JEFB Journal of
Ecology and Field Biology

Calling song and phonotactic selectivity in the field cricket *Teleogryllus emma* (Orthoptera: Gryllidae)

Soojin Jang, Hyon-Gyong An and Yikweon Jang[*]

Division of EcoScience, Ewha University, Seoul 120-750, Korea

Males of the field cricket *Teleogryllus emma* produce calling songs that are attractive to receptive females. The calling songs of *T. emma* consist of two components, the long chirp that is composed of up to 12 single pulses, followed by a variable number of short chirps. Based on the analysis of coefficient of variation (CV), temporal characters of the long chirp were less variable than those of the short chirps in male calling songs. To test for phonotactic selectivity of females, we conducted a single-stimulus playback experiment in which five stimuli (standard, long chirp only, long chirp augmented, short chirps only, and short chirps augmented) were used. The standard stimulus included both long and short chirps whose characteristics were derived from the calling songs of field populations. Results of the playback experiment showed that female crickets oriented more frequently toward the stimuli that included the long chirp (standard, long chirp only, and long chirp augmented stimuli) than toward the stimuli lacking the long chirp (short chirps only and short chirps augmented stimuli), indicating that the long chirp in the calling songs was required to elicit positive phonotaxis in the female crickets. The result of CV analysis of the male calling songs and the findings of the female phonotaxis experiment suggested that the long chirp of calling songs may play a role in species recognition in *T. emma*.

Key words: coefficient of variation, geographic variation, playback experiment, species recognition

INTRODUCTION

The mating behavior of a cricket species typically consists of production of male calling song and female phonotaxis (Alexander 1962, Huber and Thorson 1985, Zuk and Simmons 1997). The primary function of such long-range mating behavior is that the male and female of a species come together to mate. Upon coming together, the male and female engage in close-range mating behaviors including antennal contact, courtship song, and mounting (Loher and Dambach 1989, Adamo and Hoy 1994, Jang et al. 2007). Acoustic communication studies, especially on species in areas of sympatry, have revealed that the long-range calling songs of many crickets are species-specific (Alexander 1962, Gerhardt and Huber 2002, Greenfield 2002). Furthermore, females prefer

the songs of conspecifics over those of heterospecifics (Doherty and Callos 1991, Hennig and Weber 1997, Gray and Cade 2000). However, calling songs can also be used in the context of sexual selection, in that females discriminate among males on the basis of certain properties of calling songs for mating (Ritchie et al. 1995, Price 1998, Ferreira and Ferguson 2002, Klappert and Reinhold 2003).

The calling song characters primarily used for species recognition are less likely to vary within and among individuals. The female preference functions associated with species recognition may be stabilizing or "unimodal," such that females prefer males with intermediate values of calling song characters (Butlin et al. 1985, Ewing and

Miyan 1986, Ferreira and Ferguson 2002, Klappert and Reinhold 2003, Saarikettu et al. 2005). When other calling song characters are used for mate selection, however, the intermale variability of these characters is typically higher than that of calling song characters used for species recognition. Female preference functions associated with the mate selection context are frequently directional or "open-ended," such that females prefer males with extreme values of calling song characters (Ritchie 1996, Shaw and Herlihy 2000).

Based on within-male variability, which was expressed as the coefficient of variation (CV), Gerhardt (1991) identified static and dynamic characters in male advertisement signals. Static characters change relatively little within and between males in natural populations, and the CV values for static characters are typically lower than 5% (Gerhardt 1991). On the other hand, dynamic characters whose CV values are higher than 12% are more variable within males and between males. The expectation that selection from female choice is stabilizing or weakly directional for static characters and is directional for dynamic characters has been largely confirmed in the North American tree frog species *Hyla versicolor* and *H. cinerea* (Gerhardt 1991) and in the Hawaiian cricket *Laupala cerasina* (Shaw and Herlihy 2000). However, females exerted stabilizing selection on pulse-repetition rate and directional selection on dominant frequency in *H. ebraccata*, and both male call characters were static (Wollerman 1998).

The Emma field cricket, *Teleogryllus emma* Ohmachi & Matsuura (Orthoptera: Gryllidae), is widely distributed throughout Korea, Japan, and China. In the Korean peninsula, *T. emma* and *T. yezoemma* are known to occur together. However, *T. yezoemma* is hardly found, as compared to the widespread distribution of *T. emma*. In the Japanese Archipelago, the distribution of *T. emma* overlaps the ranges of *T. taiwanemma* in the south and *T. yezoemma* in the north. These three species differ in characteristics of calling songs (Honda-Sumi 2004, 2005) as well as other morphological characteristics such as male external genitalia, ovipositor length, and the pattern on the upper part of the eye (Ohmachi and Matsuura 1951). Although hybrid individuals have not been found in nature, crossbreeding among these three species was possible in the laboratory (Ohmachi and Masaki 1964, Masaki and Ohmachi 1967). Here we measured geographic variation in male calling songs of *T. emma* across seven localities in Korea. We hypothesized that calling song characters with low variability may be critical for species recognition. Then, such calling song characters should elicit positive

phonotaxis by females, a necessary condition for species recognition. This prediction was tested with a playback experiment in which a series of manipulated broadcast signals were presented to *T. emma* females.

