

Does courtship behavior contribute to species-level reproductive isolation in field crickets?

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Reproductive behavior influences gene flow within and among species; thus, sexual selection may be a major contributor to the maintenance of species, and possibly their formation. Here I experimentally manipulate the courtship interactions of the field crickets *Gryllus rubens* and *G. texensis* to examine the potential of close-range courtship interactions to limit interspecific gene flow. Responses of males to females and of females to male courtship song and males per se were examined for four paired sympatric and allopatric populations. Male *G. rubens* were more likely to court conspecific females, but male *G. texensis* courted females of both species equally. If paired with conspecific males, female *G. rubens* and *G. texensis* both preferred conspecific courtship song. In none of these comparisons were the responses of males or females from allopatry different from those in sympatry. There was an asymmetry of courtship response across both sex and species: male *G. rubens* were more discriminating than male *G. texensis*, whereas female *G. texensis* were more discriminating than female *G. rubens*. Despite significant preferences for conspecifics, the net effect of courtship interactions would appear to limit interspecific gene flow only weakly. These results are consistent with courtship behavior evolving under the influence of sexual selection and only indirectly promoting species integrity. **Key words:** sexual selection, speciation, reproductive isolation, *Gryllus*. [*Behav Ecol*]

The process of speciation necessarily involves the limitation of gene flow among portions of a subdivided population, almost regardless of the species definition that is used (Avice, 2000). The role that sexual selection and changes in the mate recognition systems play in generating prezygotic isolation is thus central to the issue of species formation (Panhuis et al., 2001; Ptacek, 2000). Although both theoretical (Higashi et al., 1999; Lande, 1981; West-Eberhard, 1983) and recent empirical (Arnqvist et al., 2000; Gray and Cade, 2000; Masta and Maddison, 2002; Shaw, 1999; Uy and Borgia, 2000; Wells and Henry, 1998) studies highlight the linkage between reproductive behavior and speciation, determining the directionality of that linkage has been problematic. A key question remains: does selection to avoid unfit hybrid matings drive the evolution of reproductive behavior, or have behavioral reproductive barriers evolved via intraspecific processes of genetic drift and natural and/or sexual selection, and so preceded and significantly contributed to subsequent speciation (see, e.g., Paterson, 1985, 1993)? Here I examine behavioral reproductive isolation in crickets within a framework of basic predictions derived from the ‘classical speciation and reinforcement’ model versus the ‘sexual selection and speciation’ model of the interactions between reproductive behavior and speciation.

The classical speciation model (Mayr, 1963) suggests that behavioral reproductive barriers develop following significant divergence in other characters. The behavioral divergence is then driven by selection to avoid unfit hybrid matings and is thus expected to be stronger in areas of sympatry (Howard, 1993; Noor, 1999). Reproductive character displacement, i.e., stronger isolation in sympatry than in allopatry, is a common prediction of this model. If behavioral isolation arose due to selection to avoid unfit hybrid matings, then we might also

predict that the behavioral isolation that developed would be rather strong, permitting only minimal gene flow (Coyne et al., 2002).

If intraspecific processes, including sexual selection, drive the divergence of behaviors that may secondarily act as isolating mechanisms, our predictions would be different. First, there would be no prediction of reproductive character displacement, and the efficacy of the behaviors in preventing gene flow would be quite variable and might reflect levels of divergence in a continuum from population divergence to subspecies to species. Sexual selection theory additionally predicts that males should be less selective in their choice of mates than females (Andersson, 1994; Bateman, 1948; Trivers, 1972). Both sexual selection and classical speciation models would predict that females should be selective about their mates; females have a high proportion of their total reproductive effort at stake and so should avoid unfit matings with conspecifics and heterospecifics alike. In species without significant male nuptial gifts and little male gametic or parental investment, males might be expected to be relatively indiscriminate in matings with conspecifics. Thus, one would predict that females would show a stronger conspecific mating preference than males. Clearly, the prediction of greater female choosiness under sexual selection models, and more equal choosiness under reinforcement models, is the least definitive of the three predictions. Most workers do seem to predict male choosiness under the reinforcement model, however. Influential reviews of reinforcement have considered male contributions to prezygotic isolation, i.e., male choosiness, equally to female choosiness, suggesting that male choosiness is generally considered likely under the reinforcement model of speciation. For example, Coyne and Orr (1989) generate a prezygotic isolation index that weights tests of female choice among conspecific versus heterospecific males equally to tests of male choice among conspecific versus heterospecific females, and Noor (1999: 503) states that “males benefit from mating preferentially with females of the same species rather than wasting resources on heterospecific females.”

