the body, which results in the production of the impact sound (part C) accounting for why this component is still present after ablation of the scrapers.

Pair Formation

Males used both their tymbal and stridulatory organs to produce acoustic signals, which constituted the first step in pair formation (Supplementary Video S1). When the first male in the population began to call, more and more surrounding males followed (chorusing behaviour). Within the chorus, males of this species did not signal from stationary perches. Rather, they frequently flew from perch to perch, calling on each perch visited (‘call-fly’ behaviour). The time spent on each calling perch varied from 15 to 30 s (mean ± SD = 22 ± 4.24 s, $N = 20$). Sexually receptive females produced sounds in response to an advertising male. Thereafter, the exchange of acoustic signals between the sexes continued until copulation was achieved. During acoustic exchange, the female remained motionless, and the male ceased the ‘call-fly’ behaviour and immediately commenced his search for the acoustically responding female. The male flew directly towards and landed in the vicinity of the stationary responding female. The male then walked quickly towards the female and finally made physical contact with her (Supplementary Video S2). During copulation, both male and female fell silent and remained inactive, and the copulation lasted 22.44 ± 2.99 min (mean ± SD, $N = 11$).

Comparison of Male and Female Stridulatory Sound Production

The sound-producing movements (i.e. upward and downward movements of the forewings) performed by *S. yangi* females were the same as those observed in males (Supplementary Video S2). An upward movement of the forewings led to a file–scraper interaction, producing the upward chirp (Fig. 4a, b). The downward movement of the forewings resulted in a similar file–scraper interaction, and the downward chirp was generated (Fig. 4a, b). We found it difficult to distinguish by ear between sounds produced by males and females. For comparison, a total of 523 stridulatory sounds from 23 males and 359 stridulatory sounds from 17 females were analysed. In the frequency domain, both upward and downward chirps of males and females contained a broad spectrum of frequencies, from 1.5 to 20 kHz (Fig. 4c, d). Temporal analysis revealed that neither the duration of the upward chirp (mean ± SD = 13.37 ± 1.88 ms for males versus 13.29 ± 1.68 ms for females; Mann–Whitney *U* test: $z = -0.457$, $N_1 = 523$, $N_2 = 359$, $P = 0.648$; Fig. 4e) nor the duration of the downward chirp (mean ± SD = 4.82 ± 0.83 ms for males versus 5.03 ± 1.03 ms for females; Mann–Whitney *U* test: $z = -1.605$, $N_1 = 523$, $N_2 = 359$, $P = 0.108$; Fig. 4f) differed significantly between males and females. Furthermore, no significant difference was found in the duration of the interchirp interval (i.e. interval between upward and downward chirps) between the sexes (mean ± SD = 4.04 ± 0.99 ms for males versus 4.26 ± 1.66 ms for females; Mann–Whitney *U* test: $z = -1.189$, $N_1 = 523$, $N_2 = 359$, $P = 0.235$; Fig. 4g). These results show that the stridulatory sound signals produced by males are extremely similar, if not identical, to those of females.

