Seasonal Abundance, Sex Ratio, and Macroptery of Field Crickets[1] in Northern Florida[2]

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ABSTRACT

A total of 7911 adults of 3 species of field crickets, *Gryllus rubens* Scudder, *G. firmus* Scudder, and *G. ovisopis* Walker, were collected during 4.5 yr in pitfall traps in fields at Tall Timbers Research Station near Tallahassee, FL. *Gryllus rubens* adults were trapped throughout the year with peak numbers in July, August, and September (n=4978) and with a 2nd, smaller peak in March, April, and May (n=236). Those collected during the spring peak were 10% macropterous and 33% male, while those collected during the summer peak were 32% macropterous and 42% male. No macropterous *G. rubens* were taken between Oct. 25 and March 16. Adults of *G. firmus* were trapped between Feb. 22 and Dec. 20 with peak numbers in June and July (n=1052) and again in September, October, and early November (n=1358). During the summer peak, 15% of the *G. firmus* were macropterous and 45% were male. During the fall peak, 3% were macropterous and 52% were male. Adult *G. ovisopis* were taken between Aug. 25 and Nov. 22 (n=249). All were micropterous and 72% were male. Seasonal patterns of macroptery and sex ratio differed among the 3 species.

The literature on development rates and wing dimorphism in field crickets is extensive, but most of it deals with experiments on laboratory colonies under artificial conditions. Alexander (1968) reviewed the literature emphasizing the genus *Gryllus* in the eastern United States. Fulton (1952) studied the seasonal histories of 4 species of *Gryllus* in North Carolina. Alexander (1957, 1961, 1968), Alexander and Bigelow (1960), and Bigelow (1962) added information on the life histories of several species. In his description of *G. ovisopis,* Walker (1974) discussed seasonal patterns of *G. ovisopis* and *G. fultoni* (Alexander) in northern Florida. Evidence for the life cycles that appear in the literature has usually been from 1 or more of 3 sources: records of calling males, rearing experiments, and collections of small numbers of individuals. The value of these data are diminished by ignorance of the biology of the insects under natural conditions. Records of numbers of calling males cannot answer questions about macroptery and sex ratio in adult populations and may give inaccurate population estimates since males call more frequently at low population densities (Alexander 1961, 1968). Also, species such as *G. ovisopis* have no calling song (Walker 1974). Rearing data are sometimes difficult to relate to natural life cycles. There is usually no way to distinguish evolved, adaptive responses from artifacts.

Because small numbers of individuals were collected during most previous studies, important questions about the natural populations were unanswered. During a 5-yr study of the effects of time of soil disturbance on insect populations (Whitcomb 1973, Menke 1973), adults of 3 species of *Gryllus, G. rubens* Scudder, *G. firmus* Scudder and *G. ovisopis,* were collected in large numbers. The numerous, consecutive samples of crickets provided an opportunity to study patterns of seasonal abundance and attempt answers to questions about macroptery and sex ratio in natural populations of the 3 species.

METHODS

Field crickets for the study were collected between July 8, 1969 and Dec. 10, 1973 at Tall Timbers Research Station, Leon County, FL. All specimens were from 3 open fields partially bounded by mesic hammock and annually-burned pine forest. The fields had been in corn prior to investigations. Each field was divided into seven 0.305-ha plots. Six of the plots were plowed once each year during the 5-yr period. See Menke (1973) for the cultivation schedule. The fields were not manipulated in any other way during the studies.

A pitfall trap, as described by Harris and Whitcomb (1971), was placed in the center of each plot. The traps were emptied weekly, and the specimens were preserved in 70% ethanol. *Gryllus* were identified to species by Nickle and Walker's (1974) key.

Two maximum-minimum thermometers and a rain gauge were located in each of the 3 fields. Each thermometer was attached to the underside of a board approximately 60 cm above the soil surface and was never exposed to direct sunlight. Weekly maximum and minimum temperatures and total weekly rainfall were recorded when the pitfall traps were emptied.

