Cricket Song in Sympatry: Species Specificity of Song without Reproductive Character Displacement in *Gryllus rubens*

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ABSTRACT Previous work with the cryptic sister species pair of field crickets, *Gryllus texensis* Cade & Otte and *Gryllus rubens* Scudder, has implicated sexual selection in the speciation process. That study examined reproductive character displacement (RCD) in male song and female preference for song in *G. texensis*. No evidence of RCD was found. Here, we provide a similar analysis of RCD in *G. rubens* song and examine the songs of both species from areas of sympatry in an effort to document the species-specificity of song in sympatry and to look for individuals with songs indicative of F1 hybrid status. We 1) find no evidence for RCD in *G. rubens* song, 2) demonstrate the distinctness of song in sympatry, and 3) document the rarity of songs typical of F1 hybrids.

KEY WORDS speciation, reinforcement, crickets

MATING SIGNALS ARE PARTICULARLY interesting because they mediate behavioral interactions that affect gene flow both within and among groups of organisms. Sexual signals may be both species-specific identifiers and subject to sexual selection (Ryan 1990, Ryan and Rand 1993). During speciation events, sympatric divergence in mating traits may follow allopatric divergence in morphology, ecology, or genetic architecture and so *reinforce* the species differences (Dobzhansky 1937). Such a process is expected to produce a pattern of reproductive character displacement, in which sexual signals are more distinct in sympatry than in allopatry. At equilibrium, species-specific identifying traits may be subject primarily to stabilizing selection and so may show relatively little intraspecific variation, whereas sexually selected traits are often among the most variable phenotypic features of organisms (static and dynamic traits sensu Gerhardt 1991). Examining levels of intraspecific variation in mating signals, species differences in signals, and the pattern of geographic variation in mating signals has thus been a productive area of inquiry at the interface of behavioral and evolutionary research (Butlin and Ritchie 1994, Gerhardt 1994, Ritchie and Gleason 1995, Wells and Henry 1998, Henry et al. 1999, Ritchie et al. 1999, Tregenza et al. 2000, Tregenza 2002).

Because of the conspicuous male calling song used to attract females for mating, crickets have been exceptionally productive model systems for investigating the role of behavioral isolation in speciation (Hill et al. 1972, Walker 1974, Harrison 1985, Doherty and Storz 1992, Doherty and Howard 1996, Veech et al. 1996, Gregory et al. 1998, Roff et al. 1999, Shaw 1999, Gray and Cade 2000, Shaw and Herlihy 2000). In this context, we have examined the pulse rates in the male calling song of the field cricket *Gryllus rubens* Scudder and its broadly sympatric cryptic sister species *Gryllus texensis* Cade & Otte. Previous work with these species has shown that they are each others' closest relative (Huang et al. 2000) and are capable of producing fertile hybrids in the laboratory (Smith and Cade 1987, Cade and Tyshenko 1990). The species co-occur in the southern United States gulf region from western Florida to eastern Texas. Obvious hybrids in the field have not been found, although before the study described here, only a small portion of the geographic range in sympatry had been systematically studied, namely, the far western portion of mainland Florida (Walker 1998, 2000). Males of both species produce calling song with long trains of pulses called trills. *G. rubens* tends to produce longer trills than *G. texensis*, but the two species differ most conspicuously in the pulse rate of the calling song. *G. rubens* from Gainesville, FL, produces trills with pulse rates averaging ≈56 pulses per second at 25°C, whereas *G. texensis* from Austin, TX, trill at a much faster rate, typically 80 pulses per second at 25°C (Walker 1998, 2000; Gray and Cade 2000). Laboratory produced hybrids call with intermediate pulse rates averaging 67 ± 5 pulses per second ($n = 27$ males; unpublished data). Males also differ in the quieter close-range courtship song used just before mating (Fitzpatrick and Gray 2001). Most females can be identified based on relative ovipositor length (Gray et al. 2001), but other than song no means of distinguishing males is currently known. A previous study (Gray and Cade 2000) examined reproductive character displacement in pulse rates of *G. texensis* song and found no evidence for displacement in either male song or