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Table 1

Predictions of the classical reinforcement and sexual selection models of the relationship between reproductive behavior and speciation

	Sexual selection	Classical reinforcement
Females choosy	Yes	Yes
Males choosy	Not particularly	Yes, basically
Net effect: females choosier than males	Yes, basically	Sometimes
Reproductive character displacement	No	Yes
Effectiveness of behavior as an isolating mechanism	Variable	Strong

The set of predictions is summarized in Table 1. The prediction that best distinguishes these models is reproductive character displacement (RCD). The classical reinforcement model of behavioral evolution predicts RCD, whereas the sexual selection model does not. The remaining two predictions, while not providing complete contrast between the models, can add resolution in a synthetic way. For example, a result demonstrating that reproductive behavior is highly effective at preventing gene flow does not distinguish between the models, but a result showing that reproductive behavior is only minimally effective at preventing gene flow is clearly inconsistent with the classical reinforcement model. Likewise, both models predict that females should be choosy about their mates; selection should favor females that avoid low-quality conspecifics and that avoid costly heterospecific matings. Levels of male mate discrimination could be informative, however, because females will be choosier than males if males are relatively indiscriminate (sexual selection) or similarly choosy to males if heterospecific matings are costly or counterproductive to male interest (reinforcement). Distinguishing modes of speciation by examination of extant taxa is always difficult; thus, I adopt here a total evidence approach, as advocated by Panhuis et al. (2001). Although not all predictions necessarily have exclusive outcomes, together the set of predictions may allow us to interpret the results as more parsimoniously consistent with one model or the other.

The study system

The field crickets *Gryllus texensis* and *Gryllus rubens* show reproductive isolation primarily as a function of pulse rate differences in the calling song that males use to attract females from a distance (Gray and Cade, 2000). Once corrected for temperature, the pulse rates of the male calling songs unambiguously identify males to species (Gray and Cade, 2000; Walker, 1998, 2000); females show strong preferences for pulse rates typical of their own species (Gray and Cade, 2000). Furthermore, in *G. texensis* a strong positive genetic correlation exists between male pulse rate and female preference, and neither male song nor measures of female song recognition, discrimination, or preference show any evidence of reproductive character displacement (Gray and Cade, 2000). The species are closely related sister taxa (Huang et al., 2000), and postzygotic isolation is minimal to non-existent (Cade and Tyshenko, 1990; Smith and Cade, 1987). Laboratory-produced F1 hybrids are intermediate in both male song and female preference for song (Gray DA, unpublished data). Thus, although hybrids in the field may not be at a significant disadvantage via natural selection, we

would expect hybrids to be relatively unfit due to a mating disadvantage: both parental species discriminate against songs with pulse rates typical of F1 hybrids. Selection against heterospecific mating in areas of sympatry may thus be primarily the result of sexual selection against hybrids (see also Naisbit et al., 2001; Vamossi and Schluter, 1999).

In field crickets the male calling song and female song preference are only one aspect of behavioral premating isolation. Males produce the loud calling song when alone to attract females from a distance. Once a female has contacted a male, he produces a very distinct type of song called the courtship song (Alexander, 1961). Courtship always precedes mating, and female crickets have previously been shown to exhibit mating preferences dependent on male courtship song (Wagner and Reiser, 2000). Thus, in areas of sympatry, male and female courtship interactions may additionally function to limit gene flow among species. This is not to imply that courtship interactions are a primary mechanism of species isolation. That function is clearly served by the calling song. Nonetheless, because they are requisite preludes to mating, courtship interactions may be subject to selection as isolating mechanisms. This is especially true in dense populations where a substantial number of mating interactions may be initiated without female phonotaxis to calling song, i.e., noncalling satellite and/or silent mate searching strategies are more effective at high density (Cade and Cade, 1992; Cade and Wyatt, 1984; Hissmann, 1990). By examining courtship interactions, we can assess both male and female components of species recognition: males may or may not court females, and females may or may not mount courting males. With this in mind, I conducted an experiment to address the following: (1) Do courtship interactions serve as an effective premating isolating mechanism? (2) Are both males and females discriminating? (3) Do allopatric and sympatric populations of crickets differ in conspecific versus heterospecific discrimination?

