

Trilling Field Crickets in a Zone of Overlap (Orthoptera: Gryllidae: *Gryllus*)

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ABSTRACT A bimodal distribution of pulse rates in field recordings of calling songs suggests that the ranges of the morphologically similar field crickets *Gryllus rubens* Scudder and *G. nr. integer* Scudder (=“*integer*”) overlap for at least 300 km in western Florida. When sons were reared from 42 females collected at 5 sites on 7 trips to this region during 1977-1978, those within a sibship had similar modal pulse rates. At Milton, the westernmost site, 28 of 31 females produced sons with mean modal pulse rates typical of *G. rubens*; the other 3 were among 6 females collected 1 October 1977 and 30 September 1978 and had modal pulse rates in or near the “*integer*” range. None of the 11 females from other sites had sons with a mean modal pulse rate indicative of “*integer*.” Most progenies of females collected at Milton on 25 September 1982 were reared as 2 cohorts of contrasting initial density, and each son was recorded on 2 dates. The mean, temperature-adjusted modal pulse rates of the 39 recorded cohorts, from 22 females, showed no effect of initial density but fell nearly evenly into 2 discrete groups: 46-60 pulses s^{-1} with a mean of 52 (*G. rubens*) and 64-78 pulses s^{-1} with a mean of 71 (“*integer*”). Lack of intermediate sibships indicates that *G. rubens* and “*integer*” remain distinct in their zone of overlap. A spring-adult generation of “*integer*” in western Florida is postulated but not confirmed. Reared under the same conditions, *G. rubens* males from fall females had a significantly lower mean modal pulse rate than males from spring females (52 versus 55), indicating a parental effect. *G. rubens* males reared from fall females had a significantly higher mean modal pulse rate than captured spring-adult males (52 versus 49), and males reared from spring females had a significantly lower modal pulse rate than captured fall-adult males (55 versus 59). Because *G. rubens* is bivoltine, both of these comparisons indicate that developmental conditions affect calling-song pulse rate. Fall males of “*integer*” had a significantly higher mean modal pulse rate than males reared from fall females (79 versus 70), indicating one or both effects. These are the 1st parental and developmental effects on pulse rates reported for crickets.

KEY WORDS sibling species, calling songs, seasonal forms, Florida

CRICKETS OF THE genus *Gryllus* (field crickets) are plentiful, easily recognized, and widespread geographically and ecologically. For the first half of this century, all United States field crickets were considered a single species. Then B. B. Fulton (1952) demonstrated that 4 species occurred in North Carolina. One of these he called the “triller” field cricket because its song was nearly continuous rather than broken into discrete chirps, as in the other North Carolina species. R. D. Alexander (1957) assigned the long-synonymized name *Gryllus rubens* Scudder to Fulton’s triller and showed that its distribution included the southeastern United States from Missouri and Louisiana to Maryland and Florida. Alexander (1957) also named 4 chirping *Gryllus* from the eastern United States, and he and others subsequently named 2 others. However, *G. rubens* has remained the only trilling *Gryllus* in the eastern States. Its trill consists of long sequences of pulses (corresponding to forewing closures) produced at a rate of $\approx 56 s^{-1}$ at 25°C (Walker 1962). In fieldwork in Texas in 1964, I encountered trilling field crickets that produced much faster pulse

rates (≈ 80 at 25°C) and that tended to interrupt their trills more often and more regularly than *G. rubens*. R. D. Alexander (personal communication) identified these as *Gryllus nr. integer* Scudder (=“*integer*”), a relative of *G. rubens* he had encountered in Texas and westward and had separated from *G. rubens* by its song. He could not separate “*integer*” and *G. rubens* by morphology and was unsure of their relation where they met geographically. To determine this relation, I tape recorded songs of trilling *Gryllus* from many localities and reported that the pulse rates of the taped trills were bimodal in an area stretching from western Florida to eastern Texas and north to Oklahoma and all of Arkansas (Walker 1974). *G. rubens* and “*integer*” were apparently coexisting. However, the songs I attributed to *G. rubens* had a slightly higher average pulse rate in the zone of overlap than farther east and both species varied more in pulse rate between individuals from the same site and for the same individual from time to time than in the many other cricket species I had studied. *G. rubens* and “*integer*” were not as clearly separated by their songs as other sympatric

pairs of sibling species of crickets (e.g., *Oecanthus quadripunctatus* Beutenmuller and *O. celerinictus* Walker [Walker 1963], and *Orocharis saltator* Uhler and *O. luteolira* Walker [Walker 1969]).

Weissman et al. (1980) endorsed the species status of "integer" when they concluded that it was "an unnamed bivoltine species distributed from Texas and Oklahoma eastward to NW Florida." They described the song of the real *G. integer* (from California, its type locality) as a "stutter-trill," with pulses within trills occurring in pairs or trios. Smith and Cade (1987) tried all possible laboratory crosses of *G. rubens* from McAlester, Oklahoma (near the western edge of *G. rubens*' range), "integer" from Austin, TX, and *G. integer* from Davis, CA. No offspring were produced from crosses of *G. integer* with either of the others, but crosses of *G. rubens* and "integer" were as successful as the controls or nearly so, and the F₁ hybrids produced F₂ generations. Their results supported the distinction between *G. integer* and "integer" but raised doubts as to the distinctness of "integer" and *G. rubens*. They concluded that *G. rubens* and "integer" may be the same species but that that redesignation was not yet warranted.

This article describes studies of trilling field crickets in western Florida, where *G. rubens* and "integer" apparently overlap and may hybridize.

