Pulse Rates in the Songs of Trilling Field Crickets (Orthoptera: Gryllidae: *Gryllus*)

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ABSTRACT   In cricket calling songs, pulse rate is often the feature that allows females to home on the songs of conspecific males while ignoring those of other species. A previous study of the sibling species *Gryllus rubens* Scudder and *G. texensis* Cade & Otte from western Florida showed unexpected effects of developmental conditions and parental generation on the pulse rates of their songs. The current study tested for these and other effects in *G. rubens* from Gainesville, FL, and *G. texensis* from Dallas, TX. In both species, sibships from different field-fertilized females differed significantly in the effects of rearing environment on the pulse rates of their songs. Tests for effects of nymphal diapause and adult age were negative. Hybrids between the two species produced pulse rates intermediate to the rates of the control crosses. Males of *G. rubens* reared at 32°C produced faster pulse rates (at a standard temperature) than those reared at 25°C. Furthermore, pulse rates of field-collected males in this study and of field-collected and laboratory-reared males in the previous study increased in rough proportion to the known and estimated temperatures during nymphal development.

KEY WORDS   crickets, calling songs, developmental effects, age effects, hybrids

THE RESEARCH REPORTED here was prompted by an earlier study in which I concluded that two field cricket species distinguished only by the pulse rates of their calling songs occur in mixed populations in western Florida (Walker 1998). A continued dichotomy in the pulse rates of callings songs during a 6-yr study supported the hypothesis that introgression between the two species was little or lacking. Also supporting this hypothesis were the songs of laboratory-reared sons of field-fertilized females. Males of each sibship had similar pulse rates, and the mean pulse rates of sibships were clearly dichotomous. Of 21 sibships from females collected in a vacant lot in Milton, FL, 25 September 1982, 11 were *Gryllus rubens* Scudder and 10 were *G. texensis* Cade & Otte.

The most surprising conclusion of the western Florida study was that developmental conditions and parental generation affected the pulse rates of calling males. Both *G. rubens* and *G. texensis* are bivoltine as revealed by a spring peak of adult abundance, when overwintering nymphs mature, and a fall peak, when the progeny of the spring generation mature. *G. rubens* males collected in the spring had a mean pulse rate of 48.6, whereas males reared from fall-collected females (which in the field would have been spring males) had a mean pulse rate of 51.8. *G. rubens* males collected in the fall had a mean pulse rate of 58.6 and males reared from spring-collected females had a mean pulse rate of 55.3. Thus, both spring and fall generation *G. rubens* males differed in pulse rate depending on whether they developed under field or laboratory conditions. Field-reared *G. rubens* differed in pulse rate depend-

ing on their generation, and males reared in the laboratory under similar conditions differed in pulse rate depending on the generation of their parents. No spring generation *G. texensis* were collected, but fall males of *G. texensis* and the sons of fall-collected females had mean pulse rates of 77.6 and 70.6, respectively, the same relationship as exhibited by the corresponding classes of *G. rubens* (58.6 and 51.8)

In crickets, pulse rate of a given species at a given temperature generally varies little and is an important determinant of female response to the song (Walker 1957, 1962; Doherty and Callos 1991). In fact, the songs of trilling species that sing together frequently differ only in their pulse rates. Therefore, developmental effects on pulse rate, which would make the calls less species-specific, should have reproductive disadvantages and be minimized by natural selection. In the only case where pulse rate differences attributable to developmental environment have been sought, Walker (1962) found the songs of spring and fall generation *Oecanthus argentinus* Saussure indistinguishable, though the songsters developed under contrasting temperatures and photoperiods.

In the current study, I used *G. rubens* from Gainesville, FL, and *G. texensis* from Dallas, TX, to test whether the following factors influence pulse rate: sibship (mother), parental generation, temperature and photoperiod during development, nymphal diapause, adult age, and interspecific hybridization.

