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SEASONAL AND DAILY CHIRPING CYCLES IN THE NORTHERN SPRING AND FALL FIELD CRICKETS, *GRYLLUS VELETIS* AND *G. PENNSYLVANICUS*¹

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ABSTRACT

In southeastern Michigan, *Gryllus veletis* chirps from mid-May until early August, barely or not at all overlapping with its sympatric sibling, *G. pennsylvanicus*, which chirps from early August until mid-November. When nights are warm, both species chirp chiefly at night; when nights are cold, they chirp solely by day.

SEASONAL RELATIONSHIP OF ADULT POPULATIONS

Several investigators have discussed the seasonal relationships of adult populations of the northern spring field cricket, *Gryllus veletis* (Alexander and Bigelow), and the northern fall field cricket, *G. pennsylvanicus* Burmeister, using various common names for the two species. Walker (1904) noted that, in Ontario, *G. veletis* matures "about the third week in May" and "the chirping of the males becomes more and more infrequent towards the close of July, and apparently disappears before that of [*pennsylvanicus*] . . . begins." The latter, he said, begins to mature "about the second week in August" and is "very numerous" in September and October. Criddle (1925) reported that in Manitoba there is "very little" overlapping of adults and gave "May 1 to August 1" and "August 1 to winter" as the adult seasons for the two forms. Severin (1926) stated that, in South Dakota, there also is "very little" overlapping of adults in July, with *G. veletis* beginning to mature in late May and dying "during July," *G. pennsylvanicus* beginning to mature "during the fourth week in July" and many adults living "until a heavy freeze destroys them." Cantrall (1943) found that, in Michigan, *veletis* begins to mature about the last week of May and peaks about two weeks later, with few left by the middle of July: "It is possible that a few may survive until, or even for a short time after, the fall population (*pennsylvanicus*) makes its appearance." He said that *G. pennsylvanicus* begins to mature the first week of August, peaks in about ten days, is killed off by successive frosts, and disappears "before the end of November." Fulton (1952) lacked sufficient mid-season observations in North Carolina, but suggested, in a life-history diagram, that the break or overlap occurs sometime in August. Alexander (1957b) stated that, in Ohio, *G. veletis* sings from "early May until about mid-July" and *G. pennsylvanicus* "from mid-July until frost," with a slight overlap of adults in mid-July: "Although very few adults can be seen or heard at this time, there were at least a few singing males on The Ohio State University campus every night from May to October during the three years of this study." Bigelow (1958) stated that, in Quebec, *G. veletis* matures as early as May 12 and dies off "near the end of July" with *G. pennsylvanicus* maturing "rather suddenly, in early August." He also noted that "near the end of July . . . chirping almost, but not quite disappears altogether."

For Nova Scotia, where only *G. pennsylvanicus* is known, Vickery (1961) gave July 29 and November 5 as earliest and latest dates for adults. *Gryllus veletis* is not known to occur anywhere without *G. pennsylvanicus*.

Alexander and Bigelow (1960) summarized the opinions of these investigators,

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all of whom seem to agree that both species mature a little later in the north, that more *G. pennsylvanicus* are killed by frost in the north than in the south, and that the mid-season overlap is at most very slight at any latitude and probably less extensive and somewhat later in the north. No investigator, however, has studied the precise relationship of adult populations of these two species in one particular spot, a subject of special interest because of the involvement of these two species in an hypothesis of speciation by accidental seasonal separation rather than by geographic isolation (Alexander and Bigelow, 1960).