MATERIALS AND METHODS

Sampling localities

The habitats of *T. emma* include grasslands, farms, and hills. In Korea, *T. emma* undergoes one generation per year in the field, overwintering in the egg stage and maturing to adulthood between August and October. *T. emma* can be readily distinguished by a V-shaped white marking on the forehead. We recorded calling songs of *T. emma* from seven localities between August and September in 2005. The recording localities were Ganghwa,
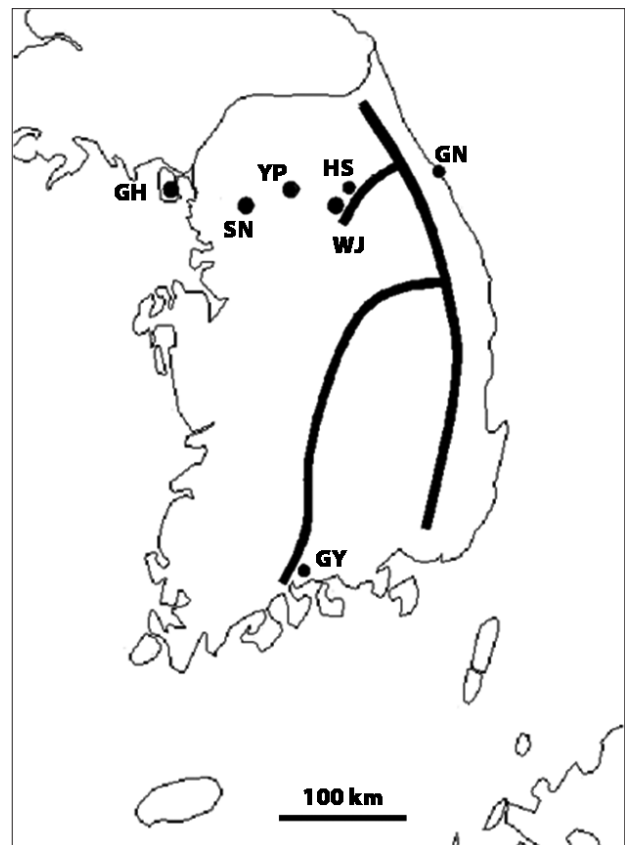

Fig. 1. Collecting and recording localities of *Teleogryllus emma*. Calling songs were recorded in seven localities: Ganghwa, Incheon (GH), Seongnam, Gyeonggi-do (SN), Yangpyeong, Gyeonggi-do (YP), Wonju, Gangwon-do (WJ), Hoengseong, Gangwon-do (HS), Gangneung, Gangwon-do (GN), and Gwangyang, Jeollanam-do (GY). Thick lines indicate major mountain ranges in Korea.

Incheon (GH, 9), Seongnam, Gyeonggi-do (SN, 8), Yang-pyeong, Gyeonggi-do (YP, 10), Hoengseong, Gangwon-do (HS, 4), Gangneung, Gangwon-do (GN, 17), Wonju, Gangwon-do (WJ, 12), and Gwangyang, Jeollanam-do (GY, 5) (Fig. 1). The parentheses above are abbreviations of the locality and the total number of recordings for that locality. One male cricket contributed to only one record-ing. Calling songs were recorded in the field using a tie-clip microphone (TCM 110; In Young Electron Co., Ltd., Taipei, Taiwan; flat frequency response from 50 to 18,000 Hz). We placed the microphone as close as possible to a singing male and recorded his calling song for more than 50 s. Output from the microphone was fed into a DAT re-corder (PCM-M1; Sony Corp., Tokyo, Japan) at a sampling rate of 44.1 kHz. The temperature near the calling male was noted using a HOBO data logger (H08-004-02; Onset Computer Corp., Pocasset, MA, USA).