In articles published before 2000, *G. texensis* was called *G. integer* Scudder, even though the former species was judged distinct from *G. integer* as early as

1980 (Weissman et al. 1980). Smith and Cade (1987) showed that *G. integer* from California (its type locality) would not produce offspring in laboratory crosses with "integer" from Austin, TX, or with *G. rubens* from McAlester, OK. Walker (1998) confirmed the distinctness of *G. rubens* and *G.* "integer" where they overlap, and Cade and Otte (2000) described "integer" as *G. texensis.*

Materials and Methods

Specimens. Robert L. Crocker collected fall generation *G. texensis* by broadcasting synthetic *G. texensis* calling song at Dallas, TX, 10 October 1996. On 20 May 1997, he collected spring generation *G. texensis* at Dallas, and at a nearby site in Ft. Worth, by broadcasting synthetic calling song and by inspection. At Gainesville, FL, I collected *G. rubens* using broadcasts of synthetic *G. rubens* song (Walker 1996). Fall generation females were collected 21 and 24 September 1996 and spring generation females were collected 17 May 1997. Males were collected in 11 of the 14 mo between September 1996 and October 1997.

Rearing. Crickets were reared as described by Wineriter and Walker (1988). The 3.8-liter rearing jars were serviced weekly. Six to eight field-collected females representing each generation and species were placed individually in jars with damp sand for oviposition and held in a rearing room at 25 ± 1°C and a long-day photoperiod of 16:8 (L:D) h. Females were removed no later than the week after first hatch. No later than 4 wk after first hatch, most sibships that had >120 juveniles were divided evenly among three fresh jars. For each of these sibships, one jar was left in the rearing room under 25°C and long days (16:8 [L:D] h); another was placed in a Florida Reach-In environmental chamber (Walker et al. 1993) that maintained a short day (11:13 [L:D] h) and 25.0 ± 0.2°C; and a third was placed in a similar chamber at 32.0 ± 0.2°C and a photophase of either 16 or 11 h. For spring- and fall-collected female *G. rubens* and for spring-collected *G. texensis*, three sibships each were divided as described above. For fall-collected *G. texensis*, no female produced >35 progeny; therefore, 5 wk after initial hatch, the 65 progeny in a jar that had held three field-collected females were divided into three cohorts and put in fresh jars as described above. Members of this trio of cohorts were potentially from three mothers and, therefore, unlikely to be as closely related as the members of other trios, which had a single mother. To simplify references to the four rearing conditions, I used three-character abbreviations that denote their temperature (25 or 32°C) and daylength (long or short)—namely, 25L, 25S, 32L, 32S.

Hybrid Study. The four possible crosses were made between Gainesville *G. rubens* and Dallas *G. texensis*. *G. texensis* were from the F_2 generation of a colony established with fall generation parents and reared under 25L conditions. Female *G. rubens* were from the F_1 generation of a colony established with spring generation parents and reared under 32S conditions. Male *G. rubens* were collected at broadcast song, 3 May to

3 June 1997. Females to be used in the crosses were isolated from males as nymphs to ensure virginity. For each cross, five pairs of crickets were established in individual wide-mouth, 1-liter jars one-fourth filled with damp sand. Parents were removed when dead or when their progeny began to hatch. Hatchlings were transferred to 3.8-liter rearing jars corresponding to their cross and replicate. When numerous F_2 hatchlings were noted in the rearing jar of a TxR sibship, they were reared and the songs of males recorded. All crosses were made and reared in a room held at 25 ± 1°C and a photoperiod of 16:8 (L:D) h.

Tape Recording. As sons of field-collected females or laboratory-crossed pairs matured, they were transferred to individual 120-ml glass or plastic containers with screen lids, assigned an identification number, and placed in an array on a table in a windowed room kept at 25 ± 2°C. They were fed oat cereal and small pieces of apple, which also provided moisture. I initially monitored the array >4 h a day and recorded songs whenever I could. When I found that most calling occurred at dawn or when lights were turned on before or during dawn, I made that a regular time for recording. Recordings were made with a reel-to-reel tape recorder (Nagra IV, Kudelski, New York, NY) and a dynamic microphone (D33, American, New York, NY) affixed to one end of a 0.4-m shaft. In each taping session, I tried to make a 20-s recording of each calling male that had not been recorded within 24 h. Temperature was measured after each recording with an electric thermometer (BAT-12, PhysiTemp, Clifton, NJ) from a copper-constantan thermocouple at a container near the center of the array. A cylinder made from a 13 by 18-cm card surrounded each container to keep callers from seeing the approach of the microphone. Twice-recorded crickets were usually killed, pinned, labeled, and placed in the Florida State Collection of Arthropods. To determine whether pulse rate changes with adult age, eight males, from fall-collected *G. rubens* females, were taped again 25 or more days after their second taping.