Contingency tables employing chi-square as the test criterion were used for all statistical comparisons between populations of crickets (Steel and Torrie 1960). The 0.05 probability level was used for tests of significance.

RESULTS AND DISCUSSION

Of the 7911 adult *Gryllus* collected during the study, 5293 (66%) were southern field crickets, *G. rubens,* 2420 (31%) were sand crickets, *G. firmus,* and 249 (3%) were taciturn woods crickets, *G.*

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Table 2.—Number of adults (n), percentages of males, and percentages of macropterous (lw) males and females of the sand cricket, *Gryllus firmus*.

Year	Peak I April 29 to Aug. 25					Peak II Aug. 26 to Dec. 22				
	n	Mode[a]	% ♂	% ♂ lw	% ♀ lw	n	Mode[a]	% ♂	% ♂ lw	% ♀ lw
1969	85[b]	July 25	48.2	12.2	20.5	49	Oct. 10	51.0	8.0	12.5
1970[d]	393	July 3	46.6	7.7	12.9	450	Oct. 16	49.3	3.2	1.8
1971[d]	152	July 9	50.7	1.3[e]	13.3[e]	514	Oct. 22	52.9	0.7	1.7
1972	179	July 7	39.1	5.7	5.5	144	Sept. 29	45.8	0.0	2.6
1973[c,d]	247	July 6	44.1	32.1	34.8	201	Oct. 12	57.7	7.8	8.2
Combined[c,d] years	1056	July 4	45.5	12.3[e]	17.4[e]	1358	Oct. 17	51.6	2.9	3.0

[a] Mode=midpoint of the week in which maximum numbers of individuals were collected.
[b] Some data missing.
[c] % ♂ significantly different between peaks at p=0.05.
[d] % lw significantly different between peaks at p=0.05.
[e] % lw significantly different between sexes during Peak I at p=0.05.

(Fig. 2A) because no collections were made during the spring, an important period in the seasonal cycle of *G. rubens* but not of the other 2 species. In the spring, the greatest numbers of *G. rubens* were usually collected in mid-April, but sample sizes were so small that the modal weeks given in Table 1 may be unreliable. The summer population peak occurred at about the same time each year, with maximum numbers of crickets collected during the last 2 wk of August in all years except 1973 (Table 1). In 1973, the maximum number of *G. rubens* was captured during the 1st week of August although large numbers of adults were also collected in late August.

Fulton (1952) and Alexander (1961, 1968) showed that *G. rubens* has a spring and summer adult population peak. The timing of the 2 peaks in this study was similar to that found by Fulton (1952) in North Carolina. Alexander (1961) stated that the adult population was usually much greater in the summer than in the spring, as we have found. Walker (unpubl.) counted large numbers of calling males in Gainesville, FL, at times corresponding to the spring and summer population peaks, but the number of calling males was many times greater in spring than in the summer. Alexander (1961) reported that territoriality and calling increased during periods of low population density. The size of the spring peak relative to the summer peak was probably underestimated by the pitfall data and overestimated by the calling data because the crickets were traveling less but calling more in the spring. Rearing experiments have indicated that *G. rubens* is bivoltine with the offspring of the spring adults maturing during the summer peak (Fulton 1952, Bigelow 1962, Walker unpubl.). In outdoor rearing experiments at Gainesville, Walker (unpubl.) found that some offspring of early summer adults matured in the fall and that a few crickets matured at all times of the year. The seasonal distribution of *G. rubens* in this study suggested a similar pattern of maturation.

Adult *G. firmus* were not taken in the traps between Dec. 20 and Feb. 22, and only 9 individuals were captured before May 16. Large numbers of *G. firmus* were collected in June and July and again in September, October, and November (Fig. 2B). In 1969, 1972, and 1973, more *G. firmus* were collected during the summer population peak than during the fall peak, but in 1970 and 1971 this trend was reversed (Table 2). Therefore, over the 4.5-yr study, approximately the same numbers of *G. firmus* were collected during the 2 seasons (Fig. 2B, Table 2). The 2 population peaks occurred about the same time each year. In the summer, maximum numbers of *G. firmus* were usually found in the traps in early July (Table 2). The data for the summer peak of 1969 are not completely reliable since no crickets were collected before 8 July. In the fall, maximum numbers of crickets were collected in mid-October during all years except 1972 (Table 2). The fall peak in 1972 was low, and approximately equal numbers of crickets were collected each week for almost 2½ months.