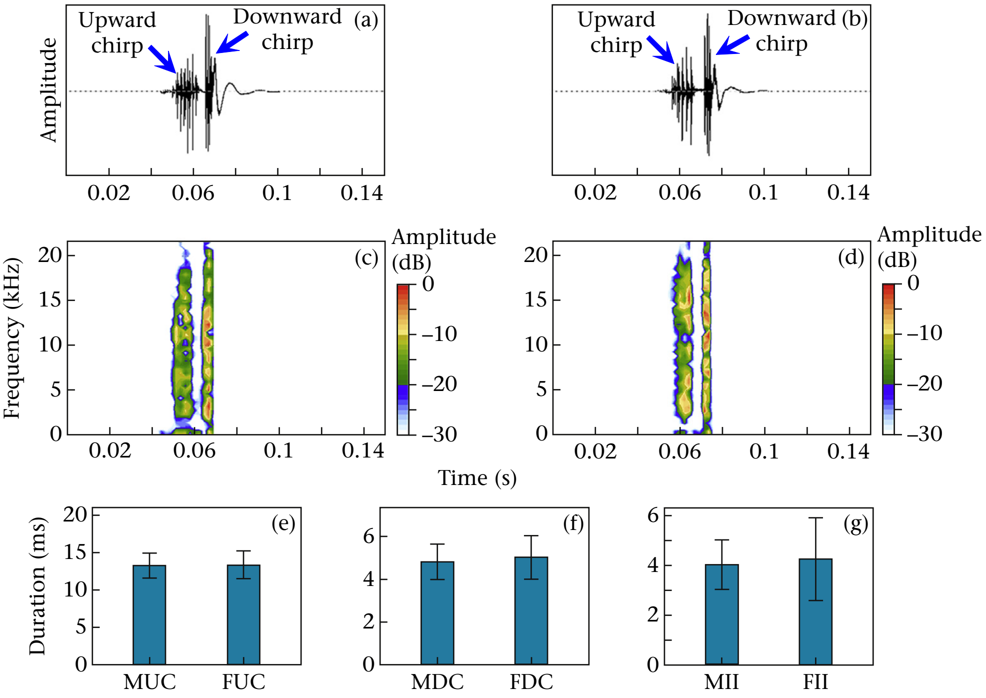

Figure 4. Comparison of male and female stridulatory sound production. (a, c) Oscillogram and spectrogram of a female stridulatory sound (i.e. upward and downward chirps). (b, d) Oscillogram and spectrogram of a male stridulatory sound. (e) Duration of male upward chirp (MUC) and female upward chirp (FUC). Data show mean ± SD. (f) Duration of male downward chirp (MDC) and female downward chirp (FDC). Data show mean ± SD. (g) Duration of male interchirp interval (MII) and female interchirp interval (FII). Data show mean ± SD.

Acoustic Playback Experiments

The playback experiments showed that neither male nor female stridulatory sounds alone could elicit acoustic responses from females (Fig. 5a). Conversely, all the females ($N = 20$) tested in this study responded acoustically to the playbacks of natural male sounds (tymbal + stridulatory sounds; Fig. 5a). In comparison with the number of females that responded to natural male sounds, the number of females (14 of 20) that responded to male tymbal sounds was significantly lower (Fisher's exact test, $P = 0.02$; Fig. 5a). Furthermore, females produced significantly more sounds in response to natural male sounds than to male tymbal sounds alone (mean $\pm$ SD $= 395.64 \pm 78.83$ for natural male sounds versus 184.57 ± 102.93 for male tymbal sounds; paired *t* test: $t_{13} = -6.048$, $P < 0.001$; Fig. 5b).

Male stridulatory sounds were as effective as female stridulatory sounds in triggering phonotactic responses from males (Fig. 5c). Some attracted males landed on and even made copulatory attempts towards the loudspeaker (Fig. 5d). None of the males tested in the playback experiments responded phonotactically to male tymbal sounds (Fig. 5c). Natural male sounds could elicit a phonotactic response from other males, but they were significantly less attractive than male stridulatory sounds alone (four of 20 for natural male sounds versus 20 of 20 for male stridulatory sounds; Fisher's exact test: $P < 0.001$; Fig. 5c).

DISCUSSION

In the cicada *S. yangi*, stridulatory file–scraper organs have evolved in both males and females in addition to the ancestral tymbal organs found in males. Our results show that males of this species produce two types of sounds utilizing both the tymbal and stridulatory mechanisms for intraspecific communication, and that females produce stridulatory sounds in response to advertising males. In insects, the most common method of sound production is the stridulatory mechanism which is especially well developed in Orthoptera (Montealegre-Z & Mason, 2005; Robinson & Hall, 2002). The tymbal mechanism is the other well-known sound production method in insects, and prominent examples are cicadas (Reid, 1971; Young & Bennet-Clark, 1995) and moths (Blest, Collett, & Pye, 1963; Skals & Surlykke, 1999). To our knowledge, a species that can use both stridulatory and tymbal mechanisms to produce sounds has not been previously reported in insects. Therefore, the unusual acoustic behaviour exhibited by *S. yangi* expands our knowledge of the diversity of sound-producing behaviours in insects.