Analysis of Taped Songs. The calls of trilling field crickets often have frequent, brief, irregularly occurring delays in what would otherwise be a uniform series of pulses. These delays interfere with measuring the fundamental pulse rate in taped songs of *G. rubens* and *G. texensis*. I overcame this difficulty by using a custom program that produces a histogram of all pulse periods (pulse plus pulse interval) in a 16.4-s digitized sample of song. The modal pulse period is noted from the histogram, and its reciprocal, the modal pulse rate, estimates the fundamental pulse rate (Walker 1998).

Pulse rate varies predictably with the temperature of the singer's immediate surroundings. I adjusted pulse rates to the standard temperature of 25°C with this formula, where R_x is the pulse rate (sec^{-1}) at temperature *x*, and R_{25} is the expected rate at 25°C:

$$R_{25} = 20R_x / (x - 5).$$

The formula assumes that pulse rate is a linear function of temperature that extrapolates to 0 at 5°C (Walker 1975). The same formula was used for both

species because estimates of the x-intercepts for the regression of pulse rate on temperature are similar for the two species: 4.8 for *G. rubens* (Walker 1962) and 4.2 and 5.7 for *G. texensis* (Souroukis et al. 1992).

When temperature adjustments were applied to the modal pulse rates of the two recordings of a single male, the rates usually became closely similar. When they did not, the discrepancy could sometimes be traced to an unusual amplitude modulation pattern within the pulses of one of the recordings. To make the elimination of such analyses objective, the difference in the two pulse-rate determinations was compared with one-tenth of their mean. If the former was greater than the latter, that male's data were eliminated from further analysis. If more than two recordings had been made of a male, the two with the most similar pulse rates were kept and the test applied.

Statistical Procedures. SAS Institute (1997) general linear models (GLM) and mixed procedures were used for most analyses. Specifics are given with results. Regression analyses were with Microsoft Excel 97. Significance was defined as $P_\alpha \leq 0.05$.

Results

Sibship Effect. Sibship, within generation, had a significant effect in both species —i.e., the mother of the sibs or half-sibs that were divided among three rearing conditions affected the mean modal pulse rate of the generation. Because no males matured in one of the 32L cohorts in *G. texensis* and because the 32°C treatments used different photoperiods in the two generations (Fig. 1), 32L and 32S treatments were omitted when applying the GLM procedure, tests of hypotheses for mixed model analysis of variance (ANOVA). In neither *G. texensis* nor *G. rubens* was the sibship × environment (within generation) interaction significant ($F = 0.76, 1.86$; df = 1, 39; 4, 103; $P = 0.39, 0.12$). Therefore, that interaction was omitted in calculating the statistics for sibship (within generation) effects. For this effect in *G. rubens*, $F = 6.44$; df = 4, 107; and $P = 0.0001$; for this effect in the fall generation of *G. texensis*, $F = 5.77$, df = 2, 39; and $P = 0.0064$. The spring generation of *G. texensis* did not contribute to the analysis because the data were from a single trio of cohorts (with three mothers, and thus not a sibship).

Generation Effect. Using SAS mixed procedure both with the full data set for each species and with the 32S and 32L data omitted, I found no effect of generation. For *G. rubens*, the ANOVA values for the full and partial data sets were $F = 3.63, 2.91$; df = 1, 4; 1, 4.40; $P = 0.13, 0.16$; for *G. texensis*, full and partial, $F = 0.28; 0.29$; df = 1, 2; 1, 2; $P = 0.65, 0.64$.

Effects of Rearing Environment. Using SAS mixed procedure for the full data set for each species, I found a significant effect of rearing environment for *G. rubens* ($F = 11.10$; df = 3, 8; $P = 0.003$) but not for *G. texensis* ($F = 0.36$; df = 3, 3; $P = 0.79$). In intrasibship comparisons of mean modal pulse rates, the 32°C treatment always had a faster pulse rate than the 25°C treatment of the same photoperiod (Fig. 1). Using the

Fisher method of combining independent t-tests (Birnbaum 1954), I found that the association of the higher temperature with the faster pulse rate was significant for *G. rubens* ($\chi^2 = 45.7$, df = 12, $P < 0.001$) but not for *G. texensis* ($\chi^2 = 9.29$, df = 6, $P = 0.32$).