Alexander (1968) reported 2 distinct adult population peaks of *G. firmus* in northern Florida. At Tall Timbers Research Station, the 2 peaks occurred later in the year than Alexander's (1968) life cycle diagram indicated. Walker (unpubl.) counted large numbers of calling ♂ *G. firmus* in Gainesville, FL, at times corresponding to the 2 population peaks at Tall Timbers, but more calling males were heard in the summer than in the fall. Our data indicated that either peak could be the larger during a given year (Table 2). Alexander (1968) and Alexander and Bigelow (1960) stated that offspring of summer adults of *G. firmus* diapause as juveniles and mature the following summer and that offspring of fall adults diapause as eggs and mature the following fall. The summer and fall populations would therefore be partially isolated. Walker (unpubl.) has evidence from outdoor rearing experiments that some of the offspring from a population peak mature in the next peak and that others develop more slowly and mature 1 peak later.

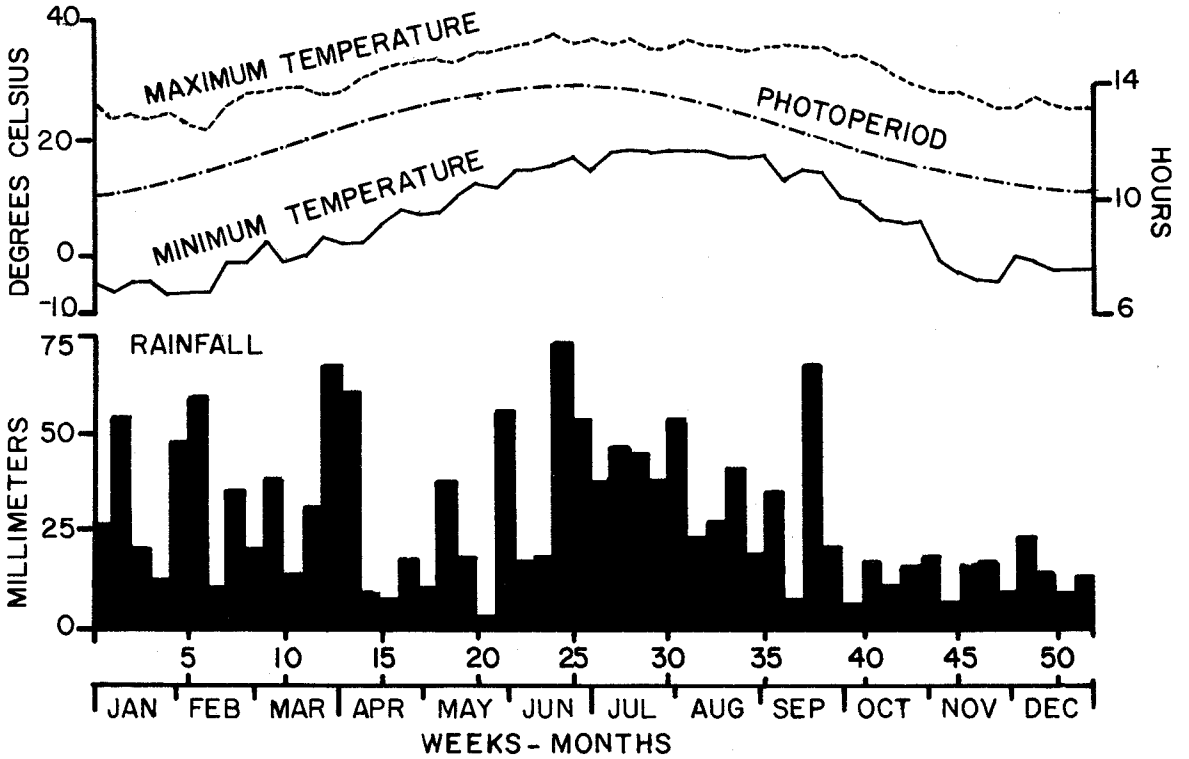

FIG. 1.—Weekly mean maximum and minimum temperatures, rainfall, and photoperiod in fields in northern Florida during July 1969 to December 1973.

