

Article

Females prefer males producing a high-rate song with shorter timbal–stridulatory sound intervals in a cicada species

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Abstract

Uncovering mate choice and factors that lead to the choice are very important to understanding sexual selection in evolutionary change. Cicadas are known for their loud sounds produced by males using the timbals. However, males in certain cicada species emit 2 kinds of sounds using respectively timbals and stridulatory organs, and females may produce their own sounds to respond to males. What has never been considered is the mate choice in such cicada species. Here, we investigate the sexual selection and potential impact of predation pressure on mate choice in the cicada *Subpsaltria yangi* Chen. It possesses stridulatory sound-producing organs in both sexes in addition to the timbals in males. Results show that males producing calling songs with shorter timbal–stridulatory sound intervals and a higher call rate achieved greater mating success. No morphological traits were found to be correlated with mating success in both sexes, suggesting neither males nor females display mate preference for the opposite sex based on morphological traits. Males do not discriminate among responding females during mate searching, which may be due to the high energy costs associated with their unusual mate-seeking activity and the male-biased predation pressure. Females generally mate once but a minority of them re-mated after oviposition which, combined with the desirable acoustic traits of males, suggest females may maximize their reproductive success by choosing a high-quality male in the first place. This study contributes to our understanding mechanisms of sexual selection in cicadas and other insects suffering selective pressure from predators.

Key words: Cicadidae, female choice, mating success, predation pressure, sexual selection.

Mating is an expensive, risky, and intimate interaction, and over an individual's life one expends time and energy on facilitating some matings and/or on avoiding others (Rosenthal 2017). Mate choice has continued to present a unique problem in evolutionary theory since the publication of Darwin's *Origin of Species* (1859), because both the formation of new species and the blending together of species via hybridization depend on individual mate-choice decisions (Rosenthal 2017). Sexual selection suggests that females may be

more choosy in selecting mates (Darwin 1871; Andersson 1994; Jennions and Petrie 1997; Rosenthal 2017) due to their relatively greater investment in gametes (Trivers 1972). Female preference favoring a male ornament can evolve under natural selection, for instance in the context of foraging or predator avoidance (Endler and Basolo 1998; Ryan 1998). Female mate choice is a central part of sexual selection, and uncovering female mate choice and the factors that lead to choice are important to understanding sexual selection

in evolutionary change (Darwin 1871; Andersson 1994; Rosenthal 2017).

Male song is a primary reproductive signal in various taxa of insects, anurans, birds, and mammals. Generally, males produce calls with distinct temporal and spectral characters, which are used by females to recognize conspecific or heterospecific males (Otte 1992; Gerhardt and Huber 2002). Meanwhile, calls may show highly intraspecific variation and can act as quality indicators of males (Alexander 1967). Many studies have revealed that female preferences on static call features are usually stabilizing, whereas preferences on dynamic acoustic features are generally directional (Gerhardt 1994; Gerhardt and Huber 2002). Female preferences on spectral properties of male calls are irregular, including stabilizing preference, weakly or strongly directional preferences, even no preferences (reviewed in Gerhardt and Huber 2002). For example, Castellano et al. (2009) found that females of the Italian treefrog *Hyla intermedia* Boulenger showed a weak stabilizing selection on male call spectral structure and a relatively stronger directional selection on call rate (CR).

In acoustic insects, cicadas are known for their loud sounds produced by males (Claridge 1985), which play a vital role in mate searching and reproduction (Luo and Wei 2015a). In most cicada species, females typically do not produce acoustic signals; they perform phonotaxis, moving toward calling males (Alexander 1967; Huber 1983). Whereas, in some cicada species, the mating system is characterized by the male's call-fly mate-searching activity toward the female acoustic responses, which result in acoustic duets (Luo and Wei 2015a, 2015b; Hou et al. 2017). Acoustic duets by airborne sound in insects are well known from Orthoptera (von Helversen et al. 2001, 2004, 2015; ter Hofstede et al. 2015), but only known in a few cicada species (Gwynne 1987; Bailey 2003), for example, New Zealand cicadas *Kikihia* spp. (Myers 1929), the tick-tock cicada *Physseema quadricincta* (Walker) (Gwynne 1987; Moulds 2012), periodical cicadas *Magicicada* spp. (Cooley and Marshall 2001) and the Chinese cicada *Subpsaltria yangi* Chen (Luo and Wei 2015a; Hou et al. 2017). In these cicada species, females can respond to the male calling song by producing their own acoustic signals with stridulatory organs (if present), or by clicking their wings to the abdomen (Sueur and Aubin 2004; Wei et al. 2009; Luo et al. 2015; Luo and Wei 2015a).

Subpsaltria yangi is a cicada species endemic to the Loess Plateau and adjacent areas in China (Luo and Wei 2015a). Females of *S. yangi* oviposit in live twigs and cause damage to their host plants, including the medicinal plants *Ephedra lepidosperma* C. Y. Cheng (Supplementary Figure S1a and b) and *Ziziphus jujuba* Mill. var. *spinosa* (Hou et al. 2019) (Supplementary Figure S1c), and *Prunus mongolica* Maxim (Supplementary Figure S1d). Besides the presence of timbals in the male, both sexes of *S. yangi* have stridulatory organs. Males of *S. yangi* produce sounds from exposed perches; whereas conspecific females produce stridulatory sounds from concealed perches, which are extremely similar in acoustic structure to those of males (Luo and Wei 2015b; Hou et al. 2017). Luo and Wei (2015a) revealed that the number of *S. yangi* females responding to natural male sounds (consisting of both timbal and stridulatory sounds) was significantly higher than those responding to male timbal sounds (MTs) alone, and females produced significantly more sounds in response to natural male sounds than to MTs alone. However, what has never been considered is the mate choice in duetting cicadas and cicadas that emit 2 kinds of sounds using, respectively, the timbals and the stridulatory organs.