Sound-Trapped *G. rubens*. Of the 113 sound-trapped *G. rubens* monitored for calling, only 27 sang often enough and long enough to be included in the analysis. When modal pulse rates of sound-trapped males were regressed on Julian day of collection, a second-order polynomial accounted for a significant amount of the variation ($r^2 = 0.24; F = 3.76$; df = 2, 24; $P = 0.038$) (Fig. 2).

Adult Age of Caller. When crickets that had been recorded on the earliest 2 d of calling were recorded again after a delay of 25 or more days, modal pulse rates had not changed significantly ($F = 0.17$; df = 1, 22; $P = 0.68$) (Fig. 3).

Diapause. When progeny of fall- or spring-collected *G. rubens* females were reared at 25°C and a photoperiod of 11:13 (L:D) h, their final molts were asynchronous and bimodal (Fig. 4A). Males maturing in the second peak had diapaused as nymphs before completing their development. To judge whether the pulse rates of diapause males differed from those of nondiapause males, modal pulse rates of males in four sibships were regressed on date of maturation. The slopes of the regressions ranged from –0.04 to +0.03, and none was significant. When I pooled the four sibships by converting dates of maturation to weeks of developmental delay, the regression was again not significant ($F = 0.22$; df = 1, 66; $P = 0.64$) (Fig. 4B),

Hybrids. In each of the crosses, three or four of the five replicates produced progeny. The songs of 4–18 males in each sibship were recorded twice. Based on SAS GLM mixed model ANOVA, both cross and sibship had significant effects (for cross, $F = 78$; df = 3, 9; $P = 0.0001$; for sibship, within cross, $F = 2.61$; df = 9, 94; $P = 0.01$). The mean modal pulse rates of the R♂×T♀ and T♂×R♀ crosses were intermediate to those of the control crosses (Fig. 5). The mean of the R×T cross was 61.9 ($n = 32$), exactly intermediate between 51.8 and 72.0, the means for the R×R and T×T crosses. The mean of the T×R cross was 59.2 ($n = 30$). The difference between the reciprocal hybrid crosses was not significant (ANOVA, least significant difference). The modal pulse rates of 14 F_2 males from one of the T×R sibships did not differ from those of 15 F_1 males from the same sibship in either variance ($F = 1.44$, df = 13,14, $P = 0.51$) or mean (58.8 versus 60.4) ($T = 0.97$, df = 17, $P = 0.34$) (SAS t-test procedure). F_2 hatchlings were noted in one of the jars in which an R×T sibship had been reared, but these were not reared and tape recorded.