ovisopis. The weekly mean maximum and minimum temperatures, rainfall, and photoperiod during the 4½-yr period are given in Fig. 1 for comparison with population patterns. Data from pitfall traps should not be used to estimate population densities (Greenslade 1964). Comparisons between species and between seasons must be made with caution because species and seasonal differences in behavior can bias pitfall catches (Greenslade 1964).

Adult *G. rubens* were found in the traps throughout the year. Only 44 *G. rubens* were collected between Nov. 4 and March 10 with 2 individuals taken between Nov. 18 and Dec. 22. More *G. rubens* were trapped in the spring and early summer (mid-March through June) than in the winter, but most of these crickets were collected in July, August, and September (Table 1, Fig. 2A). The data from 1969 were not included in the *G. rubens* histogram

Table 1.—Number of adults (n), percentage of males, and percentage of macropterous (lw) males and females of the southern field cricket, *Gryllus rubens*.

	Peak I Feb. 3 to June 16					Peak II June 17 to Oct. 27				
Year	n	Mode[a]	% ♂	% ♂ lw	% ♀ lw	n	Mode[a]	% ♂	% ♂ lw	% ♀ lw
1969	—	—	—	—	—	1837[b]	Aug. 22	42.5	16.9[e]	24.9[e]
1970[c,d,f]	84	April 17	33.3	14.3	3.6	696	Aug. 28	47.0	24.5[e]	39.6[e]
1971[d]	19	April 23	42.1	12.5	9.1	395	Aug. 20	49.9	44.7	52.0
1972[d]	93	April 14	33.3	6.5	6.5	633	Sept. 1	37.3	21.6	28.5
1973[d]	40	May 25	30.0	33.3	21.4	1417	Aug. 3	38.8	35.6[e]	47.6[e]
Combined[c,d,f] years	236	April 18	33.5	13.9	8.3	4978	Aug. 29	41.9	26.2[e]	35.8[e]

[a] Mode=midpoint of the week in which maximum number of individuals were collected.
[b] Some data missing.
[c] % ♂ significantly different between peaks at p=0.05.
[d] % lw significantly different between peaks at p=0.05.
[e] % lw significantly different between sexes during Peak II at p=0.05.
[f] Difference in % lw between sexes significantly different between peaks at p=0.05.