Materials and Methods

Tape Recording. Trilling *Gryllus* were recorded in the field for 20 s or more with a dynamic microphone, a parabolic reflector (0.61 m diameter), and a Nagra IV tape recorder at 38.1 cm s⁻¹. After each recording, air temperature at the reflector was noted. Male crickets that had been captured or reared were confined indoors in cages (usually 150-ml wide-mouth jars with screen lids) and tape recorded as in the field but with no parabola and with the microphone and thermometer a few centimeters from the calling cricket.

Collecting Sites. Collecting and tape recording were restricted to 5 towns in the supposed zone of overlap between *G. rubens* and "integer" in western Florida: Milton, Crestview, DeFuniak Springs, Chipley, and Quincy (32, 77, 118, 171, and 256 km east, respectively, of Florida's border with the "toe" of Alabama). In each town, I concentrated on a single site where trilling field crickets were relatively easy to collect—usually a treeless vacant lot littered with pieces of corrugated cardboard and other debris that could be turned over to expose crickets hiding beneath.

Rearing. Females were transported to the laboratory in Gainesville, placed individually in 3.8-liter jars with damp sand for oviposition, and held at 25 ± 1°C and a photoperiod of 16:8 (L:D) h. When hatchlings were produced in a jar (demonstrating that the female had mated before collection), the female was removed. The juveniles were reared in the same or other jars according to the procedures of Wineriter and Walker (1988) at 25 ± 1°C and a photoperiod of 16:8

(L:D) h. Males that were collected as juveniles were transported to the laboratory in Gainesville and reared to adulthood in the same manner.

Vouchers. Many field-collected specimens and representatives of most sibships are in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL.

Analysis of Taped Songs. In trilling field crickets, the sequence of pulses in a calling song is often delivered more irregularly than in other crickets. In *G. rubens* this is at least partly because the male sporadically pauses momentarily during the opening motion of the wings (when file and scraper are not engaged) (unpublished data, using the technique of Walker and Dew [1972]). Whatever the cause, the effect is to make it difficult to determine the fundamental pulse rate (i.e., the one produced when prolonged pulse periods are omitted). Nearly all the tapes in this study were analyzed originally by making audiospectrograms with a Kay 7029A Sona-Graph (Kay Elemetrics, Pine Brook, NJ) and measuring numerous short sequences of what I judged to be unprolonged pulse periods. When the calculated pulse rates failed to fit any expected pattern, I decided that a less subjective method of pulse rate determination would be needed to reach defensible conclusions. Therefore, I suspended analyses until T. G. Forrest developed software that used the output of an A/D converter (Tim Tucker Electronic Solutions QAD1, 16-bit, Tucker Davis Technology, Gainesville, FL) to objectively measure every pulse period in a recording of *Gryllus* calling song and display a frequency distribution of the results. In using Forrest's software, I ran 16.4 s of the taped song through a 3- to 7-kHz bandpass filter to the A/D converter set at a sampling rate of 25 kHz (=40 μs). The software produced an amplitude versus time display that was parsed into pulses by setting a trigger level at some proportion (usually 0.50) of the amplitude range. Pulse periods (time from start of one pulse to start of next pulse) were measured with a resolution of ±80 μs, stored in an array, and used to plot a histogram with cells beginning at 0.50-ms intervals. Because males produced numerous pulse periods that were to varying degrees longer than the modal pulse period, the modal pulse period was more appropriate than the average pulse period to calculate the fundamental rate at which a cricket had moved its wings during a tape-recorded song. To estimate the modal pulse rate for the song, I took the reciprocal of the midpoint of the histogram cell that had the most pulses. This procedure transformed continuous distributions of pulse periods into discrete pulse-rate categories separated by <1 pulses s⁻¹ at the upper end of the period range to >3 pulses s⁻¹ at the lower end.

If the same male was tape recorded more than once, all tapes were analyzed and the average temperature-adjusted modal pulse rate (see next section) was used as the modal pulse rate value for that male. Means of modal pulse rates for males of different origins were compared using 2-sample *t*-tests, analysis of variance

(ANOVA), and the Tukey multiple comparison test with Kramer's modification for unequal n 's (Zar 1996).

Adjusting Pulse Rates for Temperature Differences. Air temperature profoundly and predictably influences the pulse rates of the songs of calling crickets. For each species the pulse rate approximates a linear function of temperature, and the extrapolated lines for related crickets tend to converge at 0 pulses s^{-1} and a temperature between 0 and 5°C (Walker 1962, 1975). *G. rubens* (from Gainesville, FL), 1 of 27 species of crickets used to arrive at these generalizations, had a regression of pulse rate on temperature of $2.756 C - 13.12$ (Walker 1962). This regression extrapolates to 4.8°C at 0 pulses s^{-1} . Because the pulse rate-on-temperature regression for "integer" would be expected to extrapolate to approximately the same temperature (4.8°C) at 0 pulses s^{-1} , formulas can be derived that use the pulse rate of any trilling *Gryllus* at any Celsius temperature (x) to calculate the expected pulse rate of the same cricket at any other temperature. The following 2 formulas were used in the current study:

$$R_{20} = 15.2 * \left(\frac{Rx}{x - 4.8} \right) \text{ and } R_{25} = 20.2 * \left(\frac{Rx}{x - 4.8} \right),$$

where R_x is the rate at temperature x , and R_{20} and R_{25} are the expected rates at 20 and 25°C, respectively. The R_{20} formula was used to compare field recordings made at low temperatures. When using the R_{25} formula I excluded tapes made at temperatures <21°C, because uncertainties become greater as rates at lower temperatures are extrapolated upward.