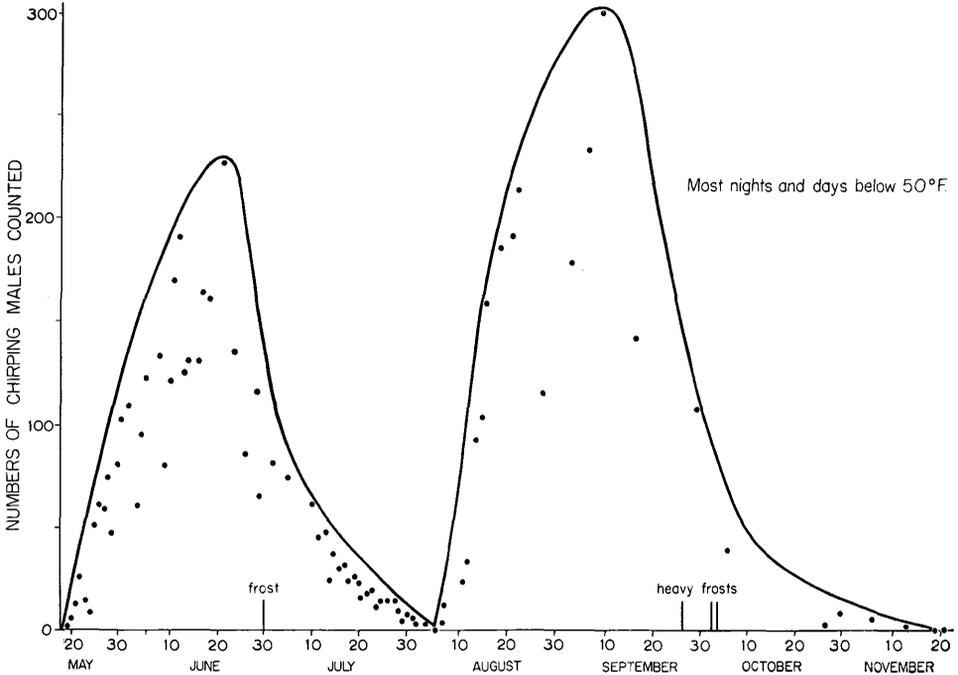


FIGURE 1. Season relationships of adult populations of *Gryllus veletis* and *G. pennsylvanicus* in a brushy pasture in southeastern Michigan, as measured by counts of chirping males during 1965. High counts were on warm, sunny days, low counts on cold, cloudy, or rainy days. Following October 1, nearly all nights were below freezing, and scarcely any days warmed up to chirping temperatures; the last six counts were made on the last six days warm enough for chirping.

During 1964, 1965, and 1966, but particularly in 1965, we studied populations of *G. veletis* and *G. pennsylvanicus* in a brushy former pasture (about three acres) near Ann Arbor, Michigan, throughout most of the summer, using numbers of chirping males as the principal sampling technique. Temperature, cloud cover, and wind were recorded each day, and marked stakes were placed near all chirping males at daily intervals (in some cases less often). In 1965, we also carried out continuous observations through one 72-hour period and another 48-hour period on the number and location of chirping males of *G. veletis* in a 50 x 150-foot area and in a 50-foot square area within the larger population (fig. 4). Juveniles of both species were collected and kept in the laboratory so that maturing times and rates of the sexes and the species could be compared (figs. 2, 3). During 1966, less frequent counts were made of chirping males in the same two populations, and a record was kept of changes in the numbers of chirping *G. veletis* males in another, nearby population (300 yards away in an area about 200' x 400') throughout a 50-hour period at mid-season (fig. 5).

Most of the results of these studies are summarized in figs. 1-5. Figure 1 shows that, in 1965, *G. veletis* males chirped between 18 May and 3 August, and *G. pennsylvanicus* males chirped between 5 August and 13 November. Because overwintering juveniles become active in late March or early April (probably a little before overwintering eggs begin to hatch), this means that the crickets are active between seven and eight months of the year at this latitude, and the combined populations contain adults during nearly six months of the year. The

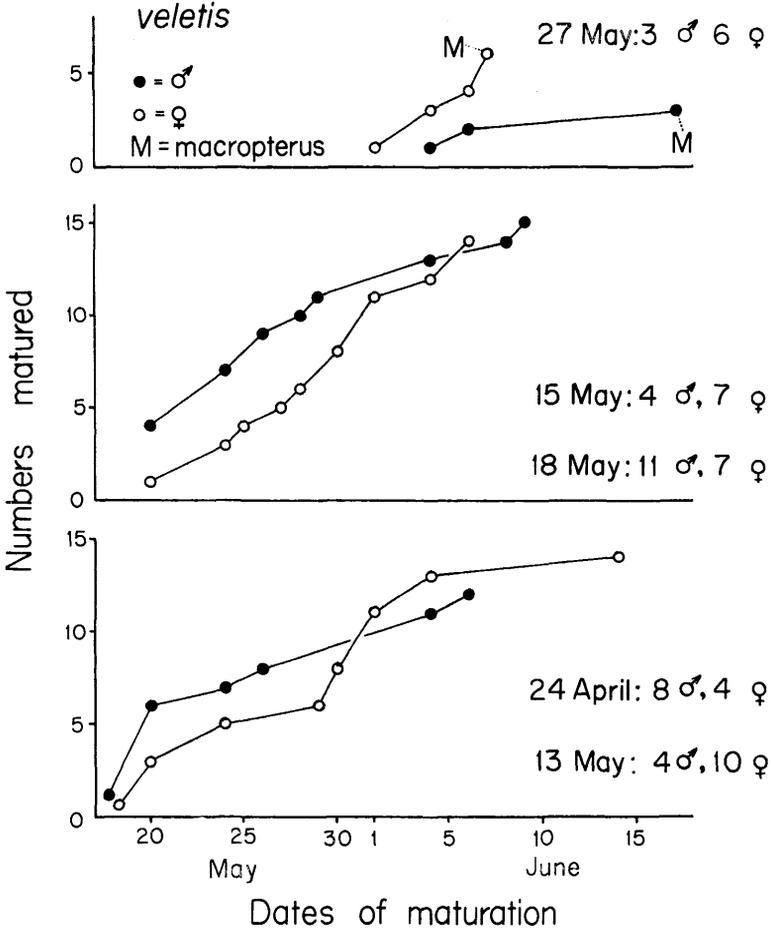


FIGURE 2. Maturation times of males and females of *G. veletis* collected at different times as late juveniles. Laboratory conditions were normal day lengths and approximately 75°F. Collections are grouped to separate collections made at greatly different times, and those in which sex ratios were not nearly 1:1. Collection dates are listed on each graph.