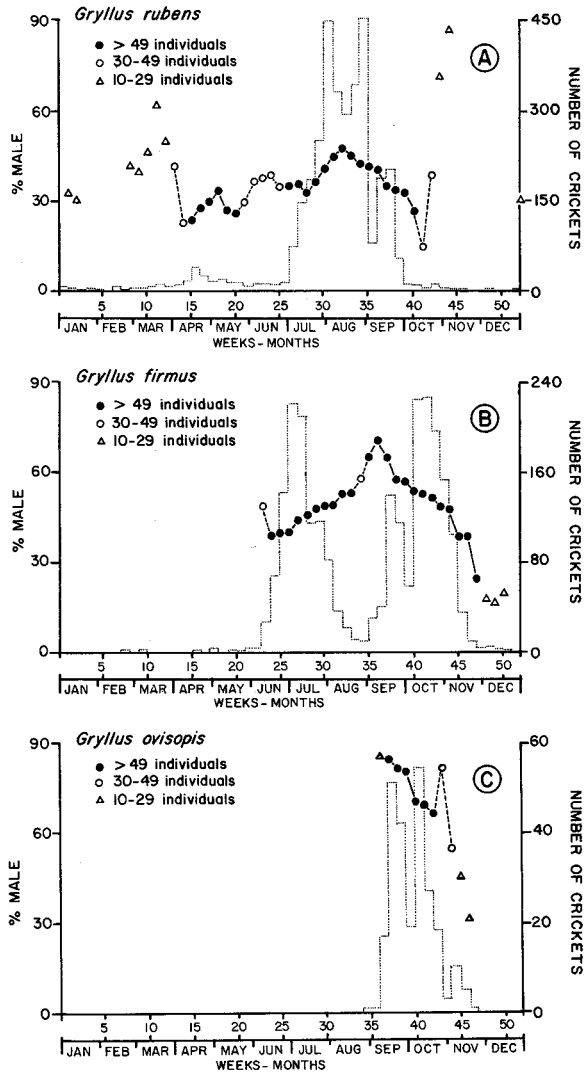

FIG. 2.—Seasonal abundance of adults of 3 species of *Gryllus* (histograms) collected in pitfall traps in fields in northern Florida and the percentages of the collections that were male. Each point represents the percentage for a 3-wk period including the week preceding and following the indicated week. The symbols indicate the number of individuals on which percentages were based; samples of less than 10 were excluded. *Gryllus rubens* (A) were from a 4-yr period, and *G. firmus* (B) and *G. ovisopis* (C) were from a 4.5-yr period.

Adult *G. ovisopis* were collected from Aug. 25 through Nov. 22 (Fig. 2C). Each year, maximum numbers of *G. ovisopis* were taken during the last 2 wk of September or the 1st 2 wk of October (Table 3). The seasonal distribution of adults was similar to that found by Walker (1974) for *G. ovisopis* near Gainesville, FL. The species is apparently always univoltine with adults present only in the fall (Walker 1974). The study plots probably did not represent a preferred habitat of *G. ovisopis* since the species occurs principally in forests (Walker 1974). The few specimens probably came from adjacent hammocks. Since *G. ovisopis* males lack a calling song (Walker 1974), mate seeking may involve more locomotion than in other *Gryllus*. A 4th species of *Gryllus, G. fultoni,* was not taken during the study although the species has been found in forests in the vicinity of the study plots. *Gryllus fultoni* may be more territorial and less mobile than *G. ovisopis* since males of *G. fultoni* have a calling song (Alexander 1961, Walker 1974).

The sex ratios of crickets in the pitfall traps could have been influenced by sexual differences in maturation rate, juvenile or adult mortality rate, or adult behavior. Walker (1974) found that the avg maturation time of ♂ *G. ovisopis* was slightly less than that of females. A male's singing (*rubens, firmus*) or searching (*ovisopis*) probably increases its chance of capture by predators. Either earlier ♂ maturation or a shortened ♂ life expectancy would result in a higher proportion of males in the population early in the breeding season than towards the end of the season. The proportion of males of all 3 species decreased in the late summer or fall (Fig. 2). However, the percentage of males of *G. rubens* and *G. firmus* followed a seasonal pattern that could not be easily explained by sexual differences in maturation or mortality rate alone (Fig. 2). Behavioral differences between the 2 sexes probably had an even greater influence on pitfall catches.

Forty-two percent of the *G. rubens* collected during the study were males. Males made up a relatively high proportion of the collection in the winter, a lower proportion in April and May, and a higher proportion in the summer (Fig. 2A). The percentage of ♂ *G. rubens* was significantly greater during the summer than during the spring in 1970 and for the combined data set (Table 1). During the summer, the maximum percentage of males was found in mid-August at the center of the population peak (Fig. 2A). Alexander (1968) states that males were collected less frequently than females because males are less mobile than females and therefore less susceptible to most trapping methods. Males of *G. rubens* were, in fact, collected in signficantly lower numbers than females except in the winter when 49% of the specimens were male. From April through September the proportion of males in the traps followed a hypothetical seasonal pattern of male territoriality. The percentage of males was low in the spring when calling and territoriality were apparently maximal and higher in the summer especially during the period of greatest population density when territoriality would be reduced (Alexander 1961, 1968).