We have shown that in the context of pair formation, females of *S. yangi* produce acoustic signals using a stridulatory mechanism. The *Subpsaltria* pair-forming system, characterized by male advertisement and female acoustic response, is similar to that observed in periodical cicadas, *Magicicada* spp. (Cooley & Marshall, 2001) and some other insects such as leafhoppers (Hunt & Nault, 1991), fireflies (Lloyd, 1966, 1971), katydids (Hartley, 1993; Spooner, 1968), grasshoppers (von Helversen & von Helversen, 1997) and lacewings (Henry, 1979; Wells & Henry, 1992). Behavioural observations indicate that, unlike the males, the females of *S. yangi* do not generate sounds spontaneously, and the female sound production occurs exclusively in response to male advertisement signals during pair formation. An acoustic signal can simultaneously convey different kinds of biologically significant information (Gerhardt, 1992). We suggest that the stridulatory sounds produced by females of *S. yangi*, being an essential element of the mating system of this insect, contain information about the species identity, sex, receptive state and location of the females. The information can be used by conspecific males to recognize and locate the females.

In the case of *S. yangi*, all males use not only tymbal but also stridulatory organs to generate sounds during pair formation. In male cicadas, the advertisement signals that are produced by

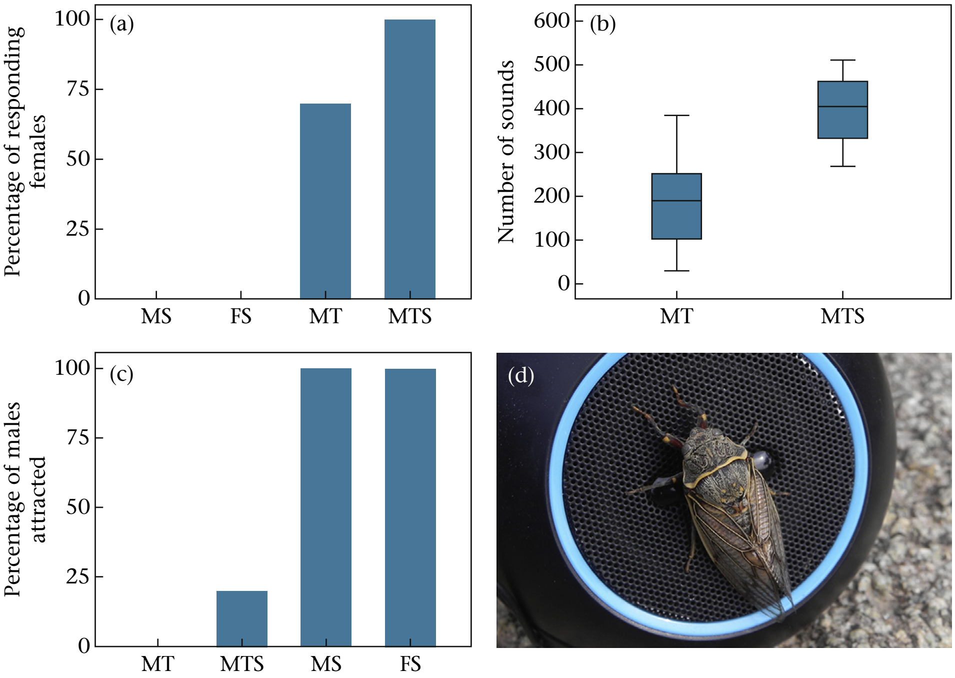

Figure 5. Acoustic playback experiments. MTS: natural male sounds consisting of both tymbal and stridulatory sounds. MT: male tymbal sounds. MS: male stridulations. FS: female stridulatory sounds. (a) The efficiency of the four types of acoustic stimuli in eliciting acoustic responses from females. (b) Number of stridulatory sounds produced by the female during the playback. Only the 14 females responding to both MTS and MT were used for analysis. The median is represented by the black line within the box, while the box indicates upper and lower quartiles. The vertical lines (whiskers) above and below the box indicate the upper and lower range of the data. (c) The efficiency of the four types of acoustic stimuli in eliciting phonotactic responses from males. (d) A male that was attracted by playback of male stridulatory sounds and landed on the loudspeaker.

tymbal organs in the context of pair formation function primarily in mate attraction or to elicit acoustic responses from conspecific females (Claridge, 1985; Sueur & Aubin, 2004; Williams & Simon, 1995). Our playbacks indicated that the tymbal sounds of *S. yangi* males, functioning as advertisement signals, can trigger acoustic responses from females. In contrast, the stridulatory sounds alone did not elicit a response from females. Acoustic analysis revealed that male stridulatory sounds were almost identical in acoustic structure to stridulatory sounds produced by acoustically responding females (i.e. female sexual signals). Furthermore, our result that both male and female stridulatory sounds elicited the same phonotactic responses from males demonstrates the extreme similarity between them.