METHODS

Crickets were reared at large population sizes under standardized laboratory conditions ($25 \pm 2^\circ\text{C}$; 14:10 h light:dark photoperiod). Crickets had ad libitum access to food (cat chow) and water in cotton plugged vials. Cultures were established from field collections in Austin, TX in 1999 and 2000 (allopatric *G. texensis*), Tuscaloosa, AL in 1999 and 2001 (both *G. texensis* and *G. rubens* in sympatry), and Gainesville, FL in 2000 and 2002 (allopatric *G. rubens*, year 2000 collections courtesy T. J. Walker and M. Velez). Adults used in the experiments were removed from culture within 48 h of the adult molt. This ensured that all crickets were virgins (Solymar and Cade, 1990). Newly molted adults were individually isolated, given food and water, and held at room temperature ($\sim 22 \pm 3^\circ\text{C}$) until a minimum adult age of five days for males and six days for females. These adults were moved to a separate room and held for testing.

To ensure sexual readiness, only calling males were used as test subjects. When I heard a male calling, I removed him from his individual container, carefully cut the right forewing just anterior to the file, and removed the entire dorsal portion of the wing modified for sound production, leaving the lateral field intact. This effectively rendered the male entirely mute, but made it very easy to see the natural wing motions when the male subsequently attempted to court. Muted males were placed in a 70 mm diam clear plastic tube with a mesh screen bottom and given a minimum of 3 min acclimation. The male in the mesh screen bottom tube was then placed directly over a high-frequency tweeter (Radioshack 40-1233,

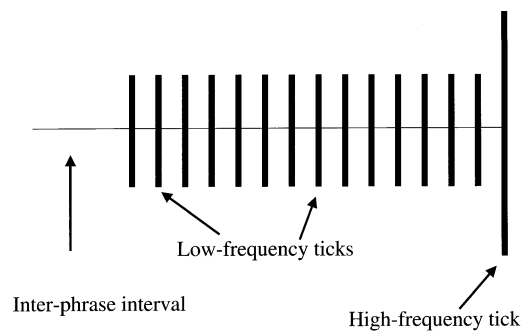


Figure 1
Schematic of generalized *Gryllus* courtship song showing features referred to in the text and in Table 1.

3.8 kHz – 30 kHz \pm 2 dB, dB re: 20 μ Pa) attached to a laptop PC. I used CoolEdit 2000 (Syntrillium software, Scottsdale, AZ) running on the laptop to generate and play back species-typical courtship song. *Gryllus* courtship songs have a series of quieter lower-frequency pulses (~5 kHz) followed by a single loud higher frequency pulse (~12 kHz peak) and a silent interval (Figure 1). I used previously recorded high and low frequency ticks to construct species-average courtship songs based on previous courtship song data corrected to 22°C (Fitzpatrick and Gray, 2001; Korody M, Osborn N, Gray DA, unpublished data). The two species' songs differ primarily in the low-frequency tick rate, the number of low frequency ticks, the inter-phrase interval, and the high-frequency tick rate. The song parameters used are given in Table 2.

To determine the combination of species of female and courtship song to be tested, I flipped a coin twice. The first flip determined female test species from available suitably aged females; the second flip determined which species' courtship song would be played if the male were to court. There were not always females of both species available for testing, however, so in those instances no coin flip was done for female species. The test female was gently introduced into the clear plastic tube and the trial time started once the crickets had contacted each other with their antennae. Males were allowed 10 min within which to court the female, otherwise the trial was ended and 'no courtship' was recorded for the male. If the male courted, I played the randomly determined courtship song during the time that the male actively courted the female. If the male stopped courting, I stopped playback; when the male resumed courting, I resumed playback, such that the male behavior and the acoustic stimulation were always presented simultaneously. I allowed for two min of cumulative courtship time for the female to mount the male, otherwise 'no mount' was recorded for female receptivity. Based on a pilot experiment, two min was judged to be ample time for receptive females to mount (for conspecific pairings during the main experiment, the mean \pm SD time to mount was 24 \pm 22 s). If the female did mount the male, I scored female receptivity as a 'mount' and noted the cumulative courtship time that had elapsed prior to mounting. In the event that a male courted a female, but then stopped prior to two min of cumulative courtship without resuming courtship within an additional five min, I scored male courtship as 'incomplete' and did not record data on female receptivity. In practice, this happened in only 11 of the trials, so these trials were simply discarded. The inclusion or exclusion of 'incomplete' courtship trials does not affect the results or conclusions. Males and females were used only once each. One-tailed statistical tests are used as appropriate for a priori directional hypotheses.