Study Protocols. Before 1977, trilling field crickets were tape recorded in the field and males were sometimes captured and taped in the laboratory. Between 18 August 1977 and 30 September 1978, I made 7 trips, approximately evenly spaced throughout the warmer seasons, to western Florida to tape record males in the field, to collect juvenile and adult males to record indoors, and to collect field-fertilized females from which to rear 1 jar of progeny each. A few sons from each jar were caged and tape recorded.

Based on the results of these initial studies I focused on Milton, the westernmost study site. Here I collected 26 females on 25 September 1982 and took them to Gainesville to rear their progeny. About 3 wk after hatchlings appeared in an oviposition jar and the female had been removed, 20 juveniles were transferred to 1 rearing jar and named the T(wenty) cohort. The remaining juveniles (usually 30–60) were transferred to another jar and named the R(emainder) cohort. This procedure was followed to produce more sons to record and to yield information on possible effects of rearing density on song. When sons of these females matured, their songs were recorded twice at an interval of ≥ 1 d.

To determine if "integer" occurred at Milton in spring as well as fall, I went there on 6 May 1983 and 23 May 1993 and tape recorded large samples of trilling field crickets.

Results and Discussion

Songs of Free and Captured Males, 1965–1982. At Milton, 27 males were taped in the field at $\geq 21^\circ\text{C}$, 27 were captured as adults and taped indoors, and 10 were captured as mid-to-late juveniles, reared, and taped. The distribution of modal pulse rates of these 64 males was continuous but bimodal, with the low between the left-hand (*G. rubens*) peak and the right-hand ("integer") peak coming at ≈ 70 pulses s^{-1} (Fig. 1A). At the other collecting sites, 7 males were taped in the field at $\geq 21^\circ\text{C}$, 39 were captured and taped, and 1 was reared from a juvenile and taped. The distribution of modal pulse rates of these 47 males matched those from Milton, except that only 15% of the males (rather than nearly half) were in the "integer" peak (Fig. 1B). Thus, a much enlarged sample of male songs, >2/3 made indoors, confirmed my earlier results (Walker 1974).

Songs of Sons of 1977–1978 Field-Fertilized Females. Between 18 August 1977 and 30 September 1978, I collected 60 adult females at the 5 sites, including 41 at Milton and 11 at Crestview. Sons were reared from 42 of the 60 females, and I succeeded in tape recording 1–10 sons per female (mean = 3.4). The frequency distribution of the modal pulse rates of these 144 reared males (Fig. 2A) was surprising for 2 reasons. First, it was nearly lacking in males that could be assigned to an "integer" peak. Second, the *G. rubens* peak was noticeably shifted to lower values than for free and captured males (Fig. 1)—with an average value of ≈ 54 pulses s^{-1} rather than ≈ 58 pulses s^{-1} . When a mean modal pulse rate was calculated for the sons of each field-fertilized female, only 3 of the 42 sibships, represented by 7 males with modal pulse rates ranging from 61.7–79.4, were presumptively "integer" (Fig. 2B). All 3 were from Milton in the fall (2 from 1 October 1977 and 1 from 30 September 1978). Three *G. rubens* sibships were from females collected on those dates.

Songs of Sons of 25 September 1982 Field-Fertilized Females from Milton. Of the 26 females collected at Milton, 23 produced offspring. Two of the oviposition jars produced only enough offspring for single cohorts of 14 and 15 juveniles. With the other sibships I set up 21 T cohorts and 21 R cohorts. R cohorts had 30–60 juveniles except for 3 that had 12, 22, and 25. Thirty-nine of the 44 cohorts produced 1–10 sons that were tape recorded twice. Of the 39, 20 cohorts had mean modal pulse rates of <60 (= *G. rubens*) and 19 had mean modal pulse rates of >64 (= "integer"). Comparing the mean modal pulse rates for the T and R cohorts in the 17 sibships that had males taped from 2 cohorts (Fig. 3), I found that 1 sibship (number 6) had a T cohort with a mean modal pulse rate of 75.2 ("integer" cluster) and an R cohort with a mean modal pulse rate of 50.4 (*G. rubens* cluster). Because the R and T cohorts of the other 16 sibships were in the same cluster, I attributed the anomaly to a mislabeled jar and excluded both cohorts of sibship number 6 from