Analysis of calling songs

Cricket calling songs were analyzed using Raven ver. 1.2 software (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Frequencies below 1 kHz were filtered out to reduce background noise. We analyzed 12 consecutive phrases from each recording for statistical analyses. The calling song of *T. emma* consisted of a series of phrases, each comprised of one long chirp followed by a variable number of short chirps (Fig. 2). We measured the begin-nings and ends of all pulses in the 12 phrases of each recording and calculated the values of the following 12 calling song characters: long chirp carrier frequency (LCCF), long chirp pulse duration (LCPD), long chirp pulse period (LCPP), long chirp pulse number (LCPN),
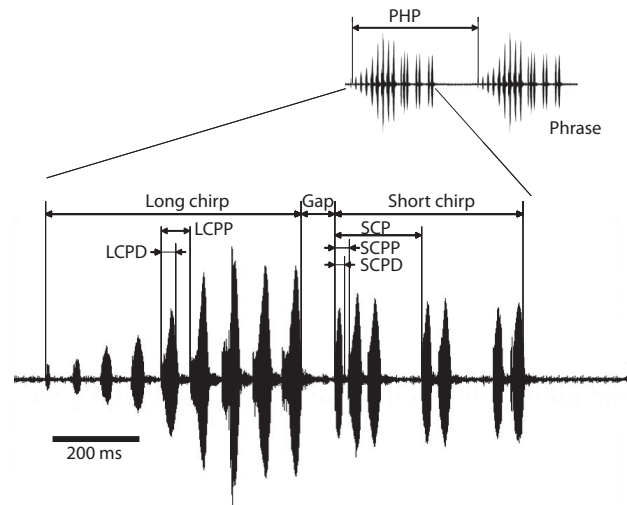

Fig. 2. Oscillogram of a typical calling song of *Teleogryllus emma*. PHP, phrase period; LCPP, long chirp pulse period; LCPD, long chirp pulse dura-tion; SCP, short chirp period; SCPP, short chirp pulse period; SCPD, short chirp pulse duration.

short chirp carrier frequency (SCCF), short chirp pulse duration (SCPD), short chirp period (SCP), short chirp pulse period (SCPP), short chirp pulse number per chirp (SCPNC), short chirp pulse number (SCPN), Gap, and phrase period (PHP). See Fig. 2 and Table 1 for definitions of these calling song characters. LCCF and SCCF were spectral characters, and all others were temporal char-acters. The definitions of calling song characters follow Bennet-Clark (1989).

Laboratory rearing

For the phonotaxis experiment, final-stage juvenile

Table 1. Definitions of calling song characters of *Teleogryllus emma*

Calling song character	Definition
Long chirp carrier frequency (LCCF)	The frequency with the most acoustic energy in the long chirp
Long chirp pulse duration (LCPD)	The time between the start and the end of a pulse in the long chirp
Long chirp pulse period (LCPP)	The time between the start of one pulse and the start of the subsequent pulse in the long chirp
Long chirp pulse number (LCPN)	The total number of pulses in the long chirp
Short chirp carrier frequency (SCCF)	The frequency with the most acoustic energy in the short chirps
Short chirp period (SCP)	The time between the start of one chirp and the start of the subsequent chirp in the short chirps
Short chirp pulse duration (SCPD)	The time between the start and the end of a pulse in the short chirps
Short chirp pulse period (SCPP)	The time between the start of one pulse and the start of the subsequent pulse in the short chirps
Short chirp pulse number (SCPN)	The total number of pulses in the short chirps
Short chirp pulse number per chirp (SCPNC)	The number of pulses per chirp in the short chirps
Gap	The time between the end of a long chirp and the start of the succeeding short chirps
Phrase period (PHP)	The time between the start of one phrase and the start of a subsequent phrase

crickets were provided by the Department of Agricultural Biology of the National Academy of Agricultural Science in Korea, which had maintained the stock population of *T. emma* for more than 2 y. Crickets were reared in an environmental room (2 × 2.5 × 2.5 m) that was maintained at 23.5 ± 1.5°C and 75% relative humidity, with a 12 h light:12 h dark photoperiod. The juveniles were housed in plastic containers with cat chow and water. Adult crickets were removed from the colony within 48 h of the final molt to ensure that all crickets used for this study were virgin. Newly emerged adults were individually housed in plastic containers (12 × 12 × 9 cm) with cat chow and vegetables. Both juveniles and adults were provided with egg cartons for shelter. Age was calculated as the number of days after the final molt.