Revealing the variation of songs of cicadas is one of the prerequisites for studying the mechanisms of mate choice that could have led to the evolution of acoustic signals. The variation in acoustic signals has been largely discussed for cicada species producing calling songs using the timbals (e.g., Quartau et al. 1999; Pinto-Juma et al. 2005; Sanborn 2006; Sofia et al. 2008; Liu et al. 2017, 2019), but association between the variations in calling songs and female mate choice has been little investigated. Besides the calling song, courtship song also exists in some cicada species, which appears to be of lower intensity than the calling song (Alexander 1967). For instance, Gwynne (1987) revealed that courtship songs of the tick-tock cicada *P. quadricincta* are produced more sporadically and at a lower rate than the calling songs. Males of *Magicicada* species (e.g., *M. septendecim* (L.) and *M. cassini* (Fisher)) can produce 2 different courtship songs when they land in close proximity to females (Alexander and Moore 1958, 1962; Alexander 1967). Pair-formation in *S. yangi* occurs when males emit calling songs, females respond, males then fly to responding females; and sometimes males emit courtship songs sporadically when they land in the vicinity of a stationary responding female (for the detailed differences between courtship songs and calling songs, see the Results section). The pair-formation of this species is relatively complex than that of other cicada species (Huber 1983; Hou et al. 2017).

Mate choice can drive the evolution of elaborate traits that hinder critical tasks such as avoiding predators, in opposition to natural selection (Rosenthal 2017). Previous studies of insect mating systems have shown that males suffer greater predation than females as a result of their courting activities, including their movements through the habitat associated with obtaining mates (e.g., Thornhill 1978; Gwynne 1987) and conspicuous displays that attract predators (Burk 1982). Similarly, Hou et al. (2017) found that only males of *S. yangi* are attacked by the robber fly *Philonicus albiceps* (Meigen), especially in their call-fly mate-seeking activity. In *S. yangi*, all observed mate encounters resulted in a successful mating characterized in terms of “love-at-first-sight”—immediate pair-formation (Hou et al. 2017). This may suggest that mate choice (if present) in this species occurs and operates on acoustic signal traits before physical contact to minimize predation pressure. A previous study revealed that males of *S. yangi* can mate multiple times, whereas females mate only once and are sexually unreceptive after copulation (Hou et al. 2017). This is contrary to females in most other cicada species which mate only once likely due to receiving a seminal plug after copulating (White 1973; Karban 1983), but similar with the periodical cicadas *M. septendecim* and *M. cassini* (Karbon 1983; Cooley and Marshall 2004). However, our recent field investigation discovered that a minority of mated females (7 out of 78 mated females) of *S. yangi* regained sexual receptivity and re-mated after laying eggs. Whether the unusual pair-formation process and re-mating behavior of *S. yangi* females are related to their dual sound-producing mechanism and predation pressure remain unknown. The answers to these puzzles may be important to evaluate the role of sound-producing mechanisms and predation pressure in influencing the evolution of mate choice of cicadas and other sound-producing insects.

Based on our previous studies of pair-formation and sound-producing organs as well as their functions in both sexes of *S. yangi* (Luo and Wei 2015a, 2015b; Hou et al. 2017), calling song variation among males and female preferences for calling song features and morphological traits (if any) in this species are investigated. We have 6 objectives in this study: to clarify the male calling song variation; to estimate the variation of body size of both sexes; to

examine the correlation between male calling song and morphological features; to reveal female preferences for properties of male calling songs; to reveal whether the body size of males/females affects mating success; and to further clarify the male-biased predation pressure and its influence on mate choice in this species.

Materials and Methods

Species and study site

This study was mainly conducted on a wild population of *S. yangi* at Chunshugou Valley (38°33.699'N, 105°55.217'E, elev. 1,400–1,600 m) located in the Helan Mountains, Ningxia Hui Nationality Autonomous Region, China in May and June from 2015 to 2017. The sampling arena consists of a core area (~0.2 ha), where most calling activities occurred, and a buffer zone (~10 m width) adjacent to the core area. Vegetation in the habitat consists mainly of drought-resistant dwarf shrubs and herbs (Supplementary Figure S2a). Adults of *S. yangi* mainly feed on *E. lepidosperma* (Hou and Wei 2019) which is the preponderant vegetation in this habitat. The host plant *E. lepidosperma* is <1 m in height (height: mean \pm SD = 24.1 \pm 6.3 cm; diameter: mean \pm SD (standard deviation) = 51.0 \pm 14.0 cm; n = 21) (Supplementary Figure S2b), which allowed easy observation of the mating behavior of *S. yangi*.

Sampling and marking techniques

In our 3-year field investigations in the Helan Mountains, censuses of this cicada species were conducted using capture-mark-recapture/re-sighted. Each census lasted for about 1 month (from 23 May to 22 June 2015, from 26 May to 25 June 2016, and from 27 May to 25 June 2017, respectively). Virgin adults of *S. yangi* (Supplementary Figure S3) were collected in the early morning after eclosion, and their head width, pronotum width, body length, forewing length (left side), and abdomen width were measured (\pm 0.01 mm) using a digital caliper (Shengtai Electronic Technology Co. Ltd., China). They were then marked with water-repellent red color (Veiao Co. Ltd., China) on the right forewing with a unique combination of 3 legible digits. In the field investigation in 2017, besides conducting morphological measurements, captured and measured individuals were also weighed (\pm 0.001 g) with an electronic scale (Changxie Electronics Factory, Dongguan, China). Marked cicadas were released at the same site they were captured.

Capture-mark-recapture technique and call recording

The core area (~0.2 ha) was divided into 20 quadrats of 10 \times 10 m. On each observation day (weather permitting), a systematic investigation of the area was conducted once every 2 h for 6 consecutive hours, mainly between 9:00 am and 15:00 pm, the time period coinciding with sustained chorus activity (Luo and Wei 2015a). To reduce any effect time of day had on insect activity, the first quadrat of the area visited was rotated each day. Remaining quadrats were then visited in ascending numerical order each day.

The advertisement calls of males were recorded between 9:00 am and 15:00 pm, this time period coinciding with the singing activity of this species, with sampling using a linear PCM recorder with stereo microphones (PCM-D100 digital recorder, 20–20,000 Hz, 44.1 kHz/16 bit, Sony, Tokyo, Japan) and saved in WAV format (Luo and Wei 2015a). Calling behavior was confirmed visually (using close-range binoculars: Pentax Papilio 8.5 \times 21, focus to 0.5 m) without disturbing them. All recordings were made at a close distance of 20–30 cm from the male (which ensured that most of the

acoustic signals recorded are of high quality), and its 3-digit identifier was noted. If a caller was unmarked, we marked, measured, and weighed it after recording its calling song. We then released it at the same site.