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female response to song. Too few *G. rubens* were caught for the previous study to include an analysis of character displacement in *G. rubens* song. Cryptic species pairs may reveal character displacement in only one species. For example, Marshall and Cooley (2000) documented character displacement in pitch and female preference for pitch in one species of periodical cicada, *Magicicada neotredecim* (Marshall & Cooley), but no change in *Magicicada tredecim* (Walsh & Riley). Here, we present the results of a follow-up study designed to address reproductive character displacement in *G. rubens* song and further examine the species specificity of song across a much broader area of sympatry than studied previously. Because *G. rubens* has a slower pulse rate than *G. texensis*, reproductive character displacement would predict that sympatric *G. rubens* should have a slower pulse rate than allopatric *G. rubens.*

It is important to note that a pattern of reproductive character displacement (RCD) is possible even in the absence of hybrid inviability (Higgie et al. 2000). In discussions of RCD, it has been generally considered that it is hybrid inviability that selects for more distinct mating signals in sympatry (Howard 1993). Some authors have interpreted this to mean that without hybrid inviability there is no a priori reason to predict a pattern of RCD. However, where it has been shown that mating success is dependent upon production of a species-typical mating signal, we may infer that hybrids with intermediate mating signals would have low fitness even if they are completely viable and fertile. That is, sexual selection can favor more distinct mating signals in sympatry (i.e., produce a pattern of RCD) due to selection on parents to avoid interspecific matings that produce hybrid offspring with unattractive intermediate mating signals and thus limited mating opportunities. That hybrid offspring would produce signals unattractive to parental populations is suggested by female preference function studies with *Ephippiger* (Ritchie 1996) and *Laupala* (Shaw 2000), and with these two species of crickets (Gray and Cade 2000).

Materials and Methods

Field crickets were collected in summer and fall of 1999 and 2002 from throughout the southeastern United States (Table 1; Fig. 1). Collection localities were designated as allopatric or sympatric based on distribution maps from T. J. Walker and T. E. Moore (2003). Singing Insects of North America (http://buzz.ifas.ufl.edu/479mc.gif and http://buzz.ifas.ufl.edu/482mc.gif), plus firsthand knowledge. We are uncertain whether Decatur, AL, should be considered as allopatric (*G. rubens*) or sympatric; we have treated it as sympatric in analyses. Because only one cricket was recorded from Decatur, we are confident that this uncertainty in no way affects our conclusions.

Crickets were collected at lights at night and by searching during the day. The 1999 collections were conducted in the fall (September–mid-October) and consisted of wild-caught females whose offspring were laboratory reared in sibling groups at 28 ± 1°C with a photoperiod of 13:11 (L:D) h. They were provided with dry cat food and water in cotton-plugged vials (Gray and Cade 2000). From one to four male offspring per wild-caught female were recorded using a Sony WM-D3 Professional Walkman, and the songs were digitized at 22.05 kHz (202 males from 107 wild-caught females, mean ± SD, 1.9 ± 0.65 males per female). To avoid pseudo-replication of data, the offspring of each wild-caught female cricket were treated