Forty-nine percent of the *G. firmus* were male. The percentage of ♂ *G. firmus* was significantly less during the summer peak than during the fall peak of 1973 and for the combined data set (Table 2). Maximum proportions of males were taken in early September (Fig. 2B). In August and September, males of *G. firmus* were collected in greater numbers than females suggesting that male territoriality may have been low at a time when population density of the species was also low (Fig. 2B). How-

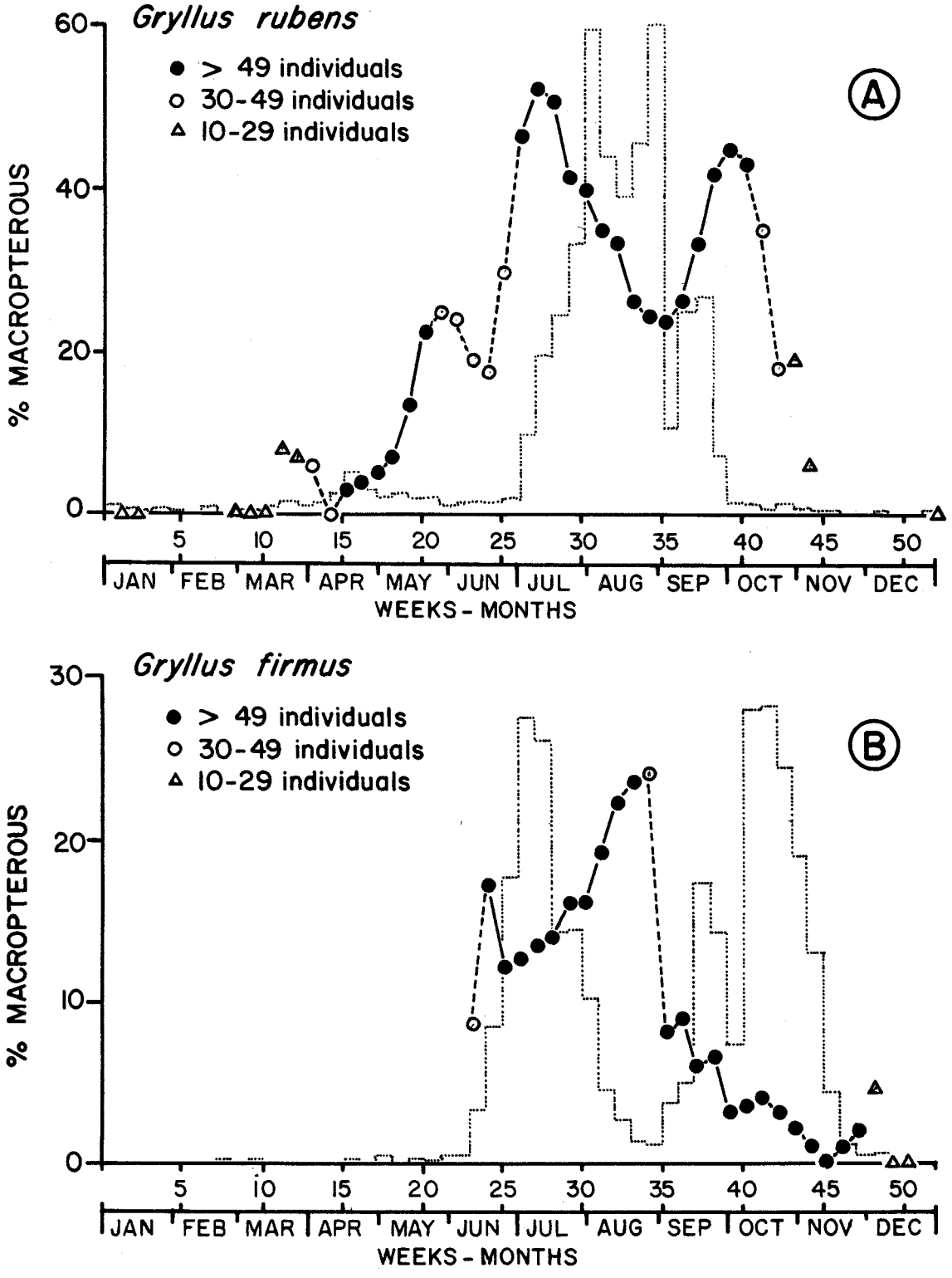

FIG. 3.—Percentages of macropterous adults of 2 species of *Gryllus* collected in pitfall traps in fields in northern Florida (histograms of seasonal abundance are as in Fig. 2). Each point represents the percentage for a 3-wk period including the week preceding and following the indicated week. The symbols indicate the number of individuals on which percentages were based; samples of less than 10 were excluded. *Gryllus rubens* (A) were from a 4-yr period, and *G. firmus* (B) were from a 4.5-yr period.