During the surveys, whenever a pair of cicadas of *S. yangi* was observed in copulation, the 3-digit identifier of both sexes was noted. When an individual was found unmarked in a mating pair, we captured it after the mating, and then marked, measured, weighed, and released it.

Call recording and acoustic analyses

Acoustic analysis was performed using Adobe Audition CC 2015 (Adobe, San Jose, CA), Raven Pro version 1.4 (The Cornell Lab of Ornithology, Ithaca, NY), and a custom-made library in R platform, Seewave (Sueur et al. 2008; R Core Team 2018). Eight calling song properties were measured: (1) the length of timbal sound (TL) (unit: ms); (2) the duration of the first syllable in timbal sound (FSD) (unit: ms); (3) the period of the first syllable in timbal sound (FSP) (unit: ms); (4) the length of stridulatory sound (SL) (unit: ms); (5) the timbal-stridulatory sound interval (TSI) (unit: ms); (6) the interval between stridulatory sound to the next timbal sound (IST) (unit: ms) (Figure 1A); (7) the dominant frequency (DF) (unit: Hz) (Figure 1B, C); and (8) the CR (unit: calls/min). CR was calculated as the ratio of the number of calls and the duration over which these calls were emitted. The time that males spent on each calling perch varied from 15 to 30 s when they performed call-fly mate-seeking activity (Luo and Wei 2015a). We randomly selected 5 complete calls of high-quality (i.e., possessing low background noise and without overlap with sounds of other individuals) from each male to measure the 7 acoustic properties (Hou et al. 2017). Mean values were then calculated for subsequent analyses.

Investigation of predation pressure on *S. yangi*

We accidentally discovered a robber fly *P. albiceps* eating a *S. yangi* male in the Helan Mountains in 2015. During the capture-mark-recapture/re-sighted experiments in 2016 and 2017, we investigated the predation pressure imposed on *S. yangi* by *P. albiceps*. When an individual of *S. yangi* was observed being attacked by *P. albiceps*, the robber fly and the cicada were captured together using a sweep net. The sex of the cicada was then identified and its identifier was noted. Besides the robber fly, a wide variety of vertebrates, for example, the Eurasian magpie *Pica pica* L. and the Alashanic ground squirrel *Spermophilus alaschanicus* Buchner also prey on *S. yangi*. We noted the number of individuals of *S. yangi* preyed upon by these 2 predators, and the sex of preyed-upon cicadas was determined based on their sound signals emitted.

In addition, a field investigation was conducted supplementarily on a wild population of *S. yangi* at Fengxiang County, Shaanxi Province (34°34.238'N, 107°32.535'E, elev. 941 m) in June 2019, aiming to further reveal if there were any other natural enemies preying on *S. yangi*. Vegetation in this habitat consisted of *Z. jujuba* var. *spinosa* (Supplementary Figure S4a) and *Sophora davidii* (Franch.) (Supplementary Figure S4b). The sex of individuals of *S. yangi* captured by the predators was determined according to the same methods mentioned above.

Statistical analyses

An index of body size for both sexes was generated through principal component analysis based on 4 morphological characters: head width, pronotum width, abdomen width, and body length.

