

Difference in calling song of three field crickets of the genus *Teleogryllus*: the role in premating isolation

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Cricket songs are species-specific signals that are important for species recognition. To prove the effectiveness of calling songs in premating isolation, studies need to take into account closely related species distributed sympatrically in nature. I compared the calling songs of three closely related cricket species that inhabit the Japanese archipelago: *Teleogryllus yezoemma*, *T. emma* and *T. taiwanemma*. *Teleogryllus emma* is widely distributed in the archipelago and overlaps the ranges of *T. taiwanemma* in the south and *T. yezoemma* in the north; *T. yezoemma* and *T. taiwanemma* are allopatric. I compared three temporal parameters (the long-chirp duration, the interphrase duration and the pulse cycle), a frequency parameter (the dominant frequency) and two structural parameters (the number of pulses in one long chirp and the number of short chirps following one long chirp). In addition, I conducted a two-speaker playback experiment using female *T. taiwanemma* to test whether they can accurately distinguish conspecific males based on their calling song. The species with partially overlapping ranges had divergent songs that females could distinguish accurately, whereas the allopatric species had similar songs that females could not accurately discriminate. These results suggest that the calling song has an important role as a premating isolation mechanism.

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Cricket song involves species-specific signals and is important for species recognition (Hill et al. 1972; Doherty & Callos 1991; Gray & Cade 2000). In particular, song has received much attention as a premating isolation mechanism in closely related sympatric species (Otte 1989; Benedix & Howard 1991; Mousseau & Howard 1998). Also of interest is reproductive character displacement, which predicts that after closely related species make secondary contact, differences in their courtship behaviours should be accentuated (Brown & Wilson 1956; Grant 1975; Yoshimura & Starmer 1997; Gerhardt 1999). Much evolutionary research of this type has been conducted on acoustic animal communication (Walker 1974; Wasserman & Koepfer 1977; Benedix & Howard 1991; Loftus-Hills & Littlejohn 1992; Gerhardt 1994; Doherty & Howard 1996; Márquez & Bosch 1997; Littlejohn 1999).

Although song differences might have been important in the speciation that determined current species distributions, it is difficult to describe the speciation events of extant species or transitions in their distribution.

Reinforcement is thought to be the primary process producing the pattern of greater species discrimination in sympatric taxa, but other explanations have been discussed (Noor 1999). For example, only species with different songs may be able to survive in parapatry or sympatry. Although it is impossible to recreate past evolutionary events exactly, data for closely related species, such as current distributions, behavioural differences and phylogenetic relationships, can provide insight into the evolutionary process (Shaw 1996a, b, 1999, 2002).

Five species of field crickets of the genus *Teleogryllus* occur in Japan. Three of these, *T. yezoemma*, *T. emma* and *T. taiwanemma*, are widely distributed within the Japanese archipelago; a fourth species, *T. boninensis*, is restricted to the Bonin Islands, and the fifth, *T. commodus*, was probably introduced into Japan from Australia in recent years. The latter two species are not considered in this paper.

Until 1951, *T. yezoemma*, *T. emma* and *T. taiwanemma* were considered a single species because of their morphological resemblance. However, they differ in the male external genitalia, ovipositor length and the pattern of white markings on the upper margin of the eye (Ohmachi & Matsuura 1951). *Teleogryllus yezoemma* is distributed from Hokkaido Island to the Kanto region; *T. emma* occurs from Hokkaido to the Kyushu region; and *T. taiwanemma*

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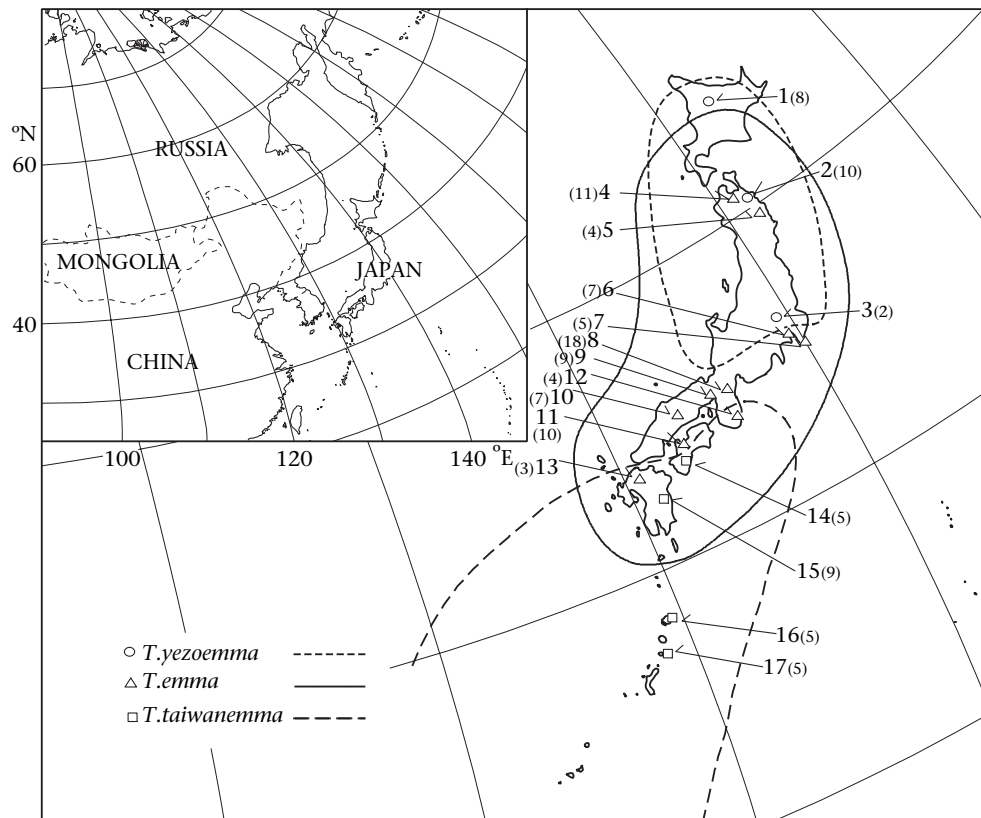