Table 3.—Number of adults (n), percentage of males, and percentage of macropterous (lw) males and females of the taciturn woods cricket, *Gryllus ovisopis*.

	Aug. 25 to Nov. 22				
Year	n	Mode[a]	% ♂	% ♂ lw	% ♀ lw
1969	19	Oct. 10	63.2	0	0
1970	102	Sept. 18	71.6	0	0
1971	82	Sept. 17	80.5	0	0
1972	22	Sept. 15	68.2	0	0
1973	24	Sept. 29 Oct. 12	54.2	0	0
Combined years	249	Oct. 10	71.9	0	0

[a] Mode=midpoint of the week in which maximum number of individuals were collected.

ever, more adults of *G. firmus* and *G. rubens* combined were collected in August and September than at any other time of the year. Territoriality of *G. firmus* males may therefore have been reduced by the presence of large numbers of adult *G. rubens*.

Seventy-two percent of the *G. ovisopis* collected during the study were male (Table 3), but the percentage of males decreased over a short adult season (Fig. 2C). If the ♂ *G. ovisopis* are not territorial and actively hunt for females, they might have encountered the pitfall traps more often than the females did. Later in the season the males may have either died or changed behavior patterns resulting in an increase in the proportion of females collected.

Macropterous adults of *G. firmus* and *G. rubens* were taken during the study, but no macropterous *G. ovisopis* were found. Alexander (1968) reported that species inhabiting forests, such as *G. ovisopis*, usually have a low incidence of macroptery. The largest proportions of macropterous individuals were collected in the summer when temperatures, rainfall, and photoperiod were near maximum (Fig. 1, 3). In 1970–73 the percentage of macropterous *G. rubens* was significantly higher during the summer population peak than during the small, spring peak (Table 1). No macropterous adults were taken in the winter between Oct. 25 and March 16. The proportion of macropterous individuals increased from mid-March through June reaching a maximum value early in July (Fig. 3A). A smaller proportion of *G. rubens* were macropterous in late August at the center of the large population peak than in either July or September (Fig. 3A). The pattern was similar in all 4.5 yr and for both sexes. In the spring a higher proportion of males than females were macropterous, but the reverse was true in the summer (Table 1). The differences in percent macroptery between the sexes decreased from the beginning to the end of the summer peak. Early in the summer peak (weeks 27–29, Fig. 3A), 59% of all females and 36% of all males were macropterous. In late August (weeks 34–36), 27% of the females and 20% of the males were macropterous. At the end of the summer season (weeks 37–39), 43% of the females and 40% of the males were macropterous.

The percentage of macropterous *G. firmus* was significantly greater during the summer peak than during the fall peak in 1970, 1971, 1973, and in the combined data set (Table 2). The maximum proportions of macropterous *G. firmus* occurred in August at the end of the summer population peak (Fig. 3B). The percentage of macropterous adults dropped suddenly at the beginning of the fall peak and decreased to zero by December (Fig. 3B). The proportion of females that were macropterous was usually higher than the proportion of males that were macropterous especially during the summer peak (Table 2). The 2 sexes had similar seasonal patterns of macroptery.