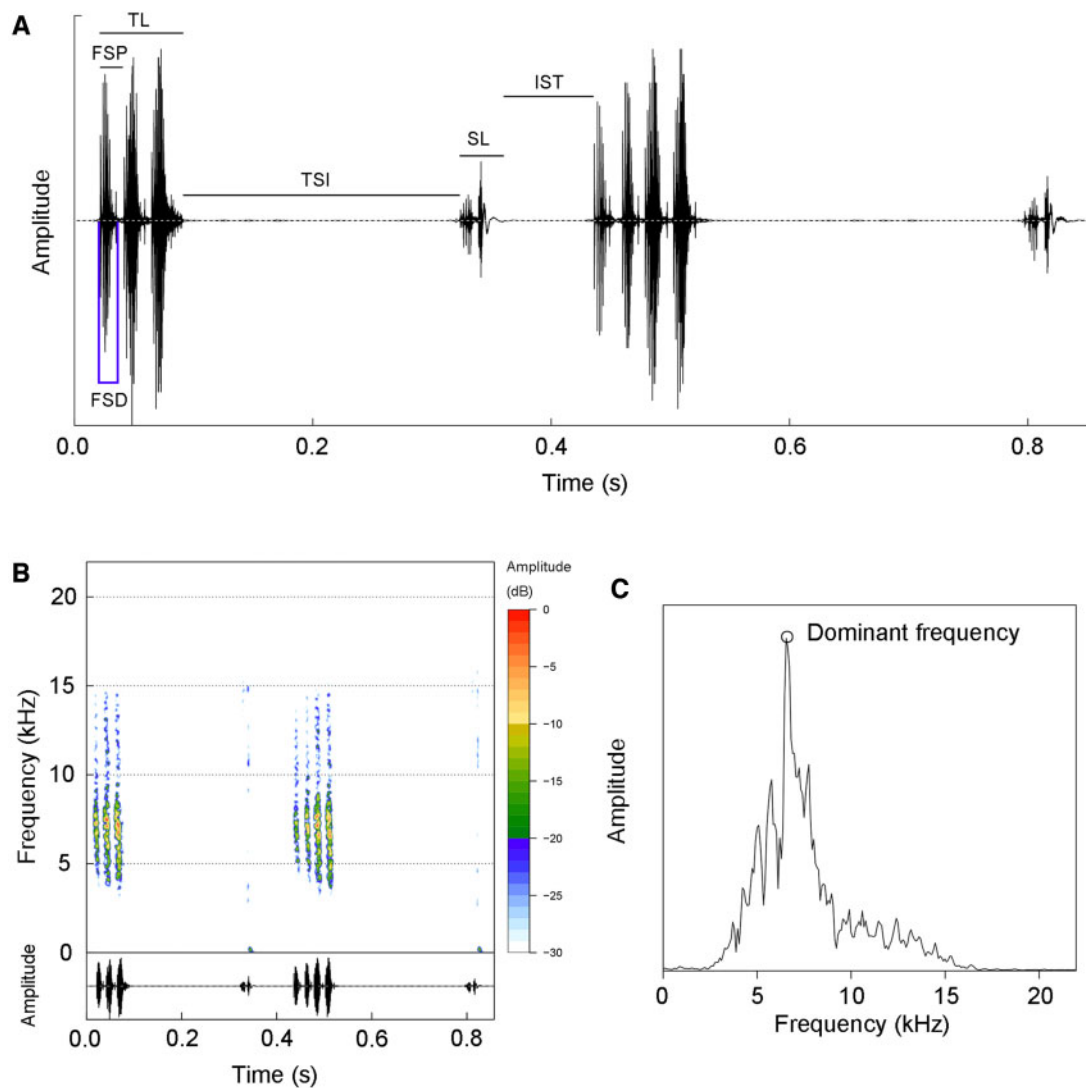


Figure 1. Acoustic analyses of the calling song of *S. yangi*. (A) Oscillogram of a sequence of the calling song. (B) Power frequency spectrum of the calling song. (C) Power spectrum showing the distribution of energy in a call with most of the energy accumulated around a single frequency (the dominant frequency).

Correlations were performed between body weight and body size, between body weight and the ratio of wing length/body length, and between body size and the ratio of wing length/body length. Correlations were performed between the 8 above-mentioned call acoustic features of male calling songs. Correlations were also performed between calling song features and 3 morphological characters of males, including body length, body size, and the ratio of wing length/body length. A paired *t*-test was conducted to check the differences of CR and DF between male calling song and courtship song. A chi-squared test was conducted to check the differences between the numbers of males and females captured by the robber fly *P. albiceps* in 2016 and 2017. A Mann–Whitney U-test and an independent sample *t*-test were performed to check the differences of the ratio of wing length/body length, and the ratio of wing length/body weight between the males captured and not captured by the robber fly, respectively. These analyses were performed using SPSS

Statistics version 20.0 (IBM, Armonk, NY). The statistical tests were considered significant at $P < 0.05$ and all *P*-values we report are 2-tailed. The figures were generated using SigmaPlot version 12.5 (Systat Software Inc., San Jose, CA).

In order to reveal how female choice (if any) operated on acoustic properties of male calling songs and morphological characters, we conducted backward-stepwise Poisson regression analysis with male mating success as the dependent variable, and male acoustic properties, males' morphological characters (body size PC1, the ratio of wing length/body length) and breeding season as independent variables. The optimal model was chosen based on the lowest Akaike's information criterion (AIC). Similarly, to reveal the relationships between female mating success and female morphological characters, female mating success was set as the dependent variable and females' morphological characters (body size PC1, the ratio of wing length/body length) and breeding season were set as

independent variables in the model. In addition, a non-parametric method, cubic regression, was used to reveal the relationships between male calling song properties and mating success.

Results

Sound communication and mating behavior

During mate searching, males of *S. yangi* produced 2 types of sounds to signal for mates, one produced by timbals and the other produced by stridulatory organs (Figure 2A). The timbal and stridulatory sounds of males' signals were produced alternately (Figure 2A). The forewing movements of both sexes caused interaction between the scraper and the file, resulting in the production of stridulatory sounds. Males produced calling songs first in pair formation. Sexually receptive females produced stridulatory sounds in response to an advertising male. Then the male flew to the responding female after locating her based on the stridulatory sounds of the female ("call-fly" behavior), sometimes emitting courtship songs (Supplementary Figure S5) sporadically when it landed in the vicinity of the stationary responding female. When physical contact was made with the female, the male stopped emitting courtship songs and mounted the female, then moved to her side and copulated (Figure 2B and Supplementary video S1). Males' courtship songs were sporadic, with a rate distinctly lower than that of calling songs (calling song: mean ± SD = 112.08 ± 16.47 calls/min; courtship song: 87.93 ± 14.40 calls/min; paired *t*-test, *n* = 14 males, *t*₁₃ = 4.241, *P* = 0.001). No significant differences were found in dominant frequency between calling and courtship songs (calling

song: 6,245.86 ± 693.75 Hz; courtship song: 6,447.66 ± 460.23 Hz; paired *t*-test, *n* = 14 males, *t*₁₃ = -0.980, *P* = 0.345). All mate encounters led to a successful mating whether or not the males emitted courtship songs.

Demography and mating frequency

In this 3-year study in the Helan Mountains, we marked 1,052 individuals in total. With the exception of 29 marked males captured and eaten by the robber fly *P. albiceps* (11 in 2016 and 18 in 2017), the remaining 1,023 individuals, including 559 males were used in our analyses. Among the 559 marked males, 331 were re-sighted at least once. The total number of re-sighted males was 112, 202, and 178 in 2015, 2016, and 2017, respectively (Figure 2C). In total, 126 males were observed mating, and the total number of matings observed was 178. The frequency distributions of male mating success in the 3 breeding seasons are similar (Figure 2D).

Morphological characteristics and their correlations with acoustic features

The first principal component for males explained 76.596% of the variance and was regarded as an index of body size of males (Supplementary Table S1). For males, body size PC1 = 0.297 × head width + 0.296 × pronotum width + 0.261 × body length + 0.287 × abdomen width. The first principal component for females explained 78.921% of the variance and was also regarded as an index of body size of females (Supplementary Table S1). For females, body size PC1 = 0.290 × head width + 0.292 × pronotum width + 0.256 × body length + 0.286 × abdomen width. Male body