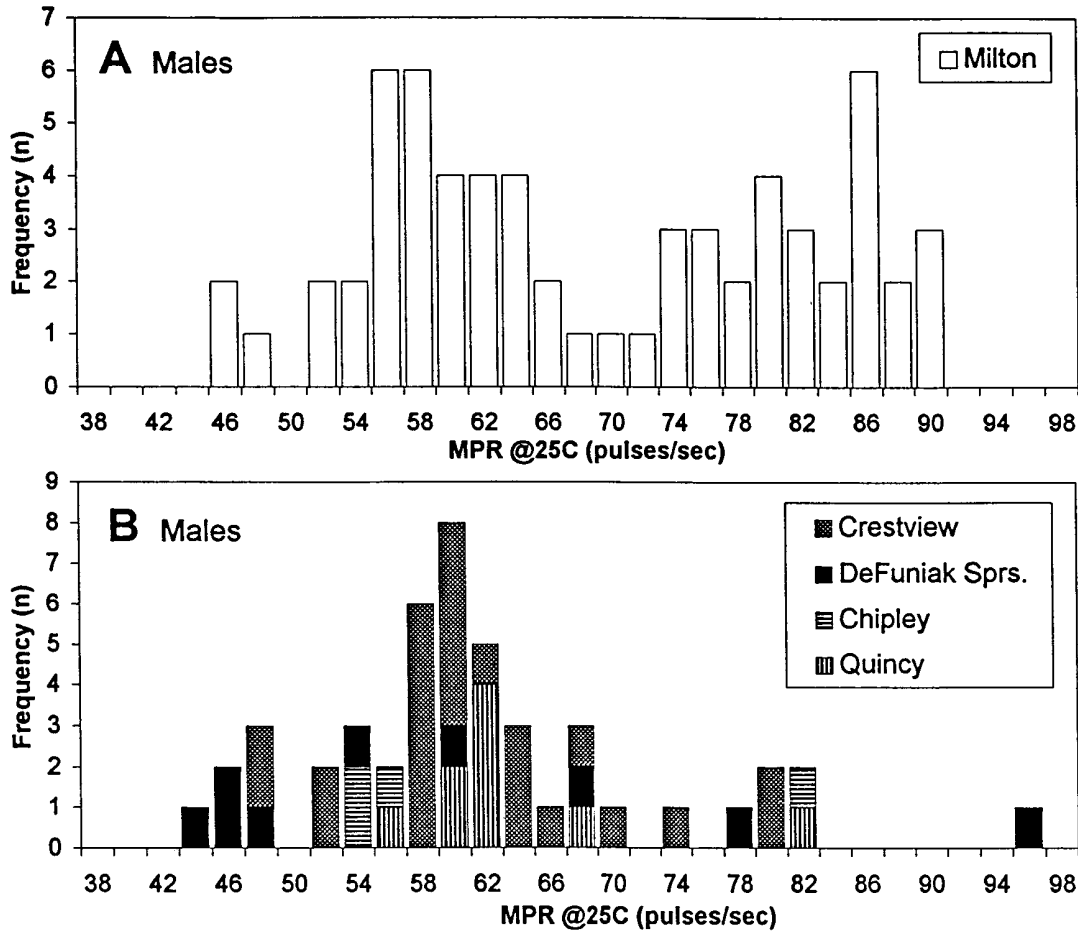


Fig. 1. Frequency distributions of temperature-adjusted modal pulse rates (MPR) for free and captured males recorded at $\geq 21^\circ\text{C}$. (A) Males from Milton ($n = 64$). (B) Males from 4 other sites in western Florida ($n = 47$). (Note: x axis labels on all bar graphs are the center values of the bars.)

all remaining analyses. (This interpretation was strengthened by there being no tapes from cohort R of sibship number 8, which had a mean modal pulse rate of 51.7 for its T cohort.) The other 16 sibships with males taped from 2 cohorts had similar mean modal pulse rates for cohorts T and R. For the 14 sibships in which the R cohort was initially at least 50% larger than the T cohort, the R cohort had a slightly higher mean modal pulse rate than the T cohort in 7 cases and a slightly lower modal pulse rate in the 7 others (Fig. 3). Males from cohorts T and R were therefore pooled for calculating the mean modal pulse rate for sibships. Sibship means fell into 2 discrete groups (Fig. 4A), identified as *G. rubens* (11 sibships with means of 47–57) and “integer” (10 sibships with means of 65–77). Sons of *G. rubens* females and sons of “integer” females were not quite disjunct in their modal pulse rates. Nonetheless, if a dividing line is drawn at 61.0 pulses s^{-1} , >98% of the 149 males are identified correctly by their song (Fig. 4B).

Why Do Modal Pulse Rates of Captured and Reared Males Differ? When songs of sons of field-fertilized females were first analyzed, the mean modal pulse rate of most sibships was substantially less than the lower, “*rubens*” peak evident in earlier recordings of free and captured males (Figs. 1 and 2). Upon finding that sibships from Milton formed tight, disjunct modal pulse rate clusters (Fig. 4A), I tried to resolve the previous loose, overlapping clusters by sorting tapes of calling songs into 4 categories based on where the males developed and when the males or their mothers had been collected. Males and field-fertilized females collected before 1 June were classified as “spring adults,” whereas those collected after 1 August were classed as “fall adults.” The few males and females collected in June and July were excluded from further analysis, as were males that had been collected as juveniles and reared to maturity in the laboratory. Tapes made outdoors were excluded, because temperatures had not been measured at the calling