Table 2

Characteristics of courtship songs used in this study

Song component	<i>Gryllus rubens</i>	<i>Gryllus texensis</i>
High-frequency tick rate	1.8 /s	3.4 /s
Tick = 14 ms pulse, 11.5 kHz peak		
Low-frequency tick rate	50 /s	62.5 /s
Tick = 8 ms pulse, 4.8 kHz		
Low frequency ticks per phrase	25	14
Inter-phrase interval	40 ms	50 ms

Songs are species-average at 22°C.

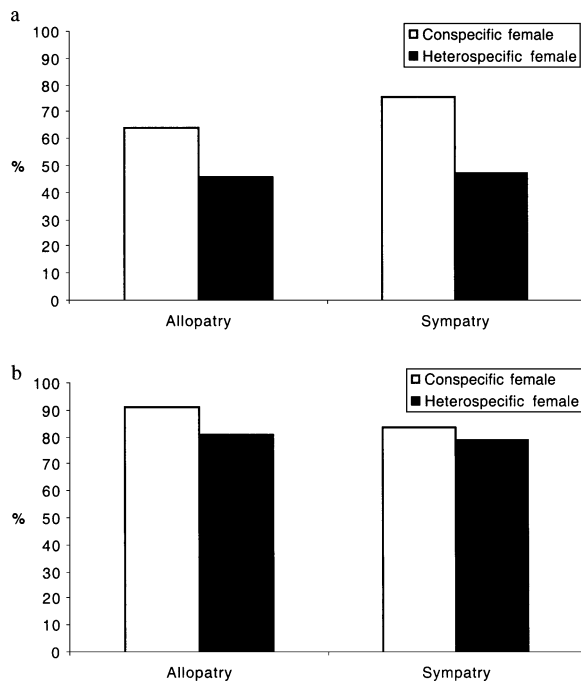
RESULTS

A total of 568 trials were completed. Trial temperatures averaged 22.7 \pm 1.6°C (mean \pm SD, range 18.7 to 26.3°C), well within the natural range of temperatures experienced by crickets in the field. Tested males ranged in age from 5–32 days old (mean \pm SD = 12.8 \pm 5.5); tested females ranged in age from 6–26 days old (mean \pm SD = 11.1 \pm 4.4). Males courted females in 363 of those trials (64%).

Given that cricket behavioral responses to acoustic cues may change with temperature (Pires and Hoy, 1992) or female age (Gray, 1999; Prosser et al., 1997), I used logistic regression to test if the probability of a female mounting a courting male was dependent on either the test temperature or female age. In no instance was test temperature close to a significant predictor within the range of trial temperatures used here (P values range from .085 to .932). Female age was likewise not significant in all cases but one (P value of .007 for allopatric *Gryllus rubens* females tested with *G. rubens* males; for other comparisons P values range from .09 to .838). In the allopatric *G. rubens* females' case, older females were less likely to mount males than were younger females (mean \pm SD age of females that mounted = 11.4 \pm 3.7 days, mean \pm SD age of females that did not mount = 16.6 \pm 5.6 days). Thus, in no case were older females more likely to mount males, as might have been expected if older virgin females discount male quality in an effort to obtain sperm.

Males of both species readily courted females of both species (Figure 2). However, *G. rubens* males were significantly less likely to court heterospecific females: *G. rubens* males courted with conspecific females in 95 of 137 trials (69%) and with heterospecific females in 81 of 174 trials (46%) (Fisher's Exact Test, one-tailed, $P < .000$). *G. texensis* males showed a similar but nonsignificant trend: *G. texensis* males courted 90 of 102 conspecific females (88%) and 97 of 121 heterospecific females (80%) (Fisher's Exact Test, one-tailed, $P = .073$). The responses of males from allopatric and sympatric populations to heterospecific females did not differ for either species (Figure 2; *G. rubens* Fisher's Exact Test, one-tailed, $P = .642$; *G. texensis* Fisher's Exact Test, one-tailed, $P = .464$).