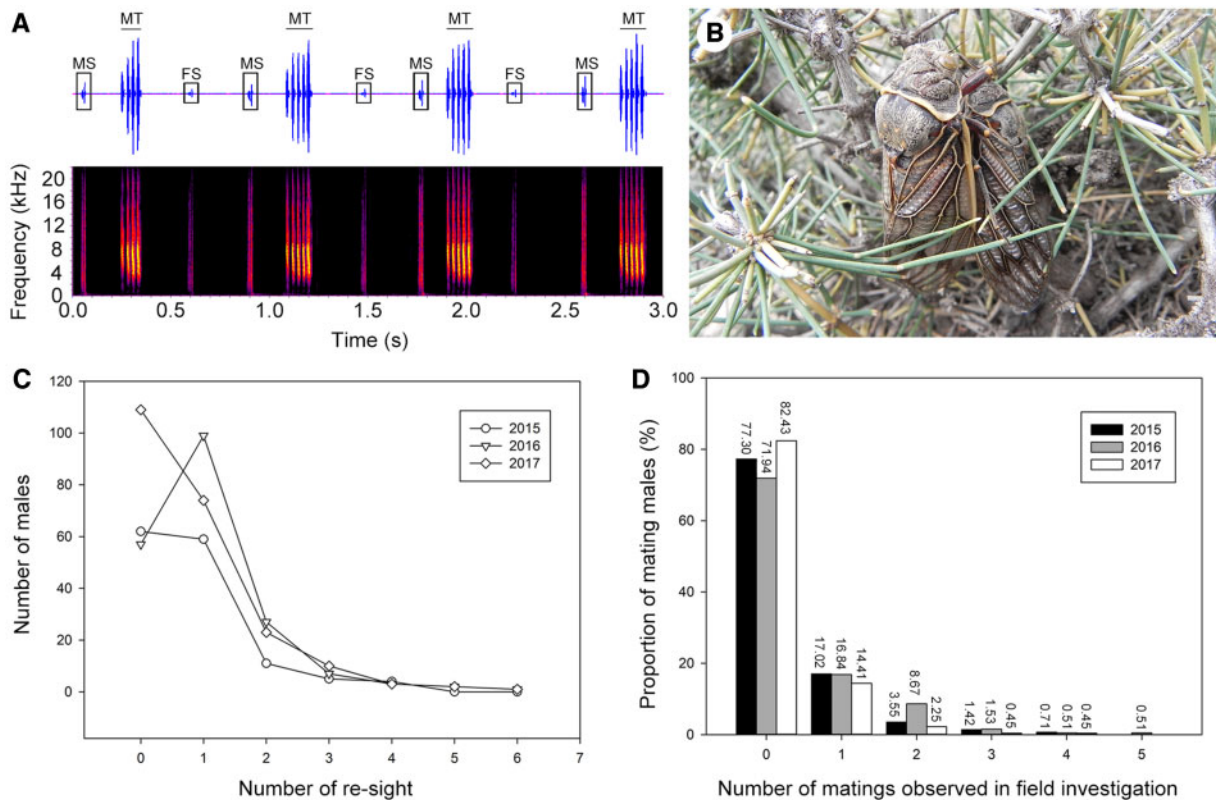


Figure 2. Demography and pair-forming in *S. yangi*. (A) Oscillogram of a sequence of duets of *S. yangi*. (B) A copulating pair of *S. yangi*. (C) Frequency distribution of the number of re-sighted males observed in field investigation. (D) Number of matings of *S. yangi* males observed in field investigation. "0" represents that no mating was observed in the field investigation, including the males without re-sighting. "1," "2," "3," "4," and "5" represent mating once, twice, 3 times, 4 times, and 5 times, respectively. FS, female stridulation, MS: male stridulation.

weight and male body size are positively correlated ($r=0.602$, $P<0.001$, $n=217$ males) (Supplementary Figure S6a). Male body weight is not correlated with the ratio of wing length/body length ($r=-0.013$, $P=0.852$, $n=217$ males) (Supplementary Figure S6b). Male body size and the ratio of wing length/body length are negatively correlated ($r=-0.463$, $P<0.001$, $n=543$ males) (Supplementary Figure S6c). Female body weight and female body size are also positively correlated ($r=0.802$, $P<0.001$, $n=121$ females) (Supplementary Figure S6d). The wing length of females is longer than body length (Supplementary Figure S6e). The female body weight and the ratio of wing length/body length are negatively correlated ($r=-0.260$, $P=0.004$, $n=121$ females) (Supplementary Figure S6e). Female body size and the ratio of wing length/body length are also negatively correlated ($r=-0.515$, $P<0.001$, $n=452$ females) (Supplementary Figure S6f).

In total, we recorded calling songs from 114 males (34.44% of recaptured/re-sighted males). The descriptive statistics of acoustic variables are shown in Table 1. Pearson correlation coefficients between calling song properties indicate most temporal features were significantly correlated with each other (Table 2). In general, males calling at a higher rate had shorter timbal sounds (TL), shorter stridulatory sounds (SL), shorter TSIs, shorter FSDs, and shorter FSPs than males with lower CRs. Among the 7 temporal features, only the FSP was significantly negatively correlated with the spectral property (DF; Table 2).

Correlations were performed between the 8 acoustic features of calling songs and the 3 male morphological characters (body length, body size, and the ratio of wing length/body length). Neither the temporal feature nor the dominant frequency was found correlated with any morphological character (Supplementary Table S2).

Correlations between acoustic features and mating success

The male mating success showed a Poisson-like distribution according to the Kolmogorov–Smirnov test ($z=0.691$, $P=0.726$, $n=114$). We revealed significant associations between male mating success and the 4 temporal properties of calling songs, that is, the positive association between mating success and CR, and the negative association between mating success and TSI, FSP, and FSD, respectively (Table 3). The model that best fits our data (the 1 with the lowest AIC index) includes only TSI and breeding season based on a stepwise approach, suggesting that males producing a shorter TSI along with a higher CR ($r=-0.831$, $P<0.01$, $n=114$ males) experienced more matings.