Figure 1. Distribution of the three *Teleogryllus* species in the Japanese archipelago. The symbols indicate the sites where each species was collected. The numbers refers to the collecting site, and the numbers in parentheses indicate the sample size at that site.

is found from south of the Kii Peninsula to the South Asian tropics (Fig. 1). *Teleogryllus emma* is widely distributed within the Japanese archipelago between 30°N and 44°N (Ohmachi & Masaki 1964; Masaki 1966), so the species overlaps with *T. yezoemma* in the north and *T. taiwanemma* in the south. In contrast, *T. yezoemma* and *T. taiwanemma* are allopatric.

Like many crickets, the three species use acoustic signals to communicate, chiefly at night, and only males produce songs. The reproductive seasons of these species partly overlap; although hybrid individuals have not been found in the field, crossbreeding appears possible in the laboratory (Ohmachi & Masaki 1964; Masaki & Ohmachi 1967). These observations suggest that strict reproductive isolation may occur in the field.

The three species have different life cycles: *T. yezoemma* and *T. emma* are univoltine, egg-diapausing species and have short-day photoperiodic responses, whereas *T. taiwanemma* is a multivoltine, juvenile-overwintering species with long photoperiodic responses. Such differences are considered adaptive to their habitat (Ohmachi & Masaki 1964; Masaki & Ohmachi 1967). The results of crossbreeding experiments of the three species plus the tropical species *T. mitratus* suggest that the three species evolved independently and at different times from a nondiapausing tropical ancestor, possibly during multiple glaciations (Masaki & Ohmachi 1967).

Crickets have a repertoire of songs; the three main types are a calling song, a courtship song and an aggressive

song. The male's calling song serves both to attract conspecific mature females and to advertise a male's presence to other males (Alexander 1962). Most studies have examined female preferences for male calling songs (Hill et al. 1972; Hedrick 1986; Brown et al. 1996; Doherty & Howard 1996). In this study I aimed to validate the function of acoustic signals as a premating isolation mechanism. I compared calling songs of the three species and used playback experiments to investigate females' discrimination ability for males' calling songs. To explore the effect of sexual experience on song preference, I conducted playback experiments using both virgin and nonvirgin females.

METHODS

Recording and Analysing the Calling Song

I collected male crickets from natural sites in various parts of Japan between 1997 and 2000: *T. yezoemma* from three sites, *T. emma* from 10 sites and *T. taiwanemma* from four sites (Fig. 1). Male nymphs were reared to adulthood in the laboratory (at $25 \pm 1^\circ\text{C}$, provided with dry insect food and water in cotton-plugged vials) and then their songs were recorded. Each male was placed in a separate plastic cage (12 × 20 cm and 14 cm high) and his calling song (the song produced spontaneously by a solitary male) was recorded for at least 240 s using a DAT recorder

(Sony TCD-D100) and microphone (Sony ECM-G3M). All recordings were made at $25 \pm 1^\circ\text{C}$ to control for temperature, which is known to influence the calling song (Walker 1962; Doherty & Callos 1991).

The calling songs of *T. emma* and *T. taiwanemma* are composed of phrases comprising one long chirp and a series of short chirps. To measure the parameters given below (except for the number of short chirps), I used only the long chirp portion of the phrase. The long chirp and short chirps have been termed simply 'chirp' and 'trill' (Pollack & Hoy 1979; Hennig & Weber 1997), or 'complex chirp' and 'simple chirp' (Hill et al. 1972), respectively. In this study, 'long chirp' refers to a chirp or complex chirp and 'short chirp' to a trill or simple chirp, as in a previous study of *Teleogryllus oceanicus* (Simmons et al. 2001; Zuk et al. 2001). Although a unit with a long chirp and short chirps may be defined as a song, I define it as a phrase, as in Pollack & Hoy (1979), Chow et al. (1990) and Hennig & Weber (1997).

Using the sound analysis program Avisoft SASLab-Pro (Raimund Specht, Berlin, Germany), I analysed 10 phrases from the recording (240 s or more) of each male. I measured several parameters: three temporal parameters (the long-chirp duration, the interphrase duration and the pulse cycle), a frequency parameter (the dominant frequency) and two song structural parameters (the number of pulses in a long chirp and the number of short chirps following a long chirp; Fig. 2). For *T. emma* and *T. taiwanemma*, the interphrase duration was measured as the time between the end of the short chirps and the beginning of the long chirp. Because *T. yezoemma* songs do not have short chirps, the interphrase duration for this species was measured as the time between the end of one long chirp and the beginning of the next. The mean value of each parameter was used to represent the male's song. Since modulation of pulse duration within a long chirp was detected, the last three pulse periods of a long chirp were also measured and used to calculate the pulse repetition rate (pulse cycle).

I analysed calling songs of 20 *T. yezoemma* males, 78 *T. emma* males and 24 *T. taiwanemma* males. For each parameter I used a nested analysis of variance (nested ANOVA) with species as the grouping factor and population nested within species. To examine song differences between the three species on the basis of the combined effect of the six measured parameters, I also used a principal components analysis (PCA) for long-chirp duration, interphrase duration, dominant frequency, number of pulses, number of short chirps and pulse cycle.

For calling songs of *T. emma* males only, I compared areas (sympatric with *T. yezoemma*, allopatric area and sympatric with *T. taiwanemma*) using a nested ANOVA with population nested within areas.