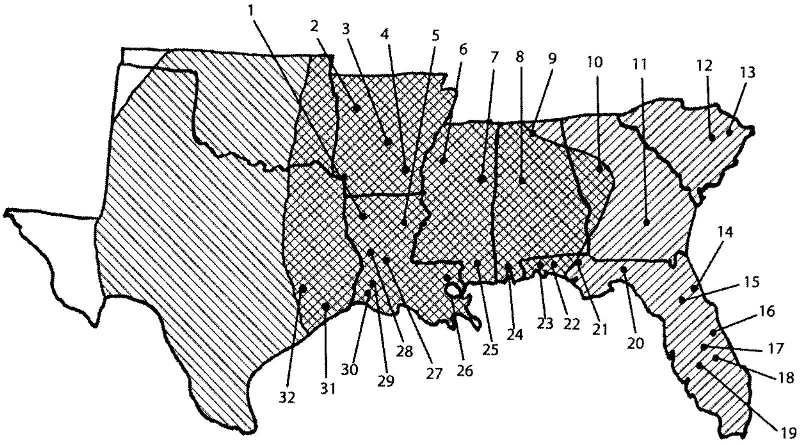

Fig. 1. Approximate geographic distributions of *G. texensis* (\\\\\ shaded area) and *G. rubens* (///// shaded area); sympatric areas are cross-hatched. Collection locality key: one Minden, LA; two Van Buren, AR; three North Little Rock, AR; four Dumas, AR; five Tallulah, LA; six Greenwood, MS; seven Starkville, MS; eight Tuscaloosa, AL; nine Decatur, LA; 10 Carrollton, GA; 11 Tifton, GA; 12 Columbia, SC; 13 Florence, SC; 14 Palatka, FL; 15 Gainesville, FL; 16 Orlando, FL; 17 Intercession City, FL; 18 Hwy 60 × Hwy 27, FL; 19 Zolfo Springs, FL; 20 Perry, FL; 21 Marianna, FL; 22 Milton, FL; 23 Pensacola, FL; 24 Mobile, AL; 25 De Soto National Forest, MS; 26 White's Kitchen, LA; 27 Alexandria, LA; 28 De Ridder, LA; 29 Sulfur, LA; 30 Kisatchee National Forest, LA; 31 Hankamer, TX; and 32 Bastrop, TX.

Table 1. Collection locality information and sample sizes

Locality	Latitude, longitude	Population type	*N G. rubens*	*N G. texensis*	Year
Alexandria, LA	31° 18′ N 91° 45′ W	SYM		7	1999
Bastrop, TX	30° 06′ N 97° 19′ W	SYM		9	1999
Carrollton, GA	33° 34′ N 85° 04′ W	SYM		3	1999
Columbia, SC	34° 03′ N 80° 59′ W	ALLO	5		2002
De Ridder, LA	30° 52′ N 93° 17′ W	SYM	3		2002
De Soto National Forest, MS	30° 34′ N 89° 07′ W	SYM	5		2002
Decatur, AL	34° 36′ N 86° 59′ W	SYM(?)	1		1999
Dumas, AR	33° 53′ N 91° 29′ W	SYM		7	1999
Florence, SC	34° 09′ N 79° 52′ W	SYM	4		2002
Gainesville, FL	29° 37′ N 82° 21′ W	ALLO	14		2002
Greenwood, MS	33° 31′ N 90° 11′ W	SYM	1	9	1999
Hankamer, TX	29° 50′ N 94° 34′ W	SYM	1	4	2002
Hwy 60 X Hwy 27, Polk county, FL	27° 54′ N 81° 36′ W	ALLO	2		2002
Intercession City, FL	28° 15′ N 81° 30′ W	ALLO	3		2002
Kisatchee National Forest, LA	31° 29′ N 93° 07′ W	SYM	3		2002
Marianna, FL	30° 46′ N 85° 13′ W	ALLO	12		1999
Milton, FL	30° 38′ N 87° 02′ W	SYM	1	3	1999
Minden, LA	32° 37′ N 93° 17′ W	SYM		10	1999
Mobile, AL	30° 41′ N 88° 02′ W	SYM		1	1999
North Little Rock, AR	34° 48′ N 92° 18′ W	SYM	3		2002
Orlando, FL	28° 27′ N 81° 18′ W	ALLO	1		2002
Palatka, FL	29° 40′ N 81° 35′ W	ALLO	3		2002
Pensacola, FL	30° 25′ N 87° 13′ W	SYM	5	3	1999
Perry, FL	30° 06′ N 83° 35′ W	ALLO	4		2002
Starkville, MS	33° 27′ N 88° 49′ W	SYM		12	1999
Sulphur, LA	30° 14′ N 93° 22′ W	SYM		3	1999
Tallulah, LA	32° 24′ N 91° 11′ W	SYM		17	1999
Tifton, GA	31° 27′ N 83° 30′ W	ALLO	8		2002
Tuscaloosa, AL	33° 10′ N 87° 31′ W	SYM	9	3	1999, 2002
Van Buren, AR	35° 27′ N 94° 21′ W	SYM	3	2	2002
White's Kitchen, LA	30° 13′ N 89° 40′ W	SYM	8		2002
Zolfo Springs, FL	27° 29′ N 81° 47′ W	ALLO	1		2002