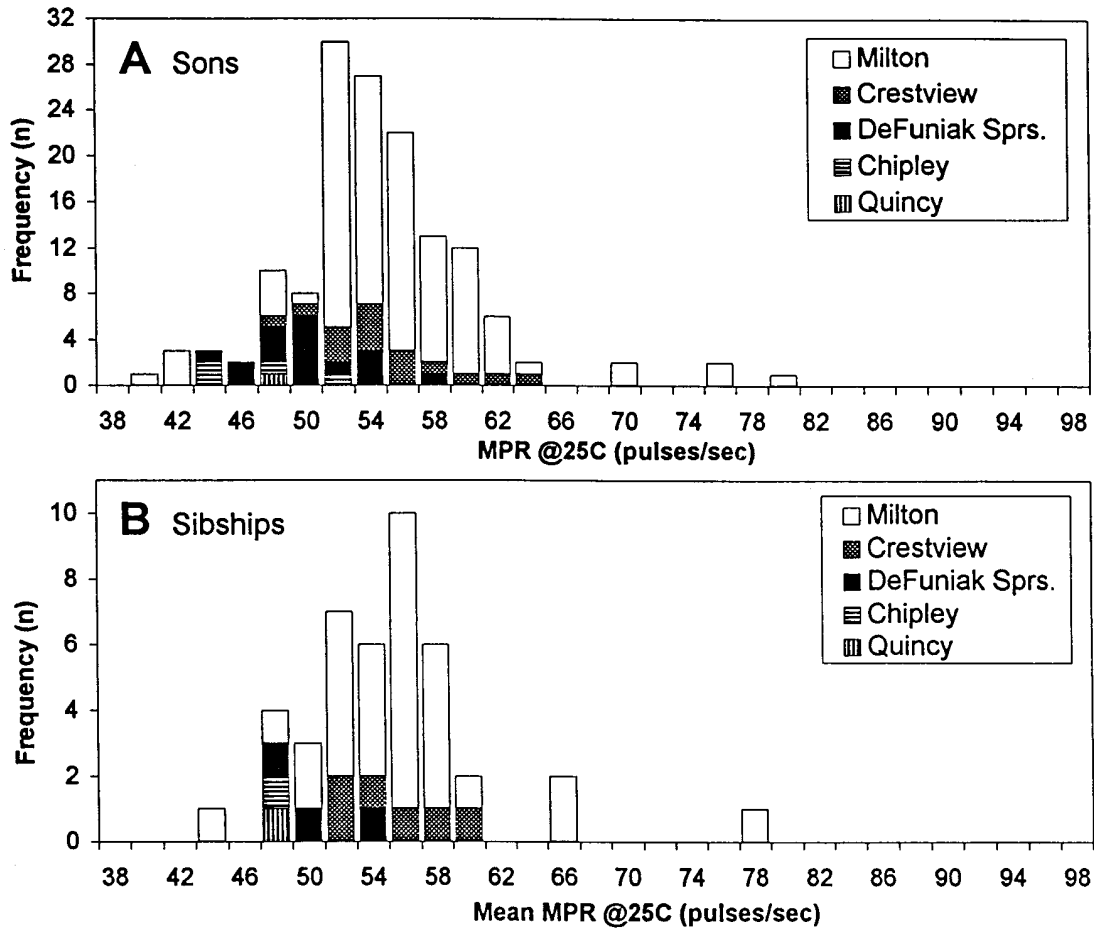


Fig. 2. Temperature-adjusted modal pulse rates of 144 sons of 42 field-fertilized females collected 18 August 1977 to 30 September 1978 at 5 sites in western Florida. (A) Frequency distribution for sons. (B) Frequency distribution of means for sibships.

cricket. With this reclassification and winnowing of the tapes, previously unrecognized patterns emerged (Fig. 5). *G. rubens* males captured in spring had a significantly lower mean modal pulse rate than those reared from fall-adult females (48.6 versus 51.8) ($P < 0.02$, 2-tail t -test). The latter males in turn had a significantly lower mean modal pulse rate than males reared from spring-adult females (55.3) ($P < 0.0003$, 2-tail t -test), and these in turn were significantly lower than males captured in fall (58.6) ($P < 0.0002$, 2-tail t -test). When the means for the 4 categories of *G. rubens* males were analyzed with the Tukey test for multiple comparisons, $P = 0.05$ for the pair of means with the least certain t -test (48.6 versus 51.8). Only 2 categories of “integer” males were represented, but their modal pulse rate relationship paralleled that of the corresponding *G. rubens* categories. The average mean sibship modal pulse rate of reared sons of fall adult females was 70.6, whereas the mean modal pulse rate of captured fall males was 77.6 or 79.0, depending

on whether 3 fall males with modal pulse rates of 68.6–71.0 are included (Fig. 5 B and D) ($P < 0.0001$, 2-tail t -test).

Are There Spring-Adult “Integer” in Western Florida? Through 1982 no adult “integer” had been recorded or collected earlier than 25 August at any of the study sites. However, only for Milton were the data extensive enough to be noteworthy. During 4 trips to Milton before mid-August (all in 1978), 31 *G. rubens* (R) and 0 “integer” (I) were identified: 18 March 1978 (2 R♂, 10 R♀), 13 May 1978 (6 R♀), 20 June 1978 (8 R♂, 2 R♀), 1 August 1978 (3 R♂). (Males were identified by their taped songs; females were identified by the songs of their sons.) On the other hand, during 5 trips to Milton after mid-August, in 5 yr, 28 *G. rubens* and 43 “integer” were identified: 31 August 1965 (2 I♂), 25 August 1973 (2 R♂, 2 I♂), 1 October 1977 (1 R♂, 1 R♀, 2 I♂, 2 I♀), 30 September 1978 (4 R♂, 2 R♀, 15 I♂, 1 I♀), 25 September 1982 (8 R♂, 11 R♀, 8 I♂, 10 I♀). This was unexpected. *G. “integer”* is bivoltine

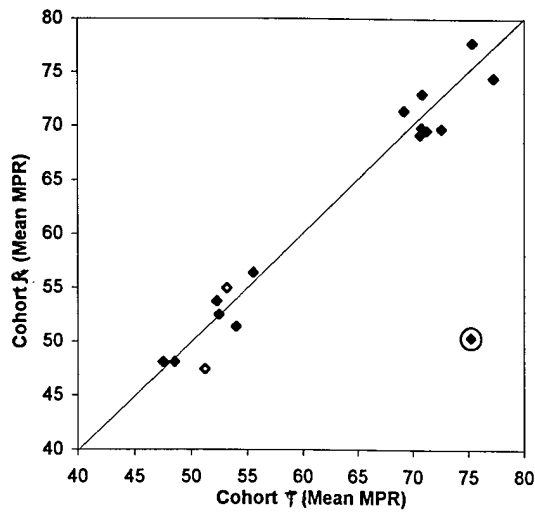


Fig. 3. Mean modal pulse rate (MPR) of cohorts T and R of 17 sibships from field-fertilized females collected 25 September 1982 at Milton. On the diagonal line, the mean of the R cohort equals the mean of the T cohort. Except for the 2 open points, the initial density of the R cohort was 50–200% greater than for the T cohort. The circled point is for sibship number 6 (see text).