Playback Experiment

Forty *T. taiwanemma* females were collected as nymphs in autumn 1999 from populations isolated from congeners on three islands in the Japanese archipelago (Amamiyoshima, Tokunoshima and Okinoerabujima Islands).

Twenty females (virgins) were separated from males before their final moult, and the other 20 (probably nonvirgins) were reared with males until the playback experiment. Females were used in playback trials 2 weeks or more after emergence.

The playback stimuli were the calling songs of one male of each species (Fig. 2). Each song was 1-kHz high-pass filtered and then recorded on a stereo cassette (Panasonic RQ-SX30). Discriminant analysis of the calling songs of the three species based on six parameters (long-chirp duration, interphrase duration, dominant frequency, number of pulses, number of short chirps and pulse cycle) indicated that the song stimuli used were distinct and characteristic of each species.

Playback trials were conducted on a platform (120×180 cm and 70 cm high) in a laboratory maintained at $25 \pm 1^\circ\text{C}$ under red light from 2100 to 0500 hours. Two loudspeakers were placed 150 cm apart and two calling songs were broadcast simultaneously, one from each speaker. Before each trial, the peak sound pressure levels (SPL) of each calling song were equalized to 72.2 ± 1.2 dB at 75 cm from the speaker with a sound level meter (Brüel & Kjær 2236D). I conducted three trials per female per night: songs were played in the following pairs (*T. taiwanemma* versus *T. emma*, *T. taiwanemma* versus *T. yezoemma* and *T. yezoemma* versus *T. emma*) in random order. The speaker from which each song was broadcast was also randomized.

Each female was kept alone in a silent room for at least 2 days before each set of trials. Each trial began with the release of the female from the release point (90 cm from the two speakers). Before the trial, the female was kept under a cup inverted on a circular pad (13 cm diameter) for at least 1 h in a dark, soundproof box. I then placed the circular pad together with the cup containing the female at the release point and allowed the female at least 5 min to settle down. I then removed the cup and playback began after 20 s, provided that the female stayed on the circular pad. The playback continued until the female approached one speaker and remained within 1 cm of the speaker for at least 3 min. If 30 min passed without the female approaching either speaker or the female fell off the platform, the trial was aborted. The song from the speaker that each female first approached in each trial was regarded as being preferred; trials in which females did not show clear positive phonotaxis were excluded from the analyses. The interval between trials was at least 70 min per female. During the trials, the female was provided only with water. After each trial, I wiped the surface of the platform with wet tissue paper.

RESULTS

Comparison of Songs between Species

There were several clear differences between the three species (nested ANOVA: long-chirp duration: $F_{2,14} = 147.97$, $P < 0.001$; interphrase duration: $F_{2,14} = 17.532$, $P < 0.001$; dominant frequency: $F_{2,14} = 43.702$, $P < 0.001$; number of pulses: $F_{2,14} = 45.284$, $P < 0.001$;