The question then arises: why do males produce female-like sound signals during pair formation? Results from our playbacks show that females of this cicada species preferentially responded to tymbal sounds with stridulatory sounds over tymbal sounds alone, and they also produced more sounds in response to acoustic stimuli containing both tymbal and stridulatory sounds. These two lines of evidence suggest that production of female-like sound signals allows males to elicit a female acoustic response more effectively.

We suggest that, in the cicada *S. yangi*, production of female-like sounds by a male is a form of intraspecific female mimicry which may enable the male to mimic a responding female. When there are fewer males than females available for mating, female–female competition for access to mates is expected (Clutton-Brock, 2007; Kvarnemo & Ahnesjö, 1996). The alternating tymbal and stridulatory sounds produced by a male are just like an acoustic interaction between a male and a female, which may give a receptive female a false impression that there is not only a potential mate but also a rival female. In this situation, the receptive female may become a more active signaller and increase her sound output to both compete with the pseudofemale and make her more attractive to the male. The results of our playbacks with females are consistent with this hypothesis.

In the case of intraspecific sexual mimicry, male-mimics or female-mimics may benefit in various ways from deceptive signalling of their sex identity. For example, they may be able to steal nuptial food resources from other males (Thornhill, 1979), to escape excessive sexual harassment by males (Cook, Vernon, Bateson, & Guilford, 1994), to sneak copulations with females guarded by large males (Hanlon, Naud, Shaw, & Havenhand, 2005), to minimize the risk of predation (Shine, Phillips, Waye, LeMaster, & Mason, 2001), or to reduce aggression from other males during breeding (Sternalski, Mougeot, & Bretagnolle, 2012). In *S. yangi*, acoustic female mimicry can make males more effective in eliciting acoustic responses from females, which may provide selective advantages for males in two ways. First, for males, eliciting a female response is a prerequisite for mating success, and therefore males could gain reproductive benefit from adopting female mimicry. Second, advertising and searching for mates is usually accompanied by a risk of predation (Cooley, 2001; Gwynne, 1987; Magnhagen, 1991). By mimicking females, males may reduce the time needed to find a mate, and thereby minimize the predation risk.

Female mimicry may impose costs on males because males are also likely to be deceived by female-like sound signals produced by other males, which may lead to male–male courtship interactions. Since same-sex sexual interactions are time consuming and could hamper male courtship efforts towards females, males that are able to minimize such costs while still achieving matings will be at a selective advantage. Our playbacks showed that, although male stridulatory sounds did have the ability to attract males, the attractiveness of male stridulatory sounds was greatly reduced when the stridulatory sounds alternated with tymbal sounds. These results suggest that males may have evolved to ignore acoustic signals consisting of alternating stridulatory and tymbal sounds to avoid detrimental courtship interactions with other males. This form of deceptive signalling appears to incur no apparent reproductive and survival costs to females. Under this condition, there were no strong selective forces to drive females to distinguish males' stridulatory sounds from those produced by females, which facilitates the retention of the deceptive function of males' stridulatory signals and leads to the persistence of female mimicry in this species.

The acoustic behaviour of other cicada species that also possess both tymbal and stridulatory organs is largely unexplored, and our results underscore the need for more acoustic studies on these remarkable cicada species. Different types of acoustic deception have been described. For example, 'cry wolf' is a form of deception where an individual utters false alarm calls to scare competitors away from food sources (Flower, 2011; Munn, 1986; Wheeler, 2009) or to prevent the departure of a receptive female from a mating territory (Bro-Jørgensen & Pangle, 2010). However, deception by acoustic sexual mimicry remains rare. We hope that our results will promote further studies of acoustic deception in animals such as birds, frogs and other acoustic insects.

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Supplementary Material

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