ALLO, allopatric; SYM, sympatric.

as a single independent data point. To achieve this, we averaged the temperature-corrected pulse rates (see below) of males within each family and used the average family values as data. Averaging within families circumvents the pseudo-replication problem, and is further justified by noting that pulse rate is a heritable trait (Gray and Cade 2000) such that the within-family variance is typically low, i.e., the within family average is generally very representative of the songs of the males of that family. We also repeated all analyses by using only one male per family (arbitrarily the first male recorded) and discarding data from siblings. Both analyses gave identical results; thus, only the family-average results are presented here. In 2002, collections were made from mid-July through mid-August. Wild-caught males were held in 500-ml individual containers provided with ad libitum dry cat food and water in a cotton plugged vial. Calling males were recorded and the songs digitized as described above. For each recording the temperature was noted to the nearest 0.1°C.

Songs from 1999 were analyzed using Canary 1.2.4 (Cornell Laboratory of Ornithology, Ithaca, NY) on a Macintosh computer; 2002 songs were analyzed on a personal computer by using CoolEdit 2000 (Syntrillium software, Scottsdale, AZ). Pulse rates for each recording were obtained by measuring the pulse period, which is the time from the start of one pulse to the start of the next pulse. We measured 50 pulse periods per male for the 1999 recordings and 25 pulse periods per male for the 2002 recordings and used the median value as representative of that male. Pulse rates in pulses per second were calculated as 1/median pulse period. We corrected the pulse rate data for recording temperature by using the slopes from regressions of pulse rates on temperature determined by previous studies (Doherty and Callos 1991, Walker 1998, Gray and Cade 2000, Martin et al. 2000, Walker 2000). Recordings were corrected to 25°C as follows: pulse rate_{adj} = pulse rate + $2.8^*(25 - T_r)$, where T_r is the recording temperature. Recording temperatures ranged from 18.9 to 30.5°C (mean ± SD, 26.4 ± 2.2°C); the regression based method of temperature correction is accurate within this range of temperatures.

Given the differences in methodology between the 1999 and 2002 recordings, it is important to note that none of the differences are likely to affect the quality of the data produced. With respect to song analysis, the computer analysis packages work similarly and for temporal data produce identical results to within 1 pulse per second. Measuring 50 pulse periods as was done for the 1999 recordings proved excessive: plots of the running median versus sample size were asymptotically stable after 10–15 measurements; therefore, measuring 25 pulse periods instead of 50 saved effort without sacrificing precision. A potentially more important, and biologically very interesting, difference between the 1999 and 2002 collections is the possible effect of rearing environment on cricket song. Several studies have now indicated that rearing temperature and/or photoperiod may influence cricket song (Walker 1998, 2000; Bertram 2002; Bertram and Bellani 2002). These fascinating studies highlight the importance of considering developmental effects on behavior from both ethological and evolutionary viewpoints. The magnitudes of the known effects of developmental environment on the songs of crickets suggest that the effects are unlikely to bias the results of this study. Both *G. rubens* and *G. texensis* are loosely bivoltine, with peaks of adult abundance in spring and fall; no spring generation crickets were used in this study. The data used in this study are from individuals caught in the field mid-July through mid-August 2002 and from individuals laboratory reared at 28°C and a photoperiod of 13:11 (L:D) h from collections made in 1999. Thus, the developmental environments of all crickets seem roughly comparable. Nonetheless, further detailed investigation of phenotypic plasticity in cricket song is clearly desirable.

Results

We found no evidence for reproductive character displacement in the pulse rate of *G. rubens* song (Fig. 2). The analysis using pulse rates averaged within families (see Materials and Methods) showed that pulse rates did not differ between allopatry and sympatry (allopatry, $N = 57$, 55.4 ± 3.9 pulses per second; sympatry, $N = 43$, 56.8 ± 4.7 pulses per second (analysis of variance [ANOVA] $F_{1,\ 98} = 2.96$; $P = 0.09$).