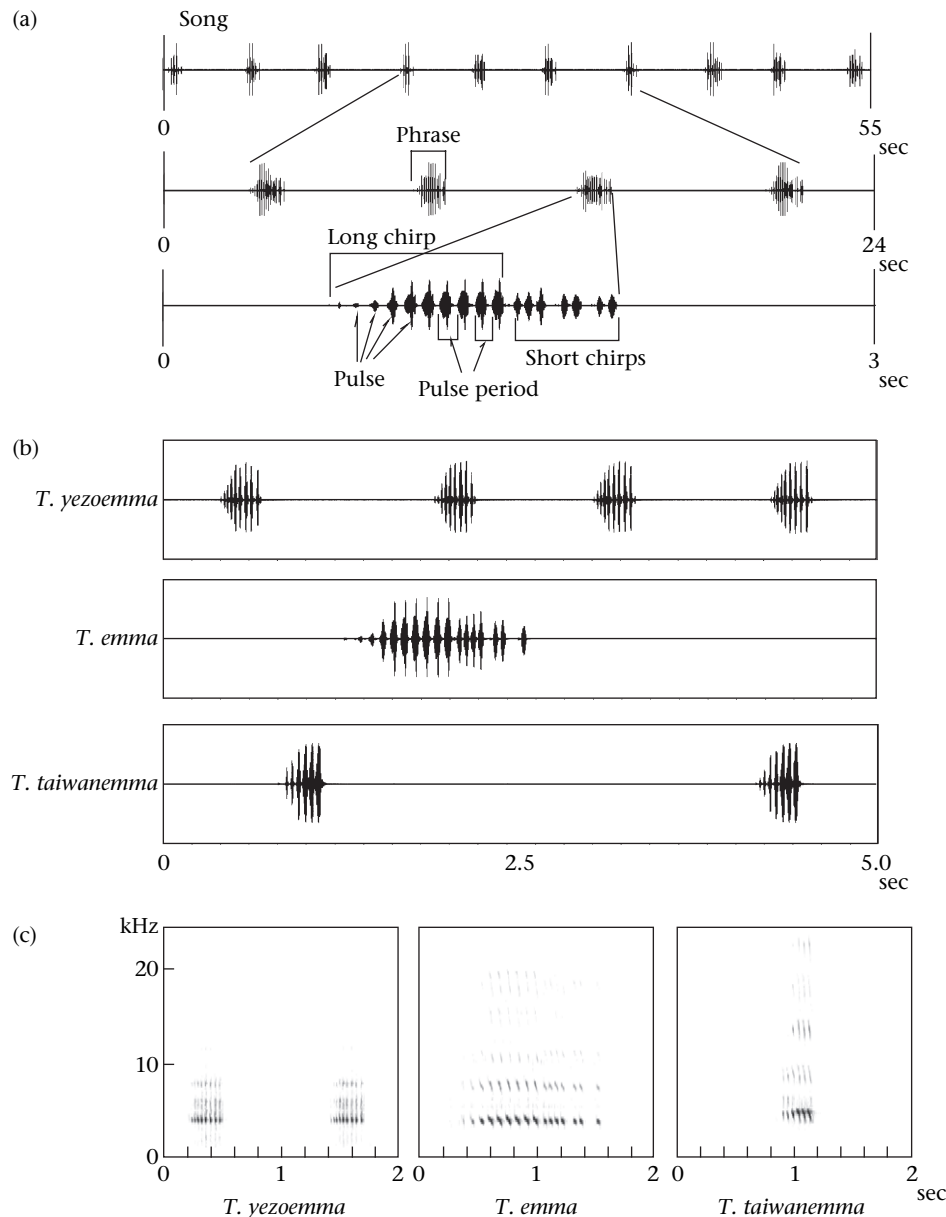


Figure 2. (a) Song structure and the temporal parameters used in the analyses using the *T. emma* calling song. A song is composed of several phrases, a phrase is composed of one long and several short chirps and chirps consist of several pulses. Pulse period is between the beginning of one pulse and the beginning of the next. Pulse period was used to calculate the pulse cycle as 1 s per pulse period. (b) Representative calling song waveforms of the three *Teleogryllus* species. (c) Representative sonograms of one phrase of the three *Teleogryllus* species calling songs. All songs were recorded at $25 \pm 1^\circ\text{C}$.

number of short chirps: $F_{2,14} = 7.309$, $P < 0.01$; pulse cycle: $F_{2,14} = 827.677$, $P < 0.001$; Fig. 3).

Of three temporal parameters, long-chirp duration and interphrase duration differed significantly both between *T. emma* and *T. taiwanemma* and between *T. emma* and *T. yezoemma* (post hoc Scheffé test: $P < 0.05$). Pulse cycle differed significantly in all pairings of the three species (post hoc Scheffé test: $P < 0.05$). Temporal parameters differed most between *T. emma* and each of the other two species. Dominant frequency differed significantly between *T. emma* and *T. taiwanemma*, and between *T. yezoemma* and *T. taiwanemma* (post hoc Scheffé test:

$P < 0.05$). Only *T. taiwanemma* had a song with a high frequency. The number of pulses in a long chirp differed significantly in all pairings of the three species (post hoc Scheffé test: $P < 0.05$). The number of short chirps also differed between the three species, significantly so between *T. emma* and each of the other two species (post hoc Scheffé test: $P < 0.05$).

The first two components of the PCA (PC1 and PC2) accounted for 73% of the total variation (Table 1, Fig. 4). The PC1 scores showed significant differences between the three *Teleogryllus* species (Kruskal–Wallis test: $H_2 = 84.4$, $P < 0.001$); they did not differ significantly between