The fit between mating success and TSI, CR, FSD, and FSP, respectively, were generated based on cubic regression (Figure 3). The cubic regression on TSI shows a monotonic decrease, confirming that there exists directional selection on this trait (Figure 3A). In

Table 1. Descriptive statistics of call acoustic properties

Acoustic properties	Mean	SD
TL (ms)	106.93	20.36
FSD (ms)	14.37	1.12
FSP (ms)	24.41	1.98
SL (ms)	22.66	1.72
(TSI (ms)	298.68	93.55
IST (ms)	137.47	41.98
DF of timbal sound (Hz)	6,297.82	694.81
CR (calls/min)	102.50	15.03

Table 2. Pearson correlation coefficients between call properties

Acoustic features	FSD	FSP	TL	TSI	SL	IST	CR
DF	0.026	-0.186*	-0.131	-0.093	0.088	-0.029	0.168
FSD	–	0.257**	0.464**	0.326**	0.267**	0.064	-0.445**
FSP	–	–	0.242**	0.490**	0.208*	-0.135	-0.449**
TL	–	–	–	0.220*	0.209*	0.035	-0.436**
TSI	–	–	–	–	0.205*	-0.295**	-0.831**
SL	–	–	–	–	–	-0.006	-0.218*
IST	–	–	–	–	–	–	-0.114

** $P<0.01$; * $P<0.05$.

contrast, the cubic regression on CR shows a monotonic increase, suggesting that there also exists directional selection on CR (Figure 3B). These results again show that male producing sounds with shorter TSI and higher CR experience more matings. But cubic regressions show that the relationships between mating success and both FSD (Figure 3C) and FSP (Figure 3D) are not monotonic, suggesting a weakly stabilizing selection on these 2 properties.

Correlations between morphological characters and mating success

Analysis of the relationship between male morphological characters and mating success reveals that male mating success also shows a Poisson-like distribution according to the Kolmogorov–Smirnov test ($z=1.142$, $P=0.148$, $n=543$). However, there is no significant association between male mating success and any of these traits in males (Supplementary Table S3). Similarly, no significant association is found between mating success and female morphological characters (Supplementary Table S4).

Predation pressure on *S. yangi*

During field investigations in the Helan Mountains in 2015, we observed a male *S. yangi* was captured and eaten by the robber fly *P. albiceps*. During field investigations in 2016, 14 *S. yangi* males that had been captured by *P. albiceps* were collected, including 11 marked males and 3 unmarked males (Supplementary Table S5). During field investigations in 2017, 22 *S. yangi* males captured by *P. albiceps* were collected, including 18 marked males and 4 unmarked males (Figure 4A). No female cicadas were ever captured by the robber fly, indicating that this predation was strongly male-biased (2016: $\chi^2=12.07$, $P<0.001$; 2017: $\chi^2=20.05$, $P<0.001$). The ratio of marked males of *S. yangi* preyed upon by the robber fly is 5.31% (11 out of 207 marked males) and 7.50% (18 out of 240 marked males) in 2016, and 2017, respectively. This indicates that a considerable number of *S. yangi* males can be preyed upon by this natural enemy during the mating season. Both the ratio of wing length/body length (Mann–Whitney *U*-test: $z=-2.812$, $P=0.005$; Figure 4B) and the ratio of wing length/body weight ($t_{233}=-5.835$, $P<0.001$; Figure 4C) of the males captured by the robber fly are significantly higher than those of males that were not captured by the robber fly. In addition, we also observed that 4 *S. yangi* males were captured and eaten by the Eurasian magpies *P. pica*, and 2 males were captured and eaten by the Alashanic ground squirrel *S. alaschanicus*.

In our field investigation in Fengxiang County, we observed 1 male of *S. yangi* was captured and eaten by a long-horned grasshopper, *Diastrammena (Tachycines)* sp. (Supplementary video S2), and 1 male of *S. yangi* was captured and eaten by the Eurasian magpie *P.*

Table 3. The effects of call acoustic properties on male mating success

Covariates	Coefficients			AIC
	Intercept	Covariate	Breeding season [†]	
CR	-3.7459 ± 0.8664***	0.0325 ± 0.0076***	-0.3966 ± 0.2484	238.78
TSI	1.3424 ± 0.3519***	-0.0058 ± 0.0013***	-0.4876 ± 0.2460*	236.17
FSP	4.9604 ± 1.5107**	-0.2140 ± 0.0627***	-0.6417 ± 0.2495*	245.35
FSD	3.5788 ± 1.6356*	-0.2687 ± 0.1156*	-0.5146 ± 0.2454*	251.36
TL	0.3038 ± 0.6149	-0.0053 ± 0.0058	-0.4722 ± 0.2474	256.29
SL	1.0424 ± 1.6019	-0.0562 ± 0.0698	-0.5455 ± 0.2510*	256.48
IST	-0.3731 ± 0.4002	0.0009 ± 0.0027	-0.4993 ± 0.2454*	257.03
DF	-1.1103 ± 1.1493	0.0001 ± 0.0002	-0.4735 ± 0.2478	256.55

^{*} $P < 0.05$; ^{**} $P < 0.01$; ^{***} $P < 0.001$. Results were obtained by using generalized linear models in which the dependent variable was assumed to be Poisson distributed. [†]The coefficient for 2017 is the sum of the intercept with breeding-season coefficients, whereas that for 2016 is just the intercept. Data are given as means ± SE (standard deviation).