Investigators have found that long photoperiods (Masaki and Oyama 1963, Saeki 1966b, Alexander 1968), high, relatively constant temperatures (Sellier 1954, Alexander 1968), and high population densities (Fuzeau-Braesch 1961, Saeki 1966a) can increase macroptery in cricket populations. Alexander (1968) hypothesized that factors that increase developmental rate may also increase macroptery. Macroptery of *G. rubens* and *G. firmus* could have been influenced by any or all of the above factors, but the exact relationships could not be predicted. The seasonal pattern of macroptery of *G. rubens* was not the same as that of *G. firmus* (Fig. 3), suggesting that the 2 species were being affected differently. Maximum macroptery in *G. firmus* occurred at a time when macroptery in *G. rubens* was at a summer low (Fig. 3).

Alexander (1968) suggested that crickets that diapause as juveniles may have a lower incidence of macroptery than crickets that diapause as eggs or crickets that develop directly, and he cited both *G. rubens* and *G. firmus* as examples to prove his point. We also found that *G. rubens* that matured in the summer had a higher incidence of macroptery, although never achieving the 75% macroptery that Alexander (1961, 1968) reported. Alexander (1968) reported a slightly higher proportion of macropterous *G. firmus* in the fall (21 of 116 specimens) than in the summer (15 of 107), but we found the opposite (Table 3B). Macropterous females of some species of crickets occur in greater numbers than macropterous males (Sellier 1954, Alexander 1968), but we often collected macropterous males in equal or greater numbers than macropterous females (Tables 2, 3). From the obvious inconsistencies in our data and that in the literature, we conclude that macroptery in crickets is a complicated phenomenon that is still poorly understood.

REFERENCES CITED

Alexander, R. D. 1957. The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). Ann. Entomol. Soc. Am. 50: 584–602.

1961. Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour 17: 130–223.

1968. Life cycle origins speciation, and related phenomena in crickets. Quart. Rev. Biol. 43: 1–41.

Alexander, R. D., and R. S. Bigelow. 1960. Allochronic speciation in field crickets, and a new species, *Acheta veletis*. Evolution 14: 334–46.

Bigelow, R. S. 1962. Factors affecting developmental rates and diapause in field crickets. Evolution 16: 396–406.

Fulton, B. B. 1952. Speciation in the field cricket. Evolution 6: 283–95.

Fuzeau-Braesch, S. 1961. Variations dans la longueur des ailes en fonction de l'effect de groupe chez quelques especes de Gryllides. Bull. Soc. Zool. Fr. 86: 785–8.

Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol. 33: 301–10.

Harris, D. L., and W. H. Whitcomb. 1971. Habitat relationship and seasonal abundance of four species of *Evarthrus* (Coleoptera: Carabidae). Coleop. Bull. 25: 67–72.

Masaki, S., and N. Oyama. 1963. Photoperiodic control of growth and wing-form in *Nemobius yezoensis* Shiraki (Orthoptera: Gryllidae). Kontyu 31: 16–26.

Menke, W. W. 1973. Response surface methodology applications to biological data from field measurements. Ecology 54: 920–3.

Nickle, D. A., and T. J. Walker. 1974. A morphological key to field crickets of southeastern United States (Orthoptera: Gryllidae: *Gryllus*). Fla. Entomol. 57: 8–12.

Saeki, H. 1966a. The effect of the population density on the occurrence of the macropterous form in a cricket, *Scapsipedus aspersus* Walker (Orthoptera, Gryllidae). Jap. J. Ecol. 16: 1–4.

1966b. The effect of the day-length on the occurrence of the macropterous form in a cricket, *Scapsipedus aspersus* Walker (Orthoptera, Gryllidae). Jap. J. Ecol. 16: 49–52.

Sellier, R. 1954. Récherches sur la morphogenese et le polymorphisme alaires chez les Orthopteres Gryllides. Ann. Sci. Nat., 11th Ser. 16: 595–740.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York.

Walker, T. J. 1974. *Gryllus ovisopis* n. sp.: A taciturn cricket with a life cycle suggesting allochronic speciation. Fla. Entomol. 57: 13–22.

Whitcomb, W. H. 1973. Natural populations of entomophagous arthropods and their effect on the agroecosystem. Pages 150–69 *in* F. G. Maxwell and F. A. Harris (ed.). Proceedings of the Summer Institute on Biological Control of Plant Insects and Diseases. Univ. Press of Miss.