Playback experiment

The acoustic stimuli used for the playback experiment were as follows: 1) standard, 2) long chirp only, 3) long chirp augmented, 4) short chirps only, and 5) short chirps augmented (Fig. 3). They were synthesized using custom-designed software with 16-bit resolution and 44.1 kHz sampling rate (Schul and Bush 2002). The standard stimulus included both long and short chirps, the characteristics of which were derived from the calling songs of field-caught males (LCPD: 37.95 ms; LCCF: 3,750 Hz; LCPP: 74.86 ms; LCPN: 10; Gap: 74.66 ms; SCPD: 29.48 ms; SCCF: 3,750 Hz; SCPP: 43.64 ms; SCPN: 3; SCP: 0.22 s; PHP: 6.53 s). The last four pulses of the long chirp and all pulses in the short chirps were at a constant amplitude. However, the amplitude of the first six pulses of the long chirp was modulated, with the magnitude of the amplitude increasing sequentially relative to the rest of the song as follows: 0.14, 0.29, 0.43, 0.57, 0.71, and 0.86. The "long chirp only" and "short chirps only" stimuli were the standard stimulus without the short chirps and long chirp, respectively. Female phonotactic responses may be biased in the long chirp only and short chirps only stimuli, because these stimuli had fewer numbers of pulses than had the standard stimulus. Thus, we eliminated this possibility by introducing two augmented stimuli whose pulse numbers were equivalent to that of the standard stimulus. The "long chirp augmented" stimulus was an elongated long chirp only stimulus, with 19 pulses instead of 10. Likewise, the "short chirps augmented" stimulus was an elongated short chirps only stimulus with 18 pulses instead of 8.

The playback experiment was conducted in a semi-anechoic chamber (2.6 × 1.7 × 2.4 m). Playback trials

were run in an octagonal arena with a 50 cm diameter. The arena was constructed on a plywood base covered with a thin layer of carpeting. The boundary of the arena was a 13-cm high acoustically transparent screen. The stimulus was played back using a CD player (Denon DN-C630; Nippon Columbia Co., Ltd., Tokyo, Japan), and the output from the CD player was sent to an amplifier (No. 1700; QSC Audio, Costa Mesa, CA, USA). The signal from the amplifier was then sent to one of two tweeters (Dayton No. 275-100; Euro series textile tweeter, Springboro, OH, USA; flat frequency 2,000-20,000 Hz). The two tweeters were placed at floor level outside the arena wall (55 cm from the center of the arena), angled at 120°. The choice of a tweeter for playback trials was switched daily to prevent any phonotactic bias that might be present in the arena. The amplitude of a stimulus played back from a tweeter was calibrated to 80 ± 0.5 dB SPL (0 dB = 20 μPa) using a Brüel and Kjær sound level meter (No. 2250; Brüel and Kjær, Nærum, Denmark). During the trials, the anechoic chamber was maintained at 23.5 ± 1.5°C in complete darkness.

Female crickets to be tested were drawn haphazardly from the stock population after eclosion. Only intact female crickets between 7 and 33 days of age were used.
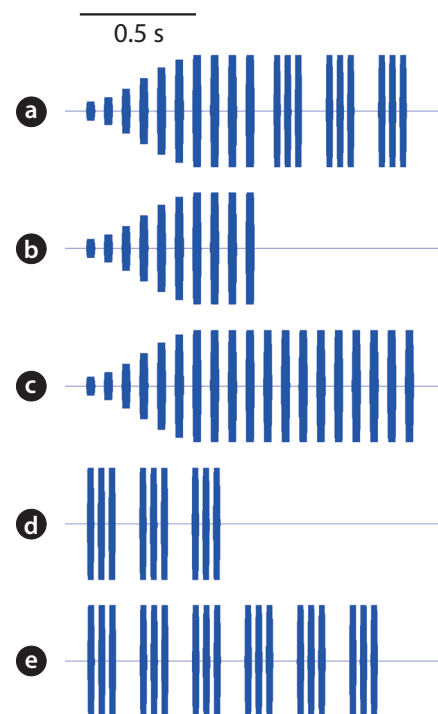

Fig. 3. Five stimuli that were used to test female phonotactic response in the single-stimulus playback experiment. These stimuli were (a) standard, (b) long chirp only, (c) long chirp augmented, (d) short chirps only, and (e) short chirps augmented.

Each trial was begun by placing a female cricket under an opaque plastic cover located in the center of the arena. The plastic cover (250 mL) had holes for sound permeation. The cricket was placed in the arena for 1 min without any sound to acclimate and was then exposed to the test stimulus broadcast from one of the tweeters for 1 min. The cricket was released by removing the cup. Female response to the stimulus was monitored using an IR camera (DSP No. HN8071R UC3; Seoul, Korea; minimum illumination: 0 Lux when IR LED on). Trials were terminated after 5 min or when the test females evidenced positive phonotaxis. A positive phonotactic response was recorded if a female oriented itself toward the tweeter and touched the wall of the arena directly in front of the loudspeaker broadcasting the test stimulus, or if a female made a 'double reversal' movement in front of the tweeter (Jang and Gerhardt 2006). That is, crickets sometimes ran toward the arena screen after release without orientation and then walked along the screen. A female cricket occasionally reversed its walking direction in front of the tweeter broadcasting the test stimulus twice in a row within close proximity of the tweeter; each reversal of direction had to cross the line between the tweeter and the female release point. The double reversal movement was a local search, and occurred when an individual was very close to the object for which it was searching (Bell 1991). Each cricket was tested only once per day, and was tested a total of five times with five test stimuli. The order in which the stimuli were presented was determined using a random number table. A total of 30 female crickets completed five stimuli in the playback experiment.