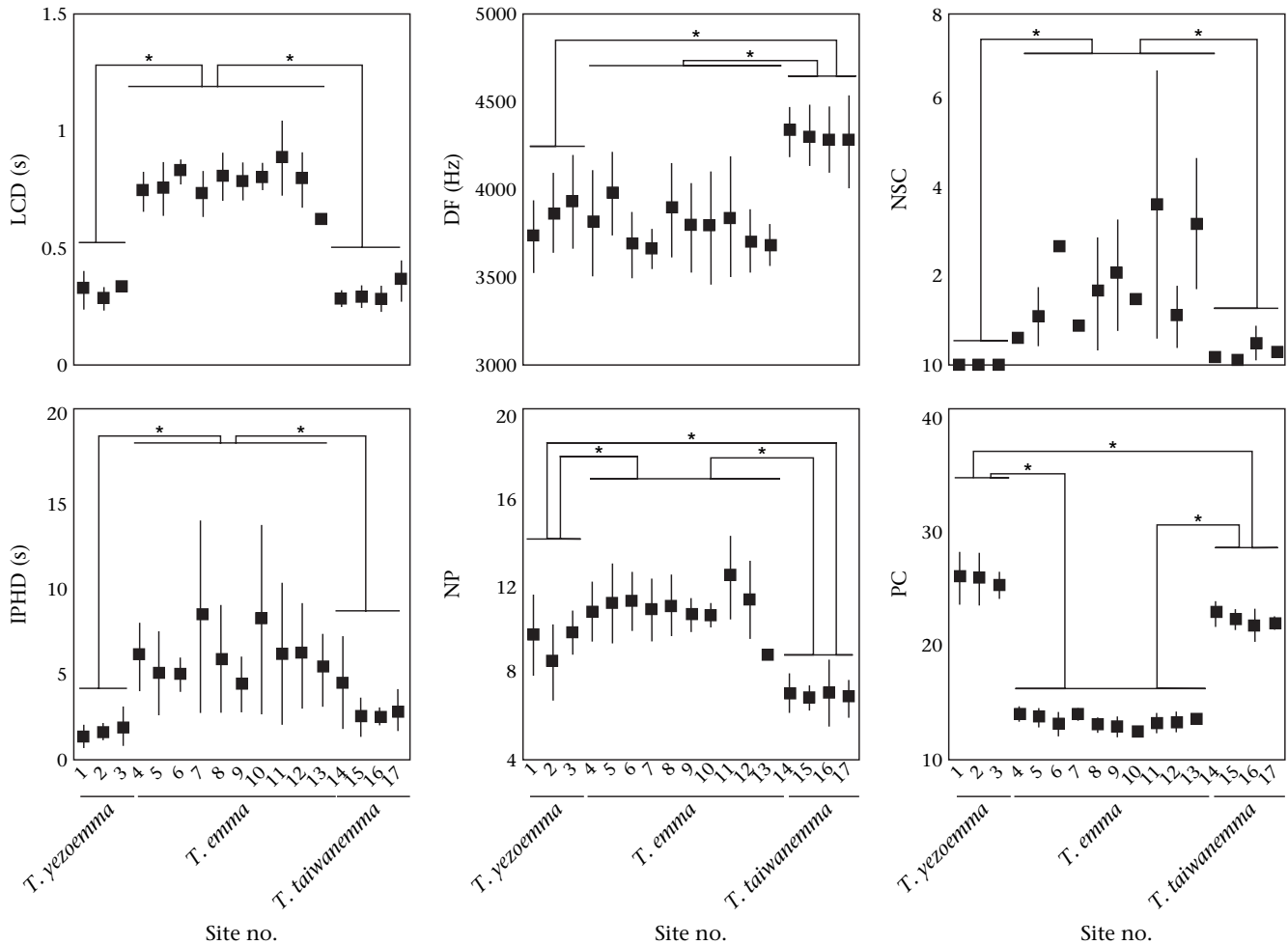


Figure 3. Comparison of six parameters in the three *Teleogryllus* species. Means are shown \pm SD. * $P < 0.05$; post hoc Scheffé test.

T. yezoemma and *T. taiwanemma*, but did between *T. emma* and each of the other two species (Scheffé test: $P < 0.05$).

No parameter of *T. emma* calling song differed significantly between areas (nested ANOVA: long-chirp duration: $F_{2,7} = 2.338$, $P = 0.143$; interphrase duration: $F_{2,7} = 0.301$, $P = 0.745$; dominant frequency: $F_{2,7} = 1.574$,

Table 1. Principal component loadings

Variable	Principal components	
	1	2
Long-chirp duration	-0.963	0.028
Interphrase duration	-0.606	-0.649
Dominant frequency	0.550	0.028
Number of pulses	-0.835	-0.011
Number of short chirps	-0.498	0.781
Pulse cycle	0.907	-0.003
Eigenvalue	3.37	1.03
Cumulative total variance (%)	56.1	73.3

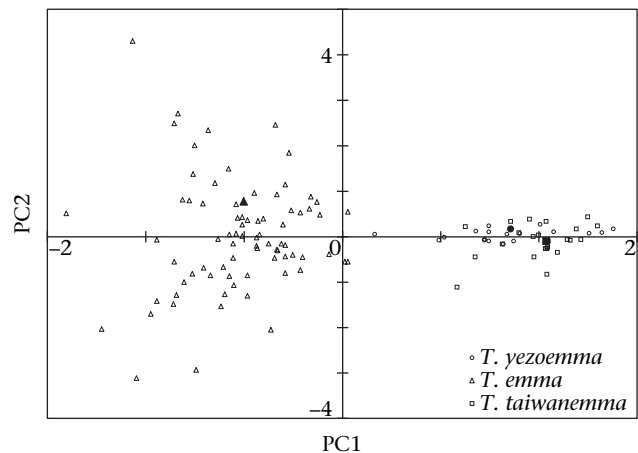


Figure 4. Results of the principal components analysis (PCA) based on six parameters (long-chirp duration, interphrase duration, dominant frequency, number of pulses, number of short chirps, pulse cycle). Solid marks indicate the calling song used as the stimulus in the playback experiments.

Table 2. Results of the playback experiment with *T. taiwanemma* females given a choice of a conspecific and a heterospecific song or two heterospecific songs

<i>T. taiwanemma</i>		<i>T. emma</i>	<i>T. yezoemma</i>	No choice	<i>p</i> *
<i>T. taiwanemma</i> versus <i>T. emma</i>					
Virgin	15	2	—	3	0.796
Nonvirgin	13	3	—	4	
<i>T. taiwanemma</i> versus <i>T. yezoemma</i>					
Virgin	14	—	6	0	0.292
Nonvirgin	11	—	6	3	
<i>T. emma</i> versus <i>T. yezoemma</i>					
Virgin	—	2	10	8	1.000
Nonvirgin	—	2	9	9	

N = 20 virgin and 20 nonvirgin females. Each female was used in three trials for each species comparison.

*Fisher's exact test comparing virgin and nonvirgin females.

$P = 0.235$; number of pulses: $F_{2,7} = 0.947$, $P = 0.419$; number of short chirps: $F_{2,7} = 1.235$, $P = 0.330$; pulse cycle: $F_{2,7} = 2.726$, $P = 0.107$). For the numbers of pulses and short chirps, there were significant effects for populations nested within areas (number of pulses: $F_{7,68} = 2.330$, $P = 0.034$; number of short chirps: $F_{7,68} = 2.242$, $P = 0.041$).

Female Response to Calling Song

In 49 of the 60 trials with virgin females and in 44 of the 60 trials with probable nonvirgin females, females showed positive phonotaxis. Although the speaker that the female approached first differed from the speaker near which the female remained for at least 3 min in four of the 93 trials, the song from the speaker that each female approached first in each trial was regarded as preferred in this analysis.

Both virgin and nonvirgin *T. taiwanemma* females preferred the conspecific song (Table 2). Furthermore, there was no difference in the reaction times of the virgin and nonvirgin females (Table 3). Since sexual experience did not appear to affect female preference, I combined the data for virgin and nonvirgin females (Fig. 5). In

playbacks of *T. taiwanemma* and *T. emma* songs, 28 of 33 females preferred the *T. taiwanemma* song (binominal test: $P < 0.001$). In playbacks of *T. taiwanemma* and *T. yezoemma* songs, 25 of 37 females preferred the *T. taiwanemma* song (binominal test: $P < 0.05$). In playbacks of *T. emma* and *T. yezoemma*, neither of which was conspecific to the females, 19 of 23 females preferred the *T. yezoemma* song (binominal test: $P < 0.01$).

DISCUSSION

My results show similarities and differences in the calling songs of three *Teleogryllus* species that are distributed across the Japanese Archipelago. Multivariate analysis showed that the sympatric species *T. yezoemma* and *T. emma*, and *T. emma* and *T. taiwanemma*, have divergent songs and that the allopatric species, *T. yezoemma* and *T. taiwanemma*, have similar songs. These differences in song between sympatric species and between allopatric species probably reflect differences in the need for species discrimination.