Female *G. rubens* mounted 71 of 95 conspecifics (75%) and 59 of 97 heterospecifics (61%); female *G. texensis* mounted 67 of 90 conspecifics (75%) and 37 of 81 heterospecifics (46%) (Fisher's Exact Tests, one-tailed, *G. rubens* $P = .028$, *G. texensis* $P = .000$). Similarly, when considering courtship song played, female *G. rubens* mounted 77 of 94 males accompanied by conspecific courtship song (82%) and 53 of 98 males accompanied by heterospecific courtship song (54%); female *G. texensis* mounted 65 of 86 males accompanied by conspecific courtship song (76%) and 39 of 85 males accompanied by heterospecific courtship song (46%) (Fisher's Exact Tests, one-tailed, *G. rubens* $P = .000$, *G. texensis* $P = .000$). Figure 3 shows these data separately for each species, with trials distinguished by whether

**Figure 2**

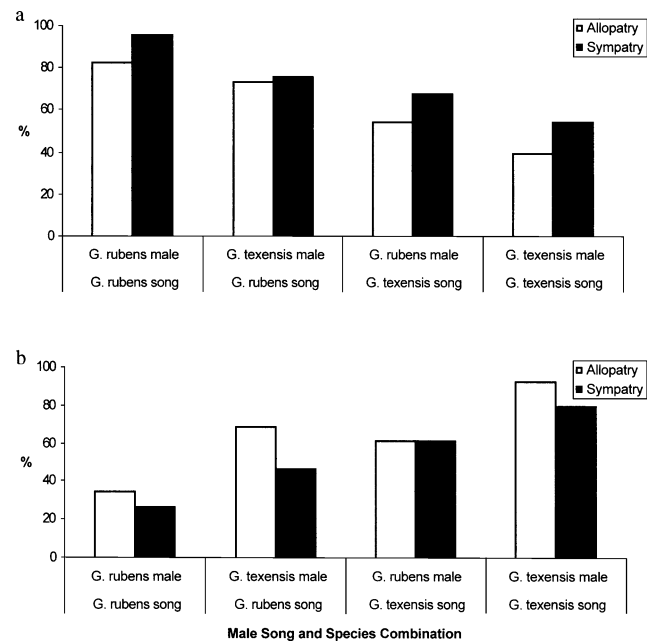
Male mate discrimination. The percentage of male *Gryllus rubens* (a) and *G. texensis* (b) that courted conspecific and heterospecific females; males from allopatric and sympatric sites are shown separately.

the female was from a sympatric or allopatric population. Allopatric and sympatric females' responses to heterospecific males or heterospecific song did not differ for either species (female *G. rubens* response to *G. texensis* males, Fisher's Exact Test, one-tailed, $P = .240$, response to *G. texensis* courtship song $P = .112$; female *G. texensis* response to *G. rubens*, Fisher's Exact Test one-tailed, $P = .429$, response to *G. rubens* courtship song $P = .092$).

These results can be subdivided more finely to address two additional questions: (1) can females use both species differences in courtship song and male species identity per se to limit heterospecific matings, and (2) are the responses of female *G. texensis* and female *G. rubens* similar, or is there asymmetry in species discrimination at the courtship level? That fact that male *G. rubens* were significantly more likely to court conspecific females (see above) suggests the presence of other species-specific cues, possibly pheromonal. Table 3 presents comparisons of female mating behavior holding constant either the species of test male or the courtship song played. Female *G. texensis* preferred both conspecific males per se and conspecific courtship song (conditional probabilities by Fisher's Exact Test, all $P < .01$). For female *G. rubens* the situation was more complex. Female *G. rubens* preferred conspecific courtship song ($P = .002$ if paired with a male *G. rubens* and $P = .004$ if paired with a male *G. texensis*). Female *G. rubens* did not show a preference for conspecific males per se if accompanied by *G. texensis* song ($P = .112$) or if accompanied by *G. rubens* song, although the results approached statistical significance ($P = .064$).

DISCUSSION

These results are of interest for several reasons. First, sexual selection theory as applied to species isolation predicts that females should be more discriminating than males in terms of

**Figure 3**

Responses of (a) *Gryllus rubens* and (b) *G. texensis* females to conspecific versus heterospecific males and conspecific versus heterospecific courtship songs for females from allopatric and sympatric populations.

conspecifics versus heterospecifics. This prediction is supported by the present data, especially in the case of *G. texensis*, in which males courted heterospecific females almost as readily as conspecifics. Second, both species identity and courtship song appear to be used in courtship interactions, although differently by males and females of each species. Male *G. rubens*, but not male *G. texensis*, were less likely to court heterospecific females. Female *G. texensis*, but not female *G. rubens*, appeared to discriminate against heterospecifics per se, irrespective of auditory cues. The non-acoustic mechanism for species identification used by male *G. rubens* and female *G. texensis* is unknown at present, but preliminary data suggest that cuticular hydrocarbon differences are one possibility (Lapaz L, Gray DA, unpublished data; see also Tregenza and Wedell, 1997).