After completing the playback experiment, female crickets were measured once for head width, thorax length, and hind femur length to the nearest 0.05 mm using a digital Vernier caliper. Head width was measured as the distance between the outer edges of the compound eyes. Thorax length was the distance between the anterior and posterior ends in the midline of the thorax. A right hind leg was removed from the thorax and placed on its side. Hind femur length was measured from the base of the femur to the joint with the tibia.

Statistical analyses

The multivariate general linear model (GLM) was used to evaluate the effect of locality on the calling song characters of *T. emma*. In the multivariate GLM, calling song characters were response variables, and temperature was a covariate. We used the CV for calling song characters to measure within-male variability. For each male, CV was calculated as the ratio of the standard deviation to the mean (Gerhardt 1991, Sokal and Rohlf 1995). Mean CV for each calling song character was the average of CV values of all recordings measured. The sample sizes for the multivariate GLM and CV analyses were reduced to 59, because seven recordings had only one short chirp in their calling songs. No SCP could be calculated for these seven recordings, and thus they were excluded from further statistical analyses. Logistic regression analysis was used to test whether female phonotactic responses differed with different stimuli. Predictor variables were age, body size, and stimulus. To estimate body size, we conducted principal component analysis (PCA) for three morphological characters: head width, thorax length, and hind femur length. The response variable was categorized as 1 for a positive phonotactic response, or 0 for all other cases. All statistical tests were conducted using SPSS ver. 11.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Variation in calling song characters

The results of multivariate GLM showed that locality was not a significant factor for any of the calling song characters, with the exceptions of LCPD and SCPD (Table 2). Temperature significantly affected most calling song characters, except for LCPD, SCPNC, and SCPN (Table 2). Carrier frequencies of both long chirp and short chirps whose CV values were less than 5% showed the lowest levels of variation (Table 3). The CV values for the temporal characters of the long chirp ranged between 9.76 and 11.72%, whereas the CV values for the temporal characters of the short chirps were greater than or equal to 12.92%. Calling song characters related to short chirp pulse number, SCP, SCPNC, and SCPN, had the most variation. Thus, the carrier frequency of calling songs may be a static character, whereas the temporal characters of the short chirps were dynamic characters in *T. emma*. The temporal characters of the long chirp were intermediate between static and dynamic characters.

Female phonotactic response

Body size was estimated on the basis of the PCA for head width, thorax length, and hind femur length. We identified only one principal component (PC) with an eigenvalue greater than 1, and this PC explained 79.8% of the total variation in female body size. Thus, PC1 was

Table 2. The result of multivariate GLM for calling song characters in *Teleogryllus emma* (*N* = 59)

Predictor variable	Response variable	*df*	MS	F	*P*-value
Temperature	LCPD	1	43.69	2.77	0.102
	LCCF	1	395,049.24	13.68	0.001
	LCPP	1	3,380.89	130.51	< 0.001
	LCPN	1	18.50	15.81	< 0.001
	Gap	1	26,752.56	30.75	< 0.001
	SCPD	1	224.08	14.90	< 0.001
	SCCF	1	419,691.65	16.18	< 0.001
	SCPP	1	1,825.98	93.46	< 0.001
	SCP	1	0.04	5.40	0.024
	SCPNC	1	0.12	0.12	0.736
	SCPN	1	1.31	0.03	0.866
	PHP	1	19.78	4.84	0.032
Locality	LCPD	6	55.99	3.55	0.005
	LCCF	6	3,801.10	0.13	0.992
	LCPP	6	16.02	0.62	0.715
	LCPN	6	1.47	1.25	0.296
	Gap	6	1,281.63	1.47	0.206
	SCPD	6	36.18	2.41	0.040
	SCCF	6	11,169.85	0.43	0.855
	SCPP	6	14.86	0.76	0.604
	SCP	6	0.01	1.06	0.397
	SCPNC	6	1.92	1.97	0.088
	SCPN	6	81.97	1.80	0.117
	PHP	6	4.26	1.04	0.410
Error	LCPD	51	15.77		
	LCCF	51	28,884.65		
	LCPP	51	25.90		
	LCPN	51	1.17		
	Gap	51	869.91		
	SCPD	51	15.04		
	SCCF	51	25,935.52		
	SCPP	51	19.54		
	SCP	51	0.01		
	SCPNC	51	0.98		
	SCPN	51	45.46		
	PHP	51	4.09		

GLM, general linear model; LCPD, long chirp pulse duration; LCCF, long chirp carrier frequency; LCPP, long chirp pulse period; LCPN, long chirp pulse number; SCPD, short chirp pulse duration; SCCF, short chirp carrier frequency; SCPP, short chirp pulse period; SCP, short chirp period; SCPNC, short chirp pulse number per chirp; SCPN, short chirp pulse number; PHP, phrase period.