Teleogryllus emma and *T. taiwanemma* are partially sympatric and sometimes reproduce synchronously, but

Table 3. Reaction times of virgin and nonvirgin *T. taiwanemma* females

	Playback stimuli		
	<i>T. taiwanemma</i> versus <i>T. emma</i>	<i>T. taiwanemma</i> versus <i>T. yezoemma</i>	<i>T. emma</i> versus <i>T. yezoemma</i>
Time to departure*			
Virgin	92.06 ± 104.10 (17)	104.55 ± 172.86 (20)	138.25 ± 88.07 (12)
Nonvirgin	96.06 ± 74.98 (16)	74.56 ± 84.95 (18)	94.18 ± 63.56 (11)
<i>U</i>	106.5	125.5	45.0
<i>P</i>	0.288	0.111	0.323
Time to reach speaker†			
Virgin	74.47 ± 60.35 (17)	121.85 ± 164.92 (20)	134.08 ± 153.72 (12)
Nonvirgin	70.25 ± 38.42 (16)	83.94 ± 52.91 (18)	49.36 ± 33.82 (11)
<i>U</i>	130.5	173.5	44
<i>P</i>	0.843	0.850	0.176

Means are given ± SD, with sample sizes in parentheses. Reaction times are compared with a Mann–Whitney *U* test.

*Time to move from circular pad (release point) after playback began.

†Time to arrival at the speaker after starting from release point.

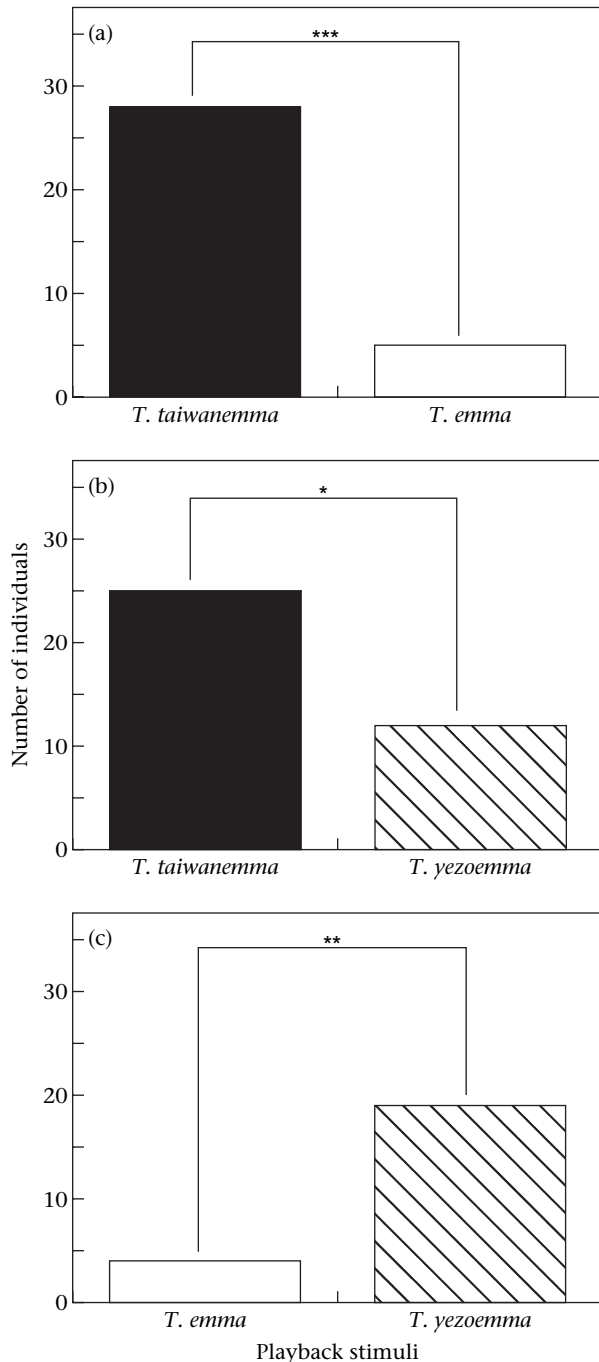


Figure 5. The results of playback experiments using *T. taiwanemma* females (virgin and probable nonvirgin females combined). The bars show the number of females that chose the song first in each two-choice experiment. Calling songs were played back in the following pairs: (a) *T. taiwanemma* versus *T. emma*, (b) *T. taiwanemma* versus *T. yezoemma* and (c) *T. emma* versus *T. yezoemma*, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (binomial test).

no hybrid has been found in nature. Although *T. emma* and *T. taiwanemma* can be crossed by mass-stress mating in the laboratory, most male nymphs develop slowly and fail to mature, and few female adults produce mature eggs (Ohmachi & Masaki 1964; Masaki & Ohmachi 1967).

Producing F_2 offspring from hybrid adults is also difficult. *Teleogryllus yezoemma* and *T. emma* have similar life cycles, but different karyotypes (*T. yezoemma* $2N = 25$, *T. emma* $2N = 27$, *T. taiwanemma* $2N = 27$). Where hybridization has a cost, songs can be an effective premating isolation mechanism if they are sufficiently different that females can consistently distinguish conspecific males from sympatric males. My results support the idea that the calling song functions as a premating isolation mechanism between *T. emma* and *T. taiwanemma*. The songs of *T. emma* and *T. taiwanemma* were significantly different in all six parameters and sufficiently different to allow *T. taiwanemma* females to distinguish them accurately.