Discussion

Sibship Effects. The design of this study assumed that sibship effects would be minor enough to allow pooling of the males from different sibships. This proved not to be the case, and the small number of sibships studied per species per generation (three or
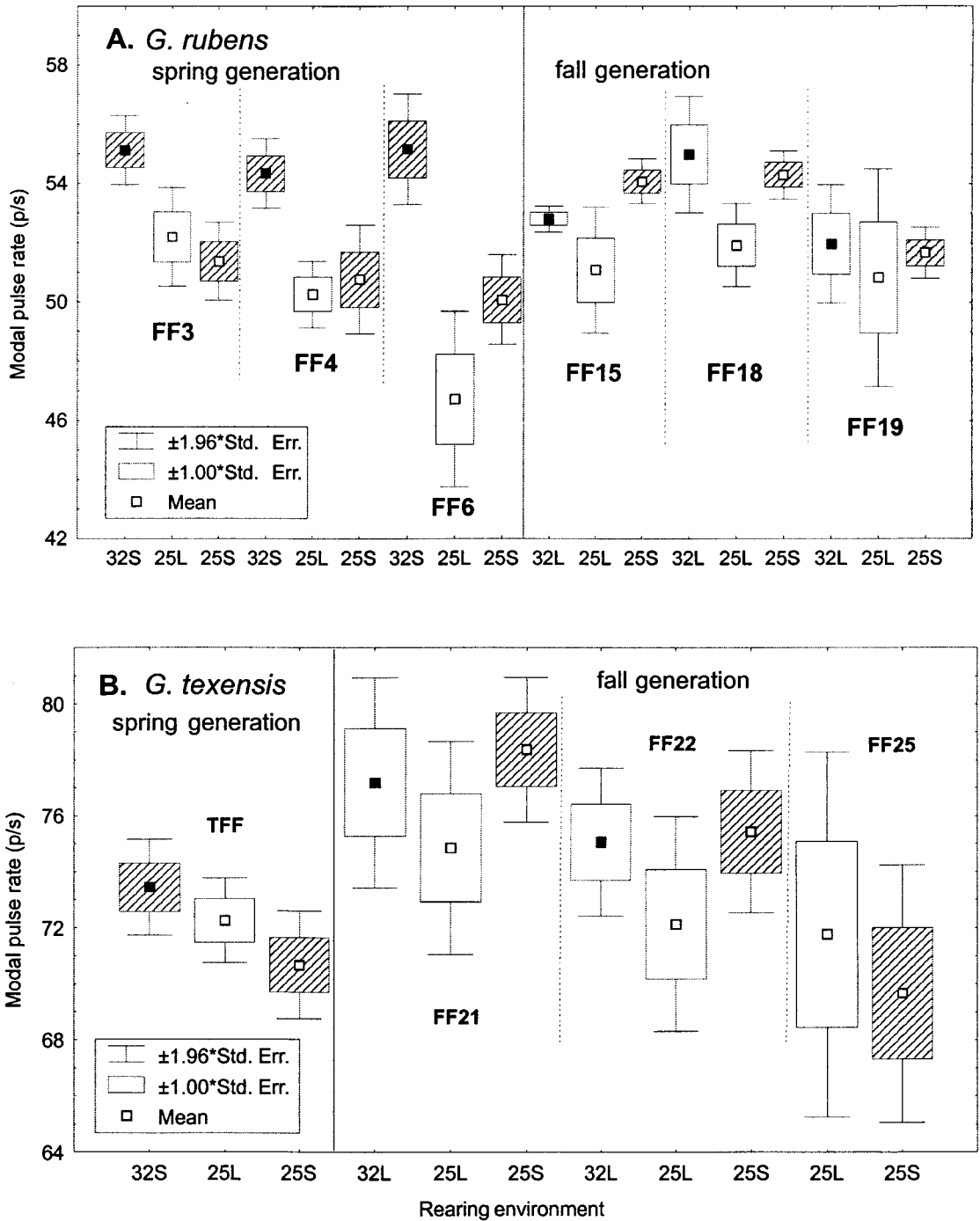
Fig. 1. Effect of sibship and rearing environment. Mean modal pulse rates and standard errors of cohorts reared at 32°C and either long day or short day (32S or 32L), 25°C and long day (25L); or 25°C and short day (25S). Vertical lines separate cohorts with different maternity. For each cohort, the rearing temperature is indicated by the mean being open (25°C) or filled (32°C); the photophase is indicated by the bar being open (long) or hatched (short). FF, field-collected female; TFF, three field-collected females. (See text for details.) A. *G. rubens*. B. *G. texensis*.

fewer) reduced the likelihood that effects of generation and rearing conditions on pulse rate would be detected.

Sibships effects are most likely genetic but could also result from maternal effects (Mousseau and Dingle 1991). The field-collected females I used had ex-
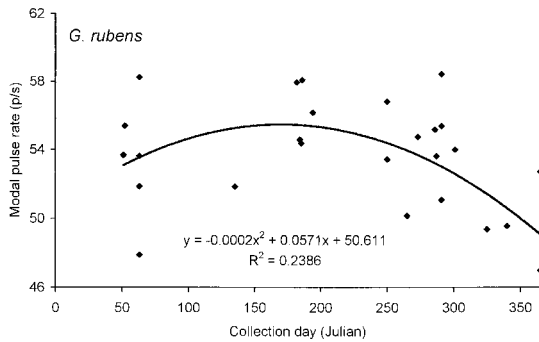
Fig. 2. Effect of season. Modal pulse rate of 27 male *G. rubens* collected at broadcast calling song on various dates between 22 September 1996 and 13 September 1997. The regression is significant ($P = 0.038$).

perienced different environments, but there is little reason to suspect that these differences influenced the pulse rates of their sons. The genetic differences among sibships of this study were probably reduced by the mothers mating with multiple males. Given the opportunity, female *Gryllus* usually mate repeatedly (Solymar and Cade 1990). Matings with different males would lead to sperm mixing (Backus and Cade 1986), which would in turn cause a female's progeny to be a mixture of sibs and half-sibs. The effect of mixed paternity would be to increase genetic variation within sibships, thus reducing the likelihood of large genetic differences among sibships.