Table 3. Mean ± standard error (SE) and coefficient of variation (CV) of calling song characters in *Teleogryllus emma* in the multivariate GLM (*N* = 59)

Character	Mean ± SE	Unit	CV
LCPD	38.91 ± 0.597	ms	11.31
LCCF	3,801.66 ± 25.575	Hz	4.64
LCPP	76.62 ± 0.766	ms	9.76
LCPN	9.93 ± 0.163		11.72
Gap	80.73 ± 4.438	ms	32.55
SCPD	30.78 ± 0.584	ms	14.30
SCCF	3,734.16 ± 24.234	Hz	4.44
SCPP	46.60 ± 0.665	ms	12.92
SCP	0.25 ± 0.013	s	42.90
SCPNC	2.95 ± 0.149		32.26
SCPN	10.82 ± 1.015		69.66
PHP	6.05 ± 0.304	s	33.27

The means of calling song characters were evaluated at the mean value of the covariate (temperature = 23.305℃) in the multivariate GLM (see Table 2). GLM, general linear model; LCPD, long chirp pulse duration; LCCF, long chirp carrier frequency; LCPP, long chirp pulse period; LCPN, long chirp pulse number; SCPD, short chirp pulse duration; SCCF, short chirp carrier frequency; SCPP, short chirp pulse period; SCP, short chirp period; SCPNC, short chirp pulse number per chirp; SCPN, short chirp pulse number; PHP, phrase period.
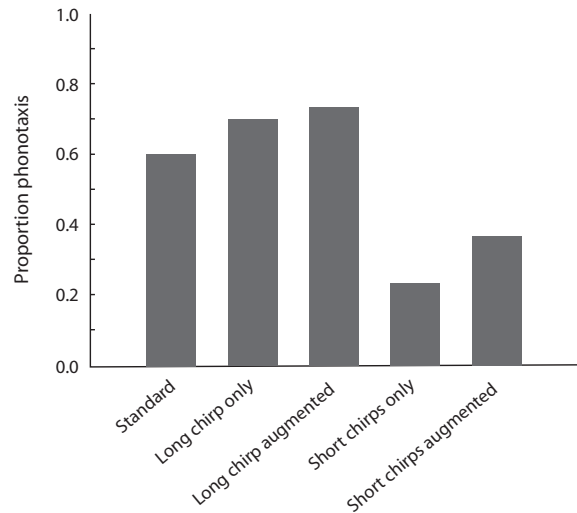

Fig. 4. The result of female phonotactic responses. In the single-stimulus playback experiment, one of the five stimuli was presented to female crickets. The standard stimulus had values representative of the calling songs of all males recorded in the field. The *Y*-axis designates the proportion of positive female phonotaxis to each stimulus (*N* = 30).

Table 4. The result of logistic regression analysis for female phonotactic response (*N* = 30)

	B	S.E.	Wald	*df*	*P*-value	Exp (B)
Age	0.076	0.062	1.516	1	0.218	1.079
Stimulus			22.611	4	< 0.001	
(Standard)	1.024	0.557	3.381	1	0.066	2.784
(Long chirp only)	1.547	0.581	7.075	1	0.008	4.695
(Long chirp augmented)	1.773	0.598	8.780	1	0.003	5.888
(Short chirp only)	-0.743	0.596	1.555	1	0.212	0.476
Body size	0.611	0.210	8.445	1	0.004	1.842
Constant	-1.686	0.963	3.061	1	0.080	0.185

S.E., standard error.

used as the body size of females tested for phonotactic trials.

When the standard stimulus was played back, 60% of the females oriented toward it (Fig. 4). The proportions of positive female phonotaxis toward the long chirp only and the long chirp augmented stimuli were greater than that of the standard stimulus. However, the proportions of positive female phonotaxis toward the short chirps only and the short chirps augmented stimuli were lower than that of the standard stimulus. The result of logistic regression analysis revealed that positive female phono-

taxis was affected significantly by stimulus and body size (Table 4). The proportion of female phonotactic orientation increased with increases in body size.

DISCUSSION

Although the findings of this study revealed that there was almost no geographic variation in the calling song characters, such findings may have been the results of insufficient sampling. The majority of the sampling localities were limited to a narrow range of latitudes. To conclusively address geographic variation in the calling songs of *T. emma*, more sampling including north-south transects will be required.