The calling songs of the allopatric species *T. yezoemma* and *T. taiwanemma* had similar temporal parameters (except pulse cycle), although they differed significantly in dominant frequency, pulse number and pulse cycle. The pulse cycle differed significantly in all pairings of the three species, but was more similar in *T. yezoemma* and *T. taiwanemma* than in *T. emma* and the other two species. Studies of acoustic animal communication have shown that temporal patterns are more important than frequency parameters for song recognition (Benett-Clark & Ewing 1969; Hill et al. 1972; Pollack & Hoy 1979; Wells & Henry 1992; Balakrishnan & Pollack 1996; Henry et al. 1999). Neurobiological data for crickets support these results (Schildberger et al. 1989). My playback experiments using nonconspecific *T. emma* and *T. yezoemma* suggest that female *T. taiwanemma* find the *T. yezoemma* song similar to the conspecific song, which in turn suggests that female crickets discriminate the male song mainly using temporal parameters.

The long chirp is more important than the short chirp for species recognition and female choice in *T. oceanicus* (Balakrishnan & Pollack 1996; Hennig & Weber 1997; Simmons et al. 2001; Zuk et al. 2001). However, *T. taiwanemma* females have responded to short chirps in playback experiments, and they seem to have separate temporal filters for long and short chirps (Honda-Sumi 2004), as does the Australian field cricket *T. commodus* (Hennig & Weber 1997). Although *Teleogryllus* species have complex songs that combine two temporal patterns (Otte & Alexander 1983; Otte 1992), the calling song of *T. yezoemma* lacks short chirps. The variation in short chirps in the songs of the three Japanese *Teleogryllus* species is of interest from the standpoint of the evolution of song differentiation.

Analysis of mitochondrial DNA (mtDNA) suggests that *T. taiwanemma* is a sister species to *T. emma*, but not to *T. yezoemma*, despite the similarity of their songs (E. Honda-Sumi & T. Sota, unpublished data). Therefore, the similarity of the calling songs and the females' inaccurate discrimination ability are not due to sister-species status. Although character similarities among species are thought to reflect the maintenance of ancestral characters and close phylogenetic relationships (Tomaru & Oguma 1994; Harrison & Bogdanowicz 1995; Huang et al. 2000), song may be an exception. Song is a mating signal and should serve as a premating isolation barrier (Wells & Henry 1998; Henry et al. 1999), especially among closely related sympatric species, whose specific mate

recognition systems should differ greatly. The calling song of *T. emma*, which differed significantly from those of the other two related species, did not differ significantly in the areas where it is sympatric with *T. yezoemma*, allopatric, or sympatric with *T. taiwanemma*. This suggests that the most divergent song of *T. emma* has not been produced as a result of secondary contact with the other two species in the Japanese archipelago. The differences in calling song and mtDNA in these three species may support the hypothesis of independent tropical origin and subsequent colonization in Japan for the three species (Masaki & Ohmachi 1967).

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References

- Alexander, R. D. 1962. Evolutionary change in cricket acoustical communication. *Evolution*, **16**, 443–467.
- Balakrishnan, R. & Pollack, G. S. 1996. Recognition of courtship song in the field cricket, *Teleogryllus oceanicus*. *Animal Behaviour*, **51**, 353–366.
- Benedix, J. H., Jr. & Howard, D. J. 1991. Calling song displacement in a zone of overlap and hybridization. *Evolution*, **45**, 1751–1759.
- Benett-Clark, H. C. & Ewing, A. W. 1969. Pulse interval as a critical parameter in the courtship song of *Drosophila melanogaster*. *Animal Behaviour*, **17**, 755–759.
- Brown, W. D., Wideman, M. C. B., Mason, A. C. & Gwynne, D. T. 1996. Female choice for an indicator of male size in the song of the black-horned cricket, *Oecanthus nigricorinis* (Orthoptera: Gryllidae: Oecanthinae). *Evolution*, **50**, 2400–2411.
- Brown, W. L. & Wilson, E. O. 1956. Character displacement. *Systematic Zoology*, **5**, 49–64.
- Chow, Y. S., Chieng, C. I., Tsai, R. S. & Kou, R. 1990. Acoustic analysis in Taiwan cricket *Teleogryllus taiwanemma* (Orthoptera: Gryllidae). *Chinese Journal of Entomology*, **10**, 201–208.
- Doherty, J. A. & Callos, J. D. 1991. Acoustic communication in the trilling field cricket, *Gryllus rubens* (Orthoptera: Gryllidae). *Journal of Insect Behavior*, **4**, 67–82.
- Doherty, J. A. & Howard, D. J. 1996. Lack of preference for conspecific calling songs in female crickets. *Animal Behaviour*, **51**, 981–990.
- Gerhardt, H. C. 1994. Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. *Animal Behaviour*, **47**, 959–969.
- Gerhardt, H. C. 1999. Reproductive character displacement and other sources of selection on acoustic communication systems. In: *The Design of Animal Communication* (Ed. by M. Hauser & M. Konishi), pp. 515–534. Cambridge, Massachusetts: MIT Press.
- Grant, P. R. 1975. The classical case of character displacement. *Evolutionary Biology*, **8**, 237–337.
- Gray, D. A. & Cade, W. H. 2000. Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 14449–14454.
- Harrison, R. G. & Bogdanowicz, S. M. 1995. Mitochondrial DNA phylogeny of North American field crickets: perspectives on the evolution of life cycles, songs, and habitat associations. *Journal of Evolutionary Biology*, **8**, 209–232.
- Hedrick, A. V. 1986. Female preferences for male calling bout duration in a field cricket. *Behavioral Ecology and Sociobiology*, **19**, 73–77.
- Hennig, R. M. & Weber, T. 1997. Filtering of temporal parameters of the calling song by cricket females of two closely related species: a behavioral analysis. *Journal of Comparative Physiology A*, **180**, 621–630.
- Henry, C. S., Wells, M. L. M. & Simon, C. M. 1999. Convergent evolution of courtship songs among cryptic species of the *Carnea* group of green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). *Evolution*, **53**, 1165–1179.
- Hill, K. G., Loftus-Hills, J. J. & Gartside, D. F. 1972. Pre-mating isolation between the Australian field crickets *Teleogryllus commodus* and *T. oceanicus* (Orthoptera: Gryllidae). *Australian Journal of Zoology*, **20**, 153–163.
- Honda-Sumi, E. 2004. Female recognition of trills in the male calling song of the field cricket, *Teleogryllus taiwanemma*. *Journal of Ethology*, **22**, 135–141.
- Huang, Y., Orti, G., Suthelin, M., Dubachek, A. & Zera, A. 2000. Phylogenetic relationships of North American field crickets inferred from mitochondrial DNA data. *Molecular Phylogenetics and Evolution*, **17**, 48–57.
- Littlejohn, M. J. 1999. Variation in advertisement calls of anurans across zonal interactions: the evolution and breakdown of homogamy. In: *Geographic Variation in Behavior* (Ed. by S. A. Foster & J. A. Endler), pp. 209–233. New York: Oxford University Press.
- Loftus-Hills, J. J. & Littlejohn, M. J. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura: Microhylidae): a reexamination. *Evolution*, **46**, 896–906.
- Márquez, R. & Bosch, J. 1997. Male advertisement call and female preference in sympatric and allopatric midwife toads. *Animal Behaviour*, **54**, 1333–1345.
- Masaki, S. 1966. Geographic variation and climatic adaptation in a field cricket (Orthoptera: Gryllidae). *Evolution*, **21**, 725–741.
- Masaki, S. & Ohmachi, F. 1967. Divergence of photoperiodic response and hybrid development in *Teleogryllus* (Orthoptera: Gryllidae). *Konchu*, **35**, 83–105.
- Mousseau, T. A. & Howard, D. J. 1998. Genetic variation in cricket calling song across a hybrid zone between two sibling species. *Evolution*, **52**, 1104–1110.
- Noor, M. A. F. 1999. Reinforcement and other consequences of sympatry. *Heredity*, **83**, 503–508.
- Ohmachi, F. & Masaki, S. 1964. Interspecific crossing and development of hybrids between the Japanese species of *Teleogryllus* (Orthoptera: Gryllidae). *Evolution*, **18**, 405–416.
- Ohmachi, F. & Matsuura, I. 1951. On the Japanese large field cricket and its allied species. *Bulletin of the Faculty of Agriculture, Mie University*, **2**, 63–72.
- Otte, D. 1989. Speciation in Hawaiian crickets. In: *Speciation and Its Consequences* (Ed. by D. Otte & J. Endler), pp. 482–526. Sunderland, Massachusetts: Sinauer.
- Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research*, **1**, 25–46.
- Otte, D. & Alexander, R. D. 1983. The Australian crickets. *Academy of Natural Sciences of Philadelphia Monograph*, **22**, 1–477.