The pulse rates of *G. rubens* and *G. texensis* are clearly distinct and virtually nonoverlapping in sympatry (Fig. 3). By using within family averages, sympatric *G. texensis* ($N = 93$) had pulse rates averaging 79.3 ± 4.4 pulses per second, whereas sympatric *G. rubens* had pulse rates averaging 56.8 ± 4.7 pulses per second (ANOVA, $F_{1,\ 134} = 737.82$; $P < 0.0001$).

Discussion

Our results clearly demonstrate three features of relevance to discussions of the role of sexual mating signals in maintaining species boundaries. First, there is no indication of RCD in *G. rubens* calling song pulse rate. Because *G. rubens* pulse rates are slower than those of *G. texensis*, RCD would predict slower pulse rates in sympatry than in allopatry. Instead, the trivial, and not statistically significant direction of difference between allopatry and sympatry was for higher pulse rates in sympatry. An absence of RCD parallels a similar finding reported previously for *G. texensis* pulse rates (Gray and Cade 2000). An absence of RCD, coupled with a lack of hybrid inviability, suggests rapid evolution of the mate recognition system, i.e., a pattern consistent with sexual selection driving diversification. It is possible that such rapid divergence in allopatry precludes the necessity for reinforcement of species differences upon secondary contact. Examination of the pulse rates of crickets from sympatry also clearly shows that the species remain distinct, and that there are few individuals with songs suggestive of F1 hybrid status. This latter result is consistent with earlier work in a restricted area of sympatry in western Florida (Walker 1998).

As suggested by Gerhardt (1994) (see also Gerhardt and Huber 2002), it is possible that RCD exists in female *G. rubens* song discrimination, rather than in male song itself. This is indeed possible; however, three considerations seem to argue against it for these species: 1) a detailed examination of female *G. texensis*

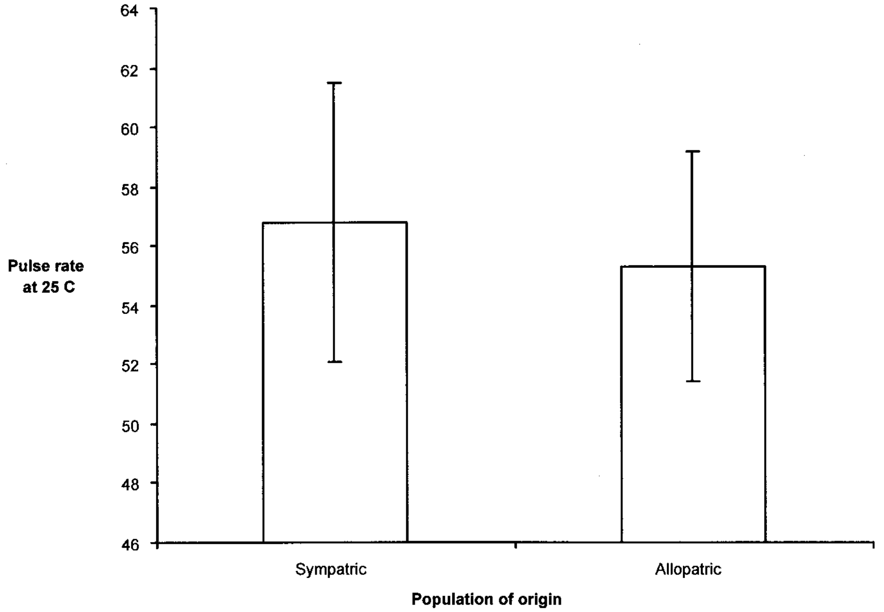

Fig. 2. Comparison of *G. rubens* pulse rates for crickets from allopatric and sympatric collection localities. All songs were corrected for recording temperature to 25°C.

preference functions shows no RCD in female preference in that species (Gray and Cade 2000); 2) available data on female *G. rubens* song preferences show strong matching between female preferences and male traits values (Gray and Cade 2000; unpublished data); and 3) RCD in female preferences *without* RCD in male song is likely to be evolutionarily unstable in the absence of additional selective influences on male song, i.e., RCD in female preference should, over time, favors male songs that match the preferences.