in Texas (Alexander 1968; W. H. Cade, personal communication 1996), yet study techniques that repeatedly confirmed 2 generations of *G. rubens* in western Florida revealed only a fall generation of “integer.” A simple way to refute the hypothesis that “integer” has no spring adults in western Florida is to tape large samples of trilling *Gryllus* in the spring and find pulse rates typical of both species. Consequently, I spent 2

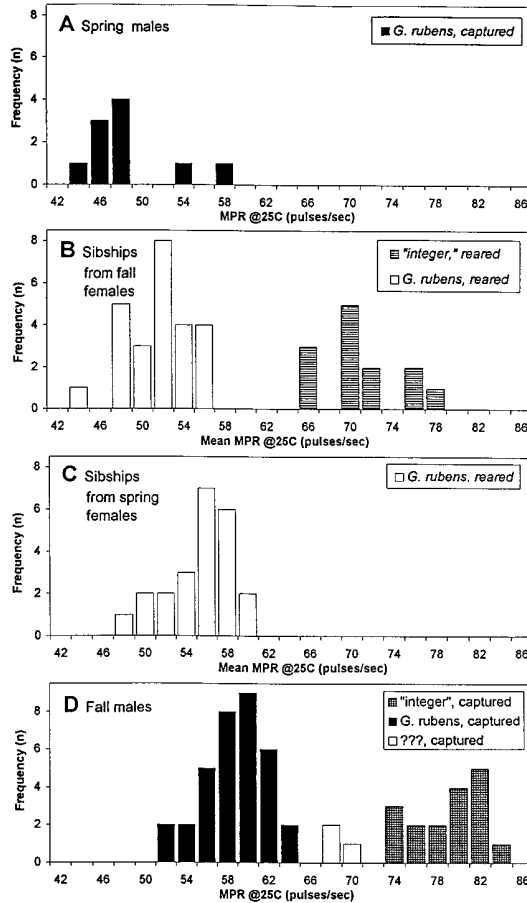


Fig. 5. Modal pulse rates of trilling *Gryllus* from 5 sites in western Florida, recorded indoors. (A) Spring-adult males, captured 18 March to 13 May ($n = 10$). (B) Mean modal pulse rates (MPR) of sibships reared from fall-adult, field-fertilized females, collected 1 August to 2 October ($n = 38$). (C) Mean MPR of sibships reared from spring-adult, field-fertilized females, collected 18 March to 13 May ($n = 23$). (D) Fall-adult males, captured 1 August to 2 October ($n = 54$).

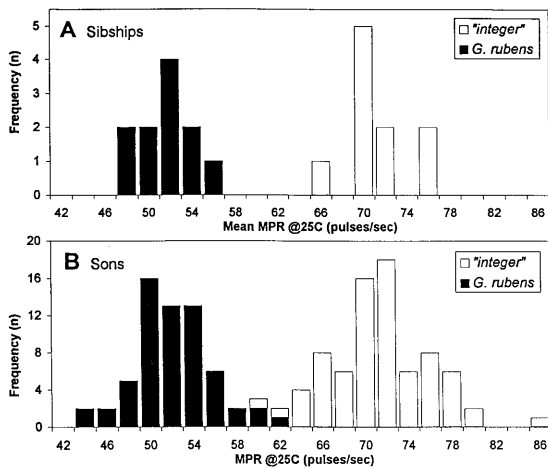


Fig. 4. Temperature adjusted modal pulse rates of 149 sons of 21 field-fertilized females collected 25 September 1982 at Milton. (A) Frequency distribution of means for sibships. (B) Frequency distribution for sons.

late-spring evenings in Milton recording as many trilling *Gryllus* as I could locate. The modal pulse rates of these recordings are displayed in Fig. 6 along with similar tapes made on the evening of 25 September 1982, when the occurrence of both *G. rubens* and “integer” was abundantly established by the progeny of captured females (Fig. 4). On all 3 evenings, temperatures were near 20°C when calling began and dropped rapidly. This was unfortunate because differences in the pulse rates of species of crickets become less as temperature drops (Walker 1962) and differences between air temperature at the parabola and at the calling cricket on the ground are probably increased. On the fall 1982 evening, songs had a wide range of temperature-adjusted modal pulse rates (42–95), including those typical of *G. rubens* and “integer” (Fig. 6A). However, songs taped on the 2 spring eve-

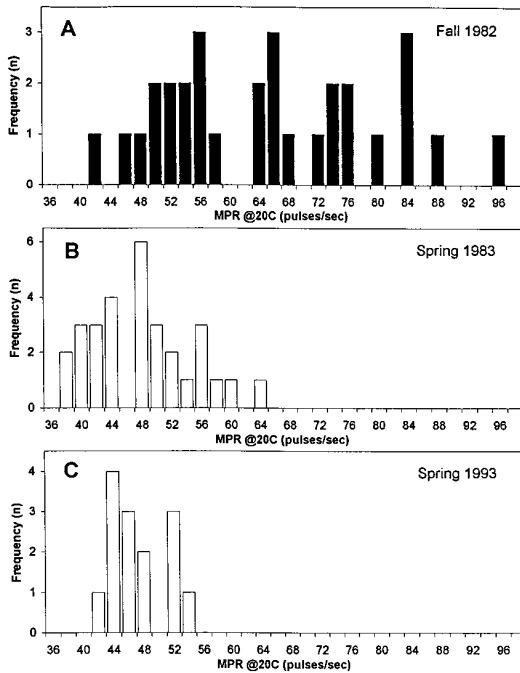


Fig. 6. Frequency distributions of temperature-adjusted modal pulse rates (MPR) for trilling *Gryllus* taped in the field at Milton on 3 evenings with similar temperatures, as measured at the parabola. (A) Fall, 25 September 1982; 16.4–21.0°C ($n = 30$). (B) Spring, 6 May 1983; 16.4–19.0°C ($n = 30$). (C) Spring, 23 May 1993; 17.2–21.2°C ($n = 14$).

nings had a much narrower range (37–64) (Fig. 6 B and C) and, except for one or a few ambiguous songs in 1983, seemed to be spring-form (i.e., low modal pulse rate) *G. rubens*. If “integer” occurs in Milton in the spring, it is strangely difficult to demonstrate.