- Pollack, G. S. & Hoy, R. R. 1979. Temporal patterns as a cue for species-specific calling song recognition. *Science*, **204**, 429–432.
- Schildberger, K., Huber, F. & Wohlers, D. W. 1989. Central auditory pathway: neuronal correlates of phonotactic behaviour. In: *Cricket Behavior and Neurobiology* (Ed. by F. Huber, T. E. Moore & W. Loher), pp. 423–459. Ithaca, New York: Cornell University Press.
- Shaw, K. L. 1996a. Sequential radiations and patterns of speciation in the Hawaiian cricket genus *Laupala* inferred from DNA sequences. *Evolution*, **50**, 237–255.
- Shaw, K. L. 1996b. Polygenic inheritance of a behavioral phenotype: interspecific genetics of song in the Hawaiian cricket genus *Laupala*. *Evolution*, **50**, 256–266.
- Shaw, K. L. 1999. A nested analysis of song groups and species boundaries in the Hawaiian cricket genus *Laupala*. *Molecular Phylogenetics and Evolution*, **11**, 332–341.
- Shaw, K. L. 2002. Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: what mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 16122–16127.
- Simmons, L. W., Zuk, M. & Rotenberry, J. T. 2001. Geographic variation in female preference functions and male songs of the field cricket *Teleogryllus oceanicus*. *Evolution*, **55**, 1386–1394.
- Tomaru, M. & Oguma, Y. 1994. Differences in courtship song in the species of the *Drosophila auraria* complex. *Animal Behaviour*, **47**, 133–140.
- Walker, T. J. 1962. Factors responsible for intraspecific variation in the calling songs of crickets. *Evolution*, **16**, 407–428.
- Walker, T. J. 1974. Character displacement and acoustic insects. *American Zoologist*, **14**, 1137–1150.
- Wasserman, M. & Koepfer, H. R. 1977. Character displacement for sexual isolation between *Drosophila mojavensis* and *Drosophila arizonensis*. *Evolution*, **31**, 812–823.
- Wells, M. M. & Henry, C. S. 1992. Behavioural responses of green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*) to synthetic mating songs. *Animal Behaviour*, **44**, 641–652.
- Wells, M. M. & Henry, C. S. 1998. Songs, reproductive isolation, and speciation in cryptic species of insects. In: *Endless Forms* (Ed. by D. J. Howard & S. H. Berlocher), pp. 217–233. Oxford: Oxford University Press.
- Yoshimura, J. & Starmer, W. T. 1997. Speciation and evolutionary dynamics of asymmetric mating preference. *Researches on Population Ecology*, **39**, 191–200.
- Zuk, M., Rotenberry, J. T. & Simmons, L. W. 2001. Geographical variation in calling song of the field cricket *Teleogryllus oceanicus*: the importance of spatial scale. *Journal of Evolutionary Biology*, **14**, 731–741.