Little is known of the genetics of calling-song pulse rates. In a study of *Gryllus firmus* Scudder, Webb and Roff (1992) found significant heritability in four morphological features and in pulse rate, but not for the other four components of song they studied. For both morphological and song features, heritability through the dam was considerably higher than heritability through the sire, suggesting the occurrence of maternal or nonadditive effects. Gray and Cade (1999)
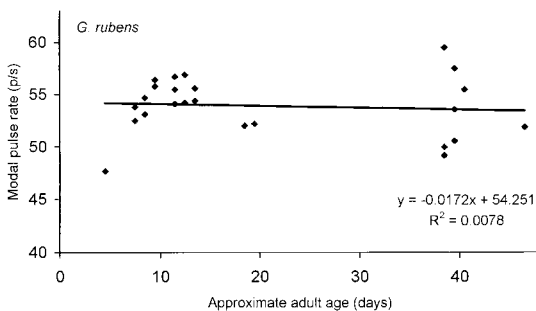

Fig. 4. Effect of nymphal diapause. (A) Time of final molt for short-day-reared sons of four field-collected *G. rubens* females. Week 0 is the week the earliest male in each sibship completed its final molt. Females FF3 and FF4 were collected 21 and 24 September 1996; FF15 and FF19 were collected 17 May 1997. (B) Modal pulse rates of 67 sons of these four females plotted against developmental delay. The regression is not significant ($P = 0.64$).

showed that ≈39% of the variation in pulses per trill in *G. texensis* was caused by additive genetic variation but reported no analysis of variation in pulse rate.

Generation Effects. In my western Florida study (Walker 1998), I reported a generation effect in *G. rubens* based on sons of fall parents (i.e., spring generation males) having significantly slower pulse rates than sons of spring parents when reared under the same rearing-room conditions (25 ± 1°C and 16:8 [L:D] h). Means were 51.8 and 55.3. In *G. texensis*, no

Fig. 3. Effect of adult age of male. Modal pulse rates of three recordings for each of eight males plotted against their approximate age on the date of recording. Each third recording (cluster at right) was made 25 or more days after the corresponding second recording. Ages are approximate because males were harvested from rearing jars weekly. (Harvested males were assigned an initial age of 3.5 d.)
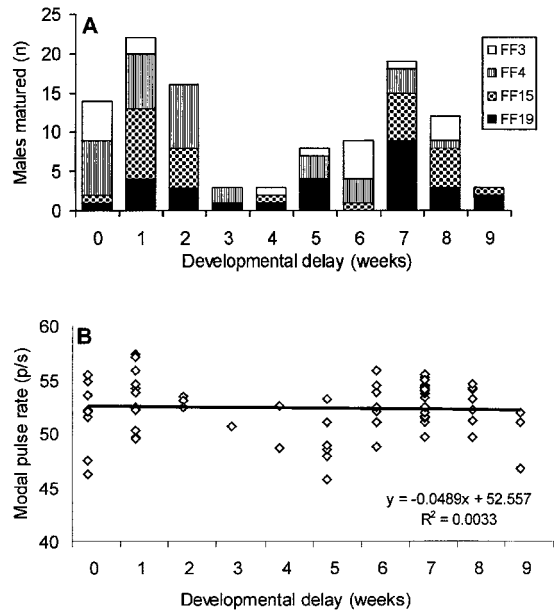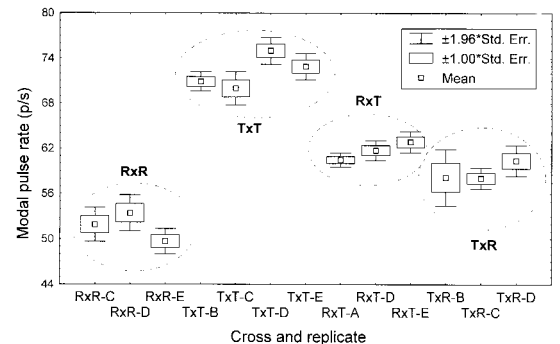

Fig. 5. Effects of crosses. Mean modal pulse rates and standard errors of replicated crosses of *G. rubens* from Gainesville, FL, and *G. texensis* from Dallas, TX. Replicates of the same cross are encircled with a dashed line.