Discussion

This study was undertaken to determine the status of *G. rubens* and “integer” in western Florida. The results suggest that the 2 species maintain their distinctness while overlapping in habitat and reproductive season. In 1977, 1978, and 1982, when females were collected September/October in vacant lots at Milton, about half produced sibships that made *G. rubens* songs and the other half produced sibships that made “integer” songs. The lack of any sibship with an intermediate mean modal pulse rate indicated that the 2 species were maintaining their genetic isolation (i.e., that no significant introgression was occurring). Another way to gauge introgression in the zone of overlap is to compare pulse rates in sympatry with those in allopatry. Introgression, unless countered by selection, would result in the songs of the 2 species being more similar in sympatry. My tapes of “integer” from allopatric sites are too few to justify a comparison, but

8 *G. rubens* males collected in late May and early June at Gainesville and taped under carefully controlled temperatures had a mean modal pulse rate of 56 (temperature-adjusted to 25°C) (Walker 1962). If these males are classed as spring adults, their western Florida counterparts are calling at a lower modal pulse rate (Fig. 5A, mean = 49), and character displacement rather than introgression is suggested. However, spring begins earlier in Gainesville, which is in northern peninsular Florida, than in western Florida; and, unlike *G. rubens* in most of its range (Alexander 1968, but see Fulton 1952), some Gainesville *G. rubens* overwinter as adults rather than as diapausing juveniles (Walker 1986). Thus, seasonal origins and developmental conditions of Gainesville late-spring males may be importantly different from the spring males of Fig. 5A. My earlier comparison of pulse rates of *G. rubens* from Gainesville and the overlap zone wrongly assumed no seasonal changes in pulse rate (Walker 1974). I now attribute the higher mean pulse rate of males in the zone of overlap to the Gainesville sample being from late spring and the overlap samples being mostly from fall.

Individual modal pulse rates of the 2 species overlapped slightly (Fig. 4B), attesting to the fact that differences other than in calling-song pulse rate are important in preventing hybrids in the field. There is ample precedence for such differences in crickets. For example, 50 heterospecific pairs of 4 *Gryllus* spp. confined in rearing jars produced no progeny, whereas 21 of 23 conspecific pairs produced progeny under those circumstances (Fulton 1952). Walker (1963) tallied the results of chance encounters between males and (mostly) virgin females of 9 pairs of closely related or sibling *Oecanthus* spp. Without benefit of cues from calling songs and without a choice of other males, females in 38 replicates of the 4 possible crosses accepted 3 spermatophores in the interspecific crosses and 136 spermatophores in the equal number of conspecific crossings. The fact that *G. rubens* and “integer” will hybridize in the laboratory (R. S. Bigelow in figure 10 of Alexander 1962; Smith and Cade 1987) does not mean that they do so in the field. For example, Bigelow (1960) produced hybrids between *G. rubens* and *G. assimilis*, but these species occur together in southern Florida without hybridizing. Contact chemoreception is probably important to reproductive isolation after chance encounters. A study of the cuticular hydrocarbons of *G. rubens* and “integer” may provide a means of separating pinned specimens of the 2 species as well as candidates for contact or short-range pheromones important to courtship (J. L. Nation and T.J.W., unpublished data).

The apparent extensive sympatry of *G. rubens* and “integer” may be of recent origin. In its area of allopatry, “integer” is a prairie species, and in the past 100 yr prairie-like habitats have become much more common in the eastern States. Two other prairie crickets, *Oecanthus argentinus* Saussure and *Neonemobius “normonius,”* have spread rapidly eastward during this period (Walker 1974).

The most serious flaw in the conclusion that *G. rubens* and "integer" are 2 similar species that maintain their genetic integrity as they occupy some of the same habitats in western Florida is the failure to find "integer" in these habitats in the spring. Below, in order of decreasing plausibility, are 4 possible explanations for the failure to find spring-adult "integer" in western Florida.

First, *G. "integer"* does not occur in the sampled habitats in spring but flies in each fall from other local habitats, or, second, it flies in from more western localities, such as coastal Alabama or Mississippi. The absence of "integer" in habitats where females surely laid eggs in the fall could result from eggs or progeny succumbing to pathogens, predators, or parasites that *G. rubens* withstands. *G. "integer"* is well known for massive fall flights (Cade 1979), and all the 1982 field-fertilized "integer" females had the long wings required for immigration, whereas only 6 of the 11 *G. rubens* females were long-winged (Walker and Sivinski 1986). The plausibility of this explanation is increased by the fact that long-winged *G. rubens* are extraordinarily abundant at flight traps but nearly absent in habitats known to breed many *G. rubens* (Walker 1987).

Third, in western Florida, "integer" is univoltine. This seems highly unlikely, because no developmental differences were noted when *G. rubens* and "integer" were reared side by side in the laboratory at 25°C and a photoperiod of 16:8 (L:D) h, and because no conditions are known to trigger egg diapause or exceptionally long juvenile diapause in either species.