The third finding of general significance is that for none of the measures used was there a difference in species-level discrimination between populations from allopatric and sympatric localities. That the responses of males and females of neither species differed between allopatric and sympatric populations suggests that the observed conspecific versus heterospecific discrimination did not develop due to selection to avoid heterospecific matings (i.e., reinforcement or a similar process). This is important in that it indicates that the differences between the species may be the result of sexual selection operating within each species, although genetic drift is also a possibility.

The final noteworthy result is that despite the statistical significance of the species-level discrimination, the observed levels of mate discrimination by both males and females are far too low to act effectively as a species-isolating mechanism. Some of the variation in mating behavior may result from the range of test temperatures; however, such variation is unlikely to produce any bias with respect to conspecific/heterospecific recognition. Combining male and female responses based on the data presented here, approximately 40% of courtship interactions between male *G. texensis* and female *G. rubens* are

Table 3

Independent effects of species of test male and song played on female response

Female species	Male species	Song played	N trials	% of trials females mounted	Fisher's Exact Test, one-tailed <i>P</i>	Tested effect
<i>G. rubens</i>	<i>G. rubens</i>	<i>G. rubens</i>	46	89%	.002	Song
		<i>G. texensis</i>	49	61%		
<i>G. rubens</i>	<i>G. texensis</i>	<i>G. rubens</i>	48	75%	.004	Song
		<i>G. texensis</i>	49	47%		
<i>G. rubens</i>	<i>G. rubens</i>	<i>G. rubens</i>	46	89%	.064	Species
		<i>G. texensis</i>	48	75%		
<i>G. rubens</i>	<i>G. rubens</i>	<i>G. texensis</i>	49	61%	.112	Species
		<i>G. texensis</i>	49	47%		
<i>G. texensis</i>	<i>G. texensis</i>	<i>G. texensis</i>	47	87%	.004	Song
		<i>G. rubens</i>	43	60%		
<i>G. texensis</i>	<i>G. rubens</i>	<i>G. texensis</i>	39	62%	.005	Song
		<i>G. rubens</i>	42	31%		
<i>G. texensis</i>	<i>G. texensis</i>	<i>G. texensis</i>	47	87%	.006	Species
		<i>G. rubens</i>	39	62%		
<i>G. texensis</i>	<i>G. texensis</i>	<i>G. rubens</i>	43	60%	.006	Species
		<i>G. rubens</i>	42	31%		

expected to result in mating. Similarly, for interactions between male *G. rubens* and female *G. texensis*, approximately 15% are expected to result in mating.

Taken together, these results can be used to assess the directionality of the interaction between reproductive behavior and speciation. If reproductive behavior evolved in response to speciation so as to limit hybridization, we would expect (1) a highly effective barrier to gene flow to result, (2) both male and female discrimination, and (3) stronger selection in sympatry. Alternatively, if reproductive behavior evolved via sexual selection within subdivided gene pools, we would expect (1) greater female mate discrimination, (2) a weaker interspecific barrier to gene flow, and (3) no reproductive character displacement. The data presented here are more consistent with the second possibility: courtship behavior evolved via intraspecific processes within gene pools largely separated by behavioral isolation via the long-range calling song. It is particularly interesting to note that the responses of the two species are not identical. *Gryllus texensis* males and females meet predictions from the sexual selection hypothesis quite well: females are choosy but males are not, neither sex shows reproductive character displacement, and the choosiness, such as it is, would not provide an effective barrier to gene flow. The results for *G. rubens*, on the other hand, appear less straightforward. However, the two strongest predictions of the classical speciation/reinforcement model, namely reproductive character displacement with a resultant effective barrier to gene flow, do not seem supported in *G. rubens*. Thus, in these species it appears that courtship behaviors may promote species integrity, but they result from sexual selection and/or genetic drift operating within species, and not as a consequence of the speciation process. These results are entirely consistent with the generally accepted notion that the cricket calling song serves a species-recognition function, whereas the courtship song potentially serves a quality signaling function (Alexander et al., 1997; Zuk and Simmons, 1997).

These results also highlight a more general, but sometimes underappreciated, issue in the study of sexual signaling and species isolation. Male signals and female responses to those signals may often interact in such a way as to reduce the

likelihood of interspecific gene flow. However, this in no way implies that limitation of gene flow is the evolved function of interspecific differences in male ornamentation and female preferences. In many systems such as this, limitation of interspecific gene flow may be an incidental consequence of sexual selection operating within species.

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