generation effect could be sought, because no spring parents were collected. In the current study, ANOVA showed no generation effect, but another means of analysis supports the hypothesis that spring generation *G. rubens* produce slower pulse rates (other things being equal) than fall generation ones, as in the earlier study. Specifically, for *G. rubens* males reared under 25S conditions, spring generation sibships had mean modal pulse rates of 51.4, 50.8, and 50.1 (grand mean = 50.8) and fall generation sibships had mean modal pulse rates of 54.1, 54.3, 51.7 (grand mean = 53.4). When the Mann–Whitney test is applied to these data, $U = 9$ ($n = 3$ and 3), which gives $P = 0.10$ for a two-tail test (similar to the $P = 0.13$ for the ANOVA) (Zar 1984). However, considering the results of the previous study, a one-tail test is appropriate and $P = 0.05$.

For *G. texensis* the same comparison of mean modal pulse rates is 70.7 (spring) versus 78.4, 75.4, and 69.7 (fall). For sibships of *G. rubens* reared under rearing room conditions, the environment used in the previous study, the spring mean modal pulse rate was 49.7, whereas the fall one was 51.3.

If there is a generation effect, it is not large. Thus, even if female responses to pulse rates did not show a matching generation effect, its influence on sexual pair formation would be small.

Effects of Rearing Environment. The link between faster pulse rates in *G. rubens* with higher temperatures during development explains most of the results of the earlier study. Specifically, it explains why fall males, which developed during the heat of summer, would have faster rates than spring males, which developed during the cooler fall and winter. It would also explain why males reared at 25°C in the laboratory would have rates faster than field-collected spring males but slower than field collected fall males.

The lack of a significant link between high temperature and fast pulse rate in *G. texensis* is attributable to the small number of its sibships reared at contrasting temperatures (Fig. 1). The data for *G. texensis* in this and the previous study are concordant with the effect of rearing temperature being similar in the two species.

No function is apparent for the demonstrated effect of rearing temperature on pulse rate, and I have none to suggest. The simplest hypothesis for its origin and maintenance is that it is an incidental consequence of developmental processes and that these processes affect female response to pulse rates in the same manner as they affect the wing-rub rate of calling males. The lack of an effect of developmental conditions in *O. argentinus*, a tree cricket (Walker 1962), indicates that such effects are not universal in crickets. Olvido and Mousseau (1995) found significant effects of developmental conditions on five characteristics of the songs of *Allonemobius faciatus* (DeGeer), a ground cricket, but they did not analyze pulse rate.

Sound-Trapped *G. rubens*. Only 24% of sound-trapped *G. rubens* males were twice recorded. Parasitism by *Ormia ochracea* (Bigot), a tachinid that is attracted to *G. rubens* song, contributed to this poor success (Walker 1986). Parasitized males die within 10 d, when one or more fly larvae emerge to pupate. Also contributing to the scanty data for sound-trapped *G. rubens* were the early, unexplained deaths of males captured in April and May 1997. Most died within 1 wk, and only one of 23 survived as long as 2 wk.

Figure 2 shows that pulse rates, on average, were faster in mid- and late summer, when temperatures of development were high, and slower at other times of year. However, the late winter pulse rates (20 February to 4 March, the leftmost six points) are not the slowest as would be expected if either generation or developmental temperatures were the principal determining factors.

Adult Age of Caller. Spring males of *G. rubens* are likely to be older than fall males, both because some mature late the previous fall and because parasitism by *O. ochracea* is absent or sparse in spring (Walker 1986, 1996). If older males produced slower pulse rates, that might explain why spring males in western Florida had slower mean pulse rates than fall males. This study found no such age effect in *G. rubens.* Similarly, Souroukis et al. (1992) found no significant effect of age on pulse rate in *G. integer* for males 6–50 d past the final molt.

Nymphal Diapause. I suspected that nymphal diapause might be associated with slower pulse rates because that association occurred in the only other ensiferan orthopteran in which developmental conditions are known to affect pulse rate. Whitesell and Walker (1978) reported that males of the katydid *Neoconocephalus triops* (L.) that had experienced adult diapause sang ≈20% slower than males that had experienced no diapause. This effect resembles, in magnitude and direction, the contrast between pulse rates in fall and spring males of western Florida *G. rubens* (Walker 1998). Spring males are likely to have spent the winter as diapausing mid- to late instar nymphs. The data in this study (Fig. 4) do not support an effect of nymphal diapause on pulse rate. However, under field conditions temperatures during diapause would have been much lower and the delay in development would have been much longer than in the 25S conditions of this study.