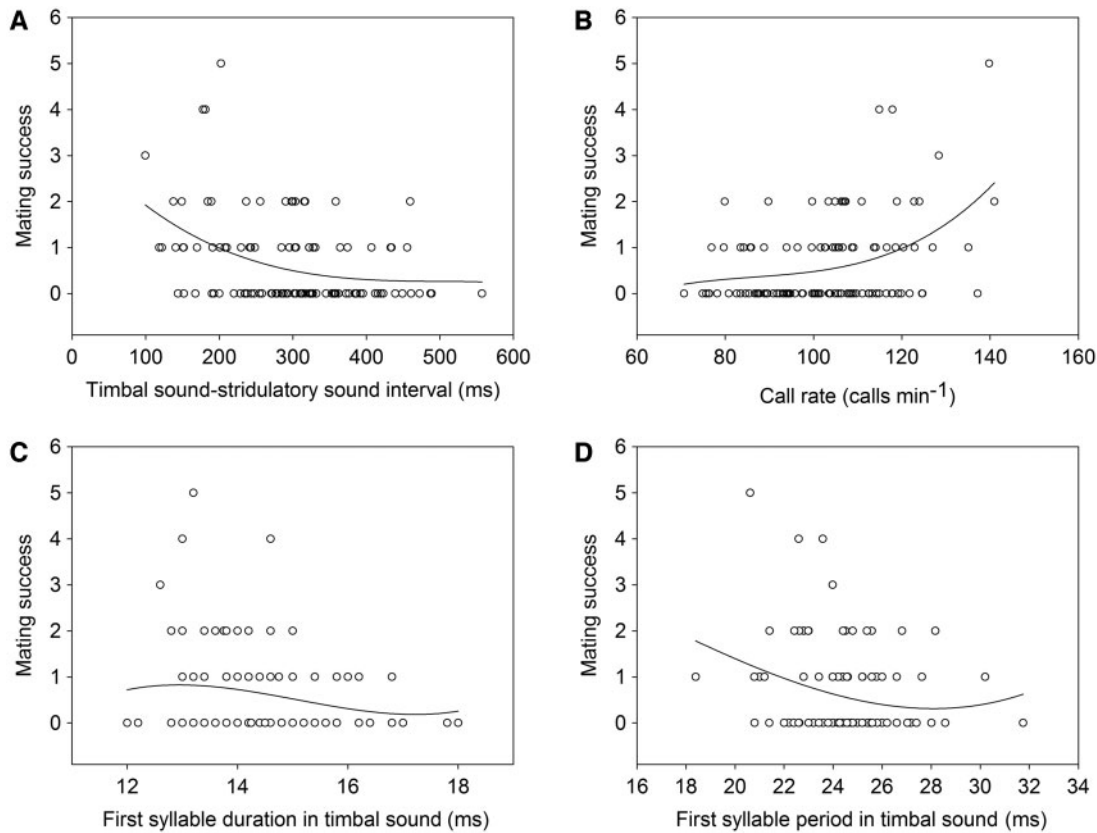


Figure 3. Non-parametric estimates of male mating success in relation to call acoustic properties: (A) TSI, (B) CR, (C) the FSD, and (D) the FSP.

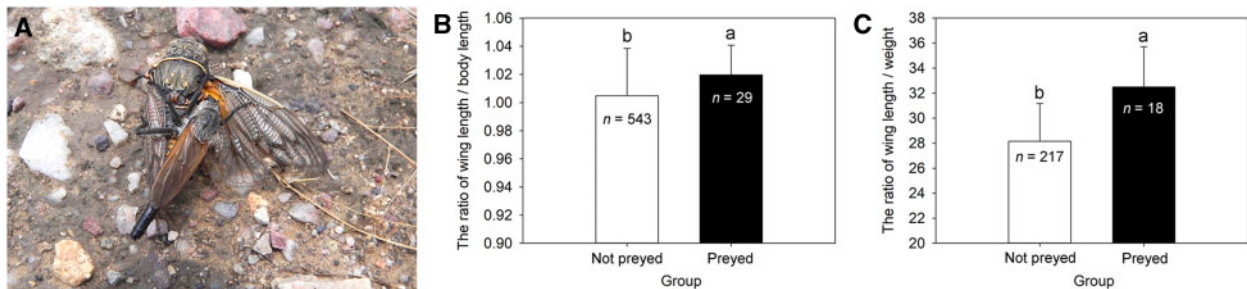


Figure 4. Predators of *S. yangi* and the differences of the character between the marked males preyed and not preyed upon by the robber fly *P. albiceps*. (A) A male captured by the robber fly *P. albiceps*. (B) The ratio of wing length/body length. (C) The ratio of wing length/body weight. Data are presented as mean ± SD.

pica. Again, no females of *S. yangi* were captured by these predators.

Discussion

Results showed that *S. yangi* males that called with shorter TSIs experienced greater mating success (Table 3 and Figure 3A). This suggests that a shorter TSI is a desirable trait for females to choose a mate. In *S. yangi*, both sexes have stridulatory organs, and stridulations produced by males are extremely similar in acoustic structure to those of females (Luo and Wei 2015a). Previous scraper-ablation experiments and acoustic playback experiments suggested that, by alternately producing timbal sound and stridulatory sound (i.e., a female-like sound signal), *S. yangi* males make themselves more effective in eliciting acoustic responses from the receptive female through “deceiving” her into treating him as a rival female or misleading her to suspect a rival female nearby (Luo and Wei 2015a). A possible explanation for the findings in our present results is that males producing calling songs with shorter TSI are more effective in eliciting female–female competition during the pair-formation process (Luo and Wei 2015a). The males of *S. yangi* appear to provide nothing to the females but sperm, yet they have elaborate ornaments for which females show preferences. This type of model has commonly been described as indirect-benefits model, because the female’s choice of males provides her with no immediate, measurable benefits (Jones and Ratterman 2009). Given that *S. yangi* males produce sounds alternately using the timbals and the stridulatory organs, signaling with shorter TSI may be more energy-costly for males and may act as an indicator of male quality. In addition to the indirect-benefits model, sensory bias model suggests that female mating preference is by-product of natural selection on sensory systems (Ryan 1998; Fuller et al. 2005). Females of *S. yangi* may exhibit a preference simply because they are predisposed to do so (Jones and Ratterman 2009). Whether mating preferences and preferred traits in *S. yangi* evolve as sensory bias, Fisherian runaway, indicator, or other mechanisms needs further investigation.

Males of *S. yangi* that called at higher rates, besides having shorter TSI (one of the contributors to high CRs), experience greater mating success than those that called at lower rates (Table 3, Figure 3B). This suggests that a higher CR is also a desirable trait for females to choose a mate. Females favoring higher CRs have also been found in other acoustic insects, for example, the variable field cricket *Gryllus lineaticeps* Stål (Wagner 1996; Wagner and Reiser 2000; Wagner et al. 2001) and various anuran species (Gerhardt 1994; Wagner and Sullivan 1995). Signaling at a higher rate is often regarded as an indicator of male quality (stamina) or has served as a handicap because it is costly (Ryan and Cummings 2005). For example, in the Mediterranean field cricket *Gryllus bimaculatus* de Geer, males signaling more rapidly incur higher energetic costs, and females may assess and choose males based on their ability to burden the costs (Mowles 2014). Thus, we infer that *S. yangi* females select mates based on their ability to bear the costs associated with the call-fly mate-seeking activity.