These results contribute to a growing understanding of the role of sexual mating signals in promoting and maintaining species diversity. Sexual signals clearly have substantial evolutionary lability. Because sexual signals are potentially subject to strong rapid directional sexual selection, divergence in mating signal traits may far exceed divergence in ecological and/or morphological traits. Species coexistence in sympatry will depend upon the effectiveness of the mating signal divergence in ensuring assortative mating, selection against hybrid individuals (including sexual selection; see Introduction), and ultimately ecological niche differentiation. Our current understanding of ecological niche differentiation between

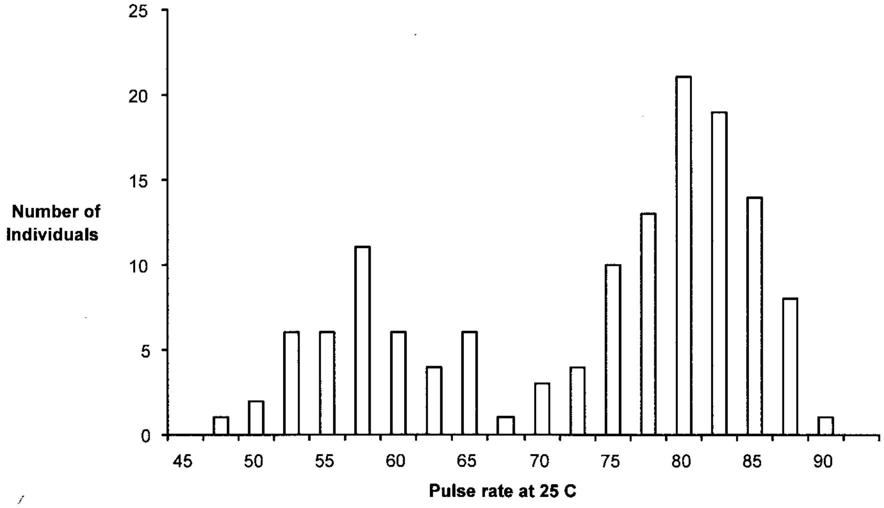

Fig. 3. Frequency histogram of the pulse rates in songs of 135 individuals of *G. rubens* and *G. texensis* from areas of sympatry. All songs were corrected for recording temperature to 25°C.

G. rubens and *G. texensis* is poor at best. Although both species can be found in exactly the same locality at the same time, some apparent differences seem worthy of further investigation. First, the difference in ovipositor length suggests that *G. rubens*, with the longer ovipositor, may be better adapted to well-drained sandy soils. Our experiences collecting crickets suggest a further difference between the species: *G. texensis* seems to be a much more vigorously eruptive species with large flights in late summer and fall (Cade 1979). Collections made at lights at night, or at places during the day that are regularly illuminated at night, e.g., 24-h gas stations along Interstate highways, typically net *G. texensis* and much less frequently *G. rubens.* Investigating the role of ecological isolation, as has been so successful in other pairs of closely related cricket species (Harrison 1985, Howard 1986, Howard and Waring 1991, Broughton and Harrison 2003), is greatly complicated in the southern gulf states and Mississippi River delta region by wholesale anthropogenic disturbances from forest clearing and agricultural practices. How this ecological disruption has affected species interactions is unknown. Our data, however, do seem to support certain criteria for continued species coexistence. First, the mating signals in sympatry are clearly distinct. Assortative mating by species seems ensured given previous measures of female phonotaxis to male calling song variants (Gray and Cade 2000) coupled with close-range courtship interactions that also promote assortative mating by species, although only with modest effect (D.A.G., unpublished data). Second, sexual selection against hybrid individuals with intermediate songs (males) or song preferences (females) should also act to promote continued species integrity.

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