Hybrids. *G. texensis* and *G. rubens* have produced viable hybrids whenever experimental crosses have been made. This study recorded and analyzed their songs. Smith and Cade (1987) and Cade and Tyshenko (1990) crossed *G. texensis* from central Texas (an area of allopatry) and *G. rubens* from SE Oklahoma and SW Arkansas (near the western extreme of the region of sympatry). Earlier I crossed the two species from Milton, FL (near the eastern extreme of sympatry) (unpublished data). In the current study, both species were from allopatric populations.

The pulse rates of the hybrid sibships were clearly different from and intermediate to the pulse rates of the control sibships (Fig. 5). If it were not for the established sibship effect, the mean pulse rates of the R×T and T×R crosses would have been judged different ($t = 6.4$; df = 13, 14; $P < 0.0001$). Songs of *G. rubens* and *G. texensis* differ in duration of the trills and in frequency of two- and three-pulse groups within

trills. These differences are less diagnostic and are less likely to be important in interspecific isolation than pulse rate. Souroukis et al. (1992) documented intraspecific variation in *G. texensis* songs as to pulses per trill, intertrill interval, and percentage of missed pulses. Wagner et al. (1995) showed that *G. texensis* females preferred songs with more pulses per trill and shorter intertrill intervals but that they did not discriminate between songs that varied in the percentage of missed pulses. The importance of pulse rate in the absence of these factors is illustrated by the fact that both *G. rubens* and *G. texensis* were collected by broadcasting continuous uniform trains of pulses at rates appropriate to the species.

The ready hybridization of the two species in the laboratory (four studies), the fertility of the hybrids (this study and Smith and Cade 1987), and the broad area of sympatry in which the two often intermingle in the same habitats (Walker 1974) suggest that the two might eventually merge. However, there is no evidence that this is occurring. The elegant studies of D. J. Howard and his co-workers on the overlap zones and hybridization of the ground crickets *Allonemobius fasciatus* (DeGeer) and *A. socius* (Scudder) may be relevant here. These two species have songs more similar than those of *G. rubens* and *G. texensis*, and females from some mixed populations did not move preferentially toward conspecific songs (Doherty and Howard 1996). Furthermore, no-choice laboratory mating experiments (such as the ones reported here) showed that interspecific crosses produced many offspring as did F₂ crosses and backcrosses (Gregory and Howard 1993). Nonetheless, within mixed populations in the field few hybrids were found and these usually had genotypes characteristic of backcrosses (Howard 1986, Howard and Waring 1991). Howard et al. (1993) found no microhabitat or phenological conditions that would isolate the species in mixed populations before mating, and showed that individuals with genotypes of mixed ancestry were quite viable in the field. Finally, Gregory and Howard (1994) found a postinsemination, prezygotic barrier that could account for the hitherto unexplained reproductive isolation between *A. fasciatus* and *A. socius*. To simplify, females typically mate more than once, and conspecific sperm, regardless of sequence of mating, are much more likely to fertilize the eggs than are heterospecific sperm. The effectiveness of calling song in isolating *G. rubens* and *G. texensis* is under study (L. Higgins, personal communication), but even if females are seldom attracted to heterospecific songs, they surely come in contact with heterospecific males in the intermingled populations that occur in the zone of overlap (Walker 1974, 1998).

The zone of overlap may be of fairly recent origin. In pre-Columbian times, prairie and woodland habitats were less intermixed than they are now. *G. rubens* is characteristic of disturbed areas throughout the southern portion of the deciduous forest biome, whereas *G. texensis* occurs in the prairie biome and in disturbed areas in the southwestern portion of the deciduous forest biome. These disturbed areas are much more extensive and prairie-like than in earlier times. Therefore, *G. texensis* may have extended its range eastward during the 20th century as have other prairie species, including the crickets *O. argentinus* and *Neonemobius nr. mormonius* (Walker 1974) The northward distribution of both *G. rubens* and *G. texensis* is apparently limited by the long growing season required to complete their bivoltine life cycles (Walker and Masaki 1989).

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