We discovered that morphological traits of *S. yangi* males are not correlated with male mating success (Supplementary Table S3). In general, male size dimorphism is usually expected to evolve in taxa with male–male competition for mates (Raihani et al. 2006). In species where males compete intensely for females or in polygynous species, male–male competition could favor large body size (Raihani et al. 2006). For example, body size has been shown to correlate with male mating success in the periodical cicada *Magicicada* spp.

(Karban 1983; English 2001). Karban (1983) revealed that males of the periodical cicada *Magicicada cassini* collected in copula were larger than those collected singly, and similar results were found by English (2001) for *M. cassini* and another periodical cicada species, *M. septendecim*. In contrast, Cooley and Marshall (2004) found that mating males were statistically smaller than chorusing males for *M. septendecim*. We found that morphological traits were not correlated with male mating success, which combined with the revealed desirable acoustic traits of males, indicate that female mate choice in *S. yangi* is operating on acoustic signal traits rather than morphological traits.

Although female mate choice is considered the norm, males also exhibit mate choice on females under some conditions (Edward and Chapman 2011). For example, Bateman and Fleming (2006) found that males of the field cricket *G. bimaculatus* would preferentially court larger females. Similarly, males of Pacific blue-eye fish *Pseudomugil signifer* Kner were capable of exercising sequential mate choice and spent more effort courting larger females (Wong et al. 2004). However, males might not pay attention to attracted females when they attract females sequentially due to the costs of missing a mating opportunity (Bateman 2001) or due to the energetic costs during mate attraction signaling (Prestwich 1994). Male mate choice has not been formally considered in cicadas because it is generally the responding females that fly to a preferred advertising male during their pair-formation (Huber 1983). However, it is the male that flies to a responding female in the pair-formation of *S. yangi*. In this study, no significant differences were found in morphological characters between mated females and presumed unmated females in *S. yangi* (Supplementary Table S4), which suggests that males displayed little direct evidence of mate preference for females with large or small body mass. In addition, males of *S. yangi* did not discriminate among responding females during their quick pair-formation process according to our field observations, suggesting that males display no mate preference for females based on acoustic features. This is consistent with that all observed mate encounters in *S. yangi* resulted in a successful mating (Hou et al. 2017). No male mate choice evolved in this species may be due to the relatively higher costs associated with their unusual call-fly mate-seeking activity and the male-biased predation pressure.

Communication systems involving visual, chemical, and acoustic signals can be exploited by predators and parasitoids (Zuk and Kolluru 1998; Marshall and Hill 2009; Ma et al. 2020). Mate searching by males is prevalent in most animals, and many studies have demonstrated conspicuous call makes males vulnerable to predation (Zuk and Kolluru 1998). Some studies analyzing predator diet found evidence to support that movement toward a signal increases exposure of mate-searching individuals to predators (Gwynne 1987; Heller and Arlettaz 1994; Raghuram et al. 2015). Our previous study revealed that the robber flies attacking *S. yangi* were not orienting to acoustic signals of cicadas but are likely visual predators. Duet calling from terrestrial or subterranean sites may help reduce predation pressure in 2 ways. First, calling from covered locations may provide concealment and physical protection from potential predators. Second, duet calling may decrease predation risk because it is more difficult for predators to detect prey which calls synchronously (Tuttle and Ryan 1982; Etzel et al. 2020). Males of *S. yangi* emit sounds at exposed perches and frequently fly from perch to perch during mate searching, attempting to both acoustically and visually locate females and mate with them, whereas females respond to males from their concealed perches (Luo and Wei 2015a; Hou et al. 2017), which may lead to the observed male-biased

predation pressure. We did reveal that all the predation on *S. yangi* was male-biased.

In addition, we found that both the ratio of wing length/body length and the ratio of wing length/body weight of the *S. yangi* males captured by the robber flies were significantly higher than those of males not being captured (Figure 4B, C). Loannou et al. (2019) provided experimental evidence in support of a widely assumed hypothesis that individual prey at the front of a moving group are most at risk from predation. Although mate-searching males of *S. yangi* do not form any moving group, the males exhibit chorus activity (Luo and Wei 2015a). We infer that males of *S. yangi* with a larger ratio of wing length/body length or a larger ratio of wing length/body weight may possess a stronger flying ability, which may perform call-fly mate-searching activity firstly within the chorus, thus they may be targeted more easily and often by predators.

The male-biased predation hypothesis argues that search and travel to a mate are risky for *S. yangi* males, which may impose an intense selective pressure on the males and influence the probability of future matings for them. We did observe that most *S. yangi* males mate once in our field investigations, although they can mate multiple times. This argues why males of *S. yangi* not discriminating among responding females are closely related to male-biased predation pressure.

Overall, we revealed a significant association of male mating success with several temporal properties of males' acoustic signals in *S. yangi*; in particular, TSIs and CR. No morphological traits were found to be correlated with mating success in either sex, suggesting neither males nor females display mate preference for the opposite sex based on morphological traits. In addition, an intensive male-biased predation pressure was confirmed for this species. We hypothesize that the "love-at-first-sight" pair-formation (immediate pair-formation) in *S. yangi* may have been shaped by the dual-sound-producing mechanism, their unusual pair-formation process, and the male-biased predation pressure. We also hypothesize that *S. yangi* females mitigate the costs of mating and maximize their reproductive success by emitting responding signals from concealed perches and choosing a high-quality male in the first place. This study is a valuable contribution to understanding the mechanisms of sexual selection in cicadas, and to understanding strategies of pair-formation, mate choice, and sexual selection in other animals also suffering selective pressure from predators.

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Authors' Contributions

C.W. and Z.H. conceived and designed the experiments; Z.H., Y.L., and S.W. conducted experiments; Z.H. and Y.L. analyzed the data; and Z.H. and C.W. wrote the manuscript. All authors read and approved the manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.

Ethical Statement

This study did not involve endangered or protected species, and the cicada *S. yangi* used in this study is not included in the "List of Protected Animals in China." Ethical approval is not required for *S. yangi* research, but we took care to reduce any possible suffering by individuals and any impacts to wild populations.

Supplementary Material

"Supplementary material can be found at <https://academic.oup.com/cz>."

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