Based on the results of our CV analysis, the carrier frequencies of both the long chirp and short chirps were identified as a static character in the male calling songs of *T. emma* (Gerhardt 1991). However, carrier frequency alone is unlikely to prove critical for species recognition in field cricket species. The carrier frequencies of most field cricket species range between 3,000 and 6,000 Hz (Bennet-Clark 1989, Greenfield 2002). When exposed to acoustic stimuli with carrier frequencies in this range, female crickets generally orient toward stimuli with temporal characters like the calling songs produced by males

of their species.

The temporal characters of the short chirps were dynamic, suggesting that these characters were unlikely to be relevant to species recognition in *T. emma*. The calling song of *T. oceanicus,* much like that of *T. emma*, consists of a long chirp followed by a series of short chirps, each with two pulses. In a survey of 15 sites within six regions in Oceania and Australia, the short chirp portion of the *T. oceanicus* calling song showed the largest variation (Zuk et al. 2001). Traits with high CV values may be subject to directional selection by females (Gerhardt 1991, Wollerman 1998, Shaw and Herlihy 2000, Klappert and Reinhold 2003). However, not all dynamic characters are necessarily subject to directional selection. In the grasshopper *Chorthippus biguttulus*, four song characters had CV values in excess of 20% (Klappert and Reinhold 2003). Results of the mate choice experiments in *C. biguttulus* revealed that females exerted directional selection on three song characters: gap duration, pause to syllable ratio, and loudness, but exerted correlative selection on song rhythm in combination with gap duration. In addition to short chirps, it is possible that the long chirp of calling songs may also be used for sexual selection by females. The proportions of female phonotaxis toward the long chirp only and the long chirp augmented stimuli were generally higher than that exhibited toward the standard stimulus. Although the CV values for the long chirp characters were lower than those for the short chirp characters, there were enough between-male variations in the long chirp characters required for mate selection by females.

The CV values for temporal characters of the long chirp were lower than 12%, suggesting a potential role in species recognition in *T. emma*. The female preference for the acoustic stimuli that included a long chirp also bolstered the hypothesis that the long chirp is important for positive phonotaxis by *T. emma* females. Sexual characteristics used for species recognition typically have low intra- and inter-male variability and are associated with the stabilizing selection exerted by females (Gerhardt 1991, Wollerman 1998, Shaw and Herlihy 2000, Klappert and Reinhold 2003). In *T. oceanicus*, the syllable period, which is equivalent to LCPP in our study, is the only character relevant to calling song recognition (Hennig and Weber 1997). Furthermore, females generally prefer calling songs with greater proportions of long chirps, although the strength and nature of selection vary across populations (Simmons et al. 2001).

Species recognition sensitively tuned to the properties of male calling songs is a matter of critical importance for

T. emma. On the Japanese Archipelago, *T. emma* occurs along with *T. yezoemma* and *T. taiwanemma*. The calling songs of the genus *Teleogryllus* are complex with two different temporal patterns: chirps and trills (long chirp and short chip in this study) (Otte 1992). The calling song of *T. yezoemma* has no short chirps, but the calling songs of *T. emma* and *T. taiwanemma* are composed very similarly, with both long and short chirps (Honda-Sumi 2004, 2005). The differences in temporal characters of the long chirp may be important for reproductive isolation among these sympatric *Teleogryllus* species. Information regarding behavioral isolation by female preference functions, as well as information concerning variation in calling song characters across a wide geographical range, will be necessary to elucidate in more detail the processes of species recognition and speciation in these *Teleogryllus* crickets.

ACKNOWLEDGMENTS

LITERATURE CITED

Adamo SA, Hoy RR. 1994. Mating behaviour of the field cricket *Gryllus bimaculatus* and its dependence on social and environmental cues. Anim Behav 47: 857-868.

Alexander RD. 1962. Evolutionary change in cricket acoustical communication. Evolution 16: 443-467.

Bell WJ. 1991. Searching Behavior: the Behavioural Ecology of Finding Resources. Chapman and Hall, London.

Bennet-Clark HC. 1989. Songs and the physics of sound production. In: Cricket Behavior and Neurobiology (Huber F, Moore TE, Loher W, eds). Cornell University Press, Ithaca, NY, pp 227-261.

Butlin RK, Hewitt GM, Webb SF. 1985. Sexual selection for intermediate optimum in *Chorthippus brunneus* (Orthoptera: Acrididae). Anim Behav 33: 1281-1292.

Doherty JA, Callos JD. 1991. Acoustic communication in the trilling field cricket, *Gryllus rubens* (Orthoptera: Gryllidae). J Insect Behav 4: 67-82.