Fourth, west Florida *G. rubens* and "integer" are phases of a single species, comparable to the solitary and gregarious phases of locusts except that complete interphase transformations occur within a single generation. Transformations of this nature are not supported by laboratory rearing, other than the apparent occurrence of cohorts of each phase within 1 of 17 split sibships (Fig. 3). In the field, the phase theory requires that winter conditions produce only the spring *rubens* phase, whereas summer conditions cause some individuals to develop into the fall *rubens* phase (faster modal pulse rate than spring *rubens*) and other individuals to develop into the "integer" phase (much faster modal pulse rate and migratory).

Until the missing spring generation of "integer" is found or explained, the status of *G. rubens* and "integer" in western Florida and elsewhere in the zone of overlap is less certain than for other pairs of sibling species of crickets. Finding some chemical or morphological feature that reliably separates specimens saved from the 2 types of sibships recognized in this study would be an important 1st step toward further studies, because it would allow field-fertilized females to be identified, and time-consuming comparisons could be done without fear that the sample included only 1 of the 2 types.

The most surprising result of this study was the evidence that normal differences in developmental

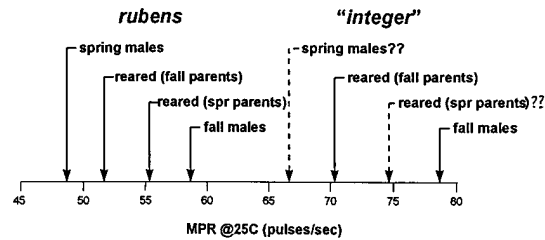


Fig. 7. Parental and developmental effects on modal pulse rates (MPR) for *G. rubens* and "integer." Solid lines point to means of data displayed in Fig. 5; dotted lines point to postulated means of categories not observed.

conditions of male crickets and their parents cause significant differences in the pulse rates of the males' calling songs (Fig. 7), effects not previously reported for any cricket species. In an early discussion of this possibility (Walker 1962), I noted there had been no experimental studies of the effects of developmental conditions on cricket calling songs and that crickets with >1 annual generation provide natural experiments when the generations develop under different conditions. As far as I knew at that time, successive cricket generations had indistinguishable calling songs. In *Oecanthus argentinus* Saussure, the one species for which I had extensive data, the late spring and late summer generations developed under different photoperiods and temperatures but produced identical pulse rates (Walker 1962).

Olvido and Mousseau (1995) were the 1st to test directly the hypothesis that developmental conditions had no effect on the characteristics of cricket calling songs, and they thoroughly refuted it. Individuals from laboratory stocks of 2 southern New Jersey populations of the ground cricket *Allonemobius fasciatus* (De Geer) were reared under spring-like (24°C, 11:13 [L:D] h) and summer-like (31°C, 15:9 [L:D] h) conditions. The songs of the resulting males (~15 from each stock, reared under each condition) were taped at 24, 28, and 31°C. Olvido and Mousseau (1995) found significant effects of developmental condition for each of the 5 characteristics they analyzed (viz., chirp rate, chirp duration, carrier frequency, pulse number, and interchirp interval). For only 1 characteristic (carrier frequency) was there a significant effect at all temperatures. They did not analyze the songs for pulse rate (often the most behaviorally significant feature of cricket calling songs), although the data for chirp duration and pulse number could have been combined to calculate it. The lack of a clearer pattern to their results may relate to the origins of the laboratory populations. Southern New Jersey is at the southern extreme of the range of *A. fasciatus*, where it has been reported to occur in mixed populations with its sibling species *A. socius* (Scudder) and where genotypes are likely to show hybrid ancestry (Howard 1986).

Whitesell and Walker (1978) described a case similar to *G. rubens* and "integer," but in a tettigoniid rather than a cricket. Males of *Neoconocephalus triops* (L.) that have overwintered in adult diapause sing with a wingstroke rate, at 25°C, that is 78% of that of males of the summer, nondiapausing generation. Slower wingstrokes in *N. triops* are correlated with diapause just as in *G. rubens*, whose spring males, believed to have overwintered in juvenile diapause, sing at a wingstroke rate (at 25°C) that is 83% of the wingstroke rate of fall males, which have not diapaused (Fig. 7). When Whitesell and Walker (1978) reared progeny of summer-adult *N. triops* under 2 photoperiods, males that developed at a photoperiod of 15:9 (L:D) h did not diapause and called with fast wingstrokes, whereas males that developed at 11:13 (L:D) h diapaused and later called with slow wingstrokes.

Both parental and developmental effects are indicated in *G. rubens*. A parental effect, probably maternal (Mousseau and Dingle 1991), is revealed by the difference between sibships reared under the same conditions but from fall and spring parents (Figs. 5 B and C and 7). The cause of the difference in spring and fall parentage seems likely to be the conditions under which the parents developed (e.g., photoperiod); however, the hypothesis that the 2 types simply alternate (each being able to produce only the other) is not refuted by the data. Developmental effects are evident in the differences in modal pulse rate between males of the same parentage exposed to different developmental environments (viz., captured males from fall parents differ from reared males from fall parents [Figs. 5 A and B and 7]), and captured males from spring parents differ from reared males from spring parents (Figs. 5 C and D and 7).

No function of parental and developmental effects in *G. rubens* and "integer" is evident, and there need not be one. Male songs and female song preferences could be affected similarly, resulting in no change in acoustic communication. Seasonal changes in acoustical interference from songs of other species could drive the system, but I have no candidate songs. The fact that the effects are correlated with diapause in both *N. triops* and *G. rubens* suggests that their song changes are an incidental consequence of physiological changes during diapause.

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