Ewing AW, Miyan JA. 1986. Sexual selection, sexual isolation and the evolution of song in the *Drosophila repleta*

group of species. Anim Behav 34: 421-429.

Ferreira M, Ferguson JWH. 2002. Geographic variation in the calling song of the field cricket *Gryllus bimaculatus* (Orthoptera: Gryllidae) and its relevance to mate recognition and mate choice. J Zool 257: 163-170.

Gerhardt HC. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. Anim Behav 42: 615-635.

Gerhardt HC, Huber F. 2002. Acoustic Communication in Insects and Anurans. University of Chicago Press, Chicago, IL.

Gray DA, Cade WH. 2000. Sexual selection and speciation in field crickets. Proc Natl Acad Sci USA 97: 14449-14454.

Greenfield MD. 2002. Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication. Oxford University Press, New York, NY.

Hennig RM, Weber T. 1997. Filtering of temporal parameters of the calling song by cricket females of two closely related species: a behavioral analysis. J Comp Physiol A 180: 621-630.

Honda-Sumi E. 2004. Female recognition of trills in the male calling song of the field cricket, *Teleogryllus taiwanemma*. J Ethol 22: 135-141.

Honda-Sumi E. 2005. Difference in calling song of three field crickets of the genus *Teleogryllus*: the role in premating isolation. Anim Behav 69: 881-889.

Huber F, Thorson J. 1985. Cricket auditory communication. Sci Am 253: 60-68.

Jang Y, Gerhardt HC. 2006. Divergence in female calling song discrimination between sympatric and allopatric populations of the southern wood cricket *Gryllus fultoni* (Orthoptera : Gryllidae). Behav Ecol Sociobiol 60: 150-158.

Jang Y, Bockhorst A, Gerhardt HC. 2007. Reproductive isolation in the wood cricket *Gryllus vernalis* (Orthoptera: Gryllidae). Ethology 113: 87-96.

Klappert K, Reinhold K. 2003. Acoustic preference functions and sexual selection on the male calling song in the grasshopper *Chorthippus biguttulus*. Anim Behav 65: 225-233.

Loher W, Dambach M. 1989. Reproductive behavior. In: Cricket Behavior and Neurobiology (Huber F, Moore TE, Loher W, eds). Cornell University Press, Ithaca, NY, pp 43-82.

Masaki S, Ohmachi F. 1967. Divergence of photoperiodic response and hybrid development in *Teleogryllus* (Orthoptera: Gryllidae). Konchu 35: 83-105.

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. Bull Fac Agric Mie Univ 2: 63-72.

Otte D. 1992. Evolution of cricket songs. J Orthoptera Res 1: 25-49.

Price T. 1998. Sexual selection and natural selection in bird speciation. Philos Trans R Soc London B Biol Sci 353: 251-260.

Ritchie MG. 1996. The shape of female mating preferences. Proc Natl Acad Sci USA 93: 14628-14631.

Ritchie MG, Couzin ID, Snedden WA. 1995. What's in a song? Female bushcrickets discriminate against the song of older males. Proc R Soc Lond B Biol Sci 262: 21-27.

Saarikettu M, Liimatainen JO, Hoikkala A. 2005. The role of male courtship song in species recognition in *Drosophila montana*. Behav Genet 35: 257-263.

Schul J, Bush SL. 2002. Non-parallel coevolution of sender and receiver in the acoustic communication system of treefrogs. Proc R Soc Lond B Biol Sci 269: 1847-1852.

Shaw KL, Herlihy DP. 2000. Acoustic preference functions and song variability in the Hawaiian cricket *Laupala cerasina*. Proc R Soc Lond B Biol Sci 267: 577-584.

Simmons LW, Zuk M, Rotenberry JT. 2001. Geographic variation in female preference functions and male songs of the field cricket *Teleogryllus oceanicus*. Evolution 55: 1386-1394.

Sokal RR, Rohlf FJ. 1995. Biometry: the Principles and Practice of Statistics in Biological Research. 3rd ed. Freeman, New York, NY.

Wollerman L. 1998. Stabilizing and directional preferences of female *Hyla ebraccata* for calls differing in static properties. Anim Behav 55: 1619-1630.

Zuk M, Simmons LW. 1997. Reproductive strategies of the crickets (Orthoptera: Gryllidae). In: The Evolution of Mating Systems in Insects and Arachnids (Choe JC, Crespi BJ, eds). Cambridge University Press, Cambridge, pp 89-109.

Zuk M, Rotenberry JT, Simmons LW. 2001. Geographical variation in calling song of the field cricket *Teleogryllus oceanicus*: the importance of spatial scale. J Evol Biol 14: 731-741.