peaks of the two adult populations are only two and a half months apart, yet in this case they overlapped either not at all or very slightly. In the laboratory, males begin to mature before females, although the results shown in figs. 2-3 suggest that some males of both *G. veletis* and *G. pennsylvanicus* mature relatively late compared to females. Laboratory observations on a variety of cricket species indicate that some females live past the last singing dates of the males.

In 1964, observations on seasonal overlap were unfortunately interrupted for three days in late July when only one or two males of *G. veletis* had been chirping for several days. Following the three-day interruption, more than 20 males of *G. pennsylvanicus* had matured and were chirping. Similar but more casual observations during several other years in this and other locations indicate that a situation at least similar to that depicted in fig. 1 is the usual one.

SIZE OF POPULATIONS

Forty "chirping locations" were mapped during the 50-hour period of observations in the small area in 1966, though no more than 14 males chirped simultane-

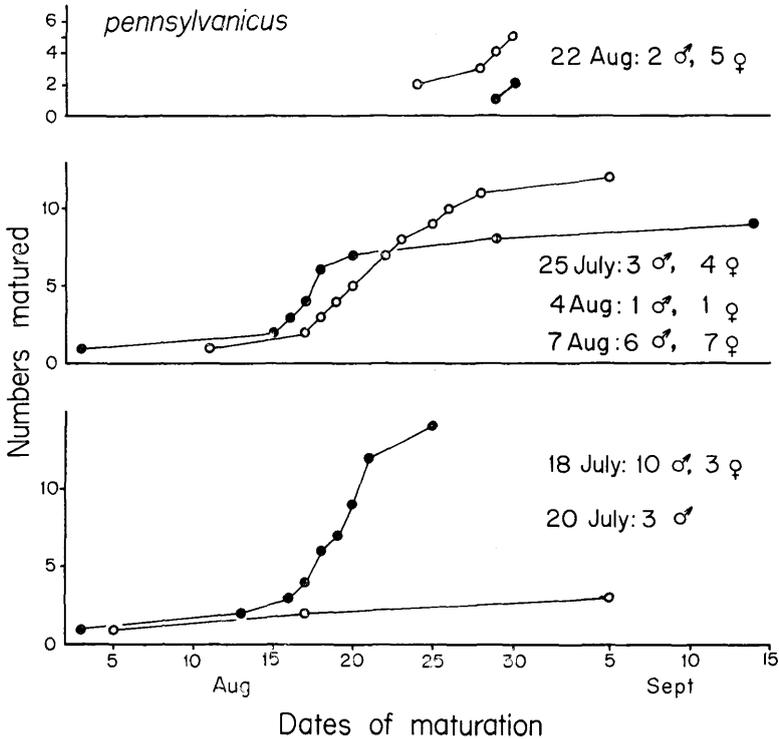


FIGURE 3. Maturation times of males and females of *G. pennsylvanicus* collected at different times as late juveniles. Laboratory conditions were normal day lengths and approximately 75°F. Collections are grouped to separate collections made at greatly different times, and those in which sex ratios were not nearly 1:1. Collection dates are listed on each graph.

ously during the counts (fig. 5), which required approximately 10 minutes each. More than 14 individual crickets were involved, for chirping often resumed from precisely the same location after silence during a previous observation period. On the night of June 27, 1966, 30 minutes of continuous walking through the area resulted in a count of 17 singing males in the same locations noted on previous evenings. On the basis of isolation from other chirping locations and the occurrence of simultaneous chirping in neighboring locations, at least eight other chirping locations from earlier evenings must have represented individual male crickets. This means that the population, during the 1966 observations, probably contained no fewer than 25 male crickets. The actual numbers of males in the larger 1965

populations cannot be estimated (fig. 1), but the shapes of the curves and their heights relative to one another are probably valid reflections of similarities and differences between the two populations. The greatest errors in counting chirping males probably occurred during times when the populations were largest, when the same male may have been counted more than once, and when some individuals may have been missed. Counts of below 50 or 75 males could be made with little evident chance of error.

DAILY CHIRPING CYCLES

Many kinds of crickets, particularly those that live only in trees, call only at night and presumably are nocturnal in most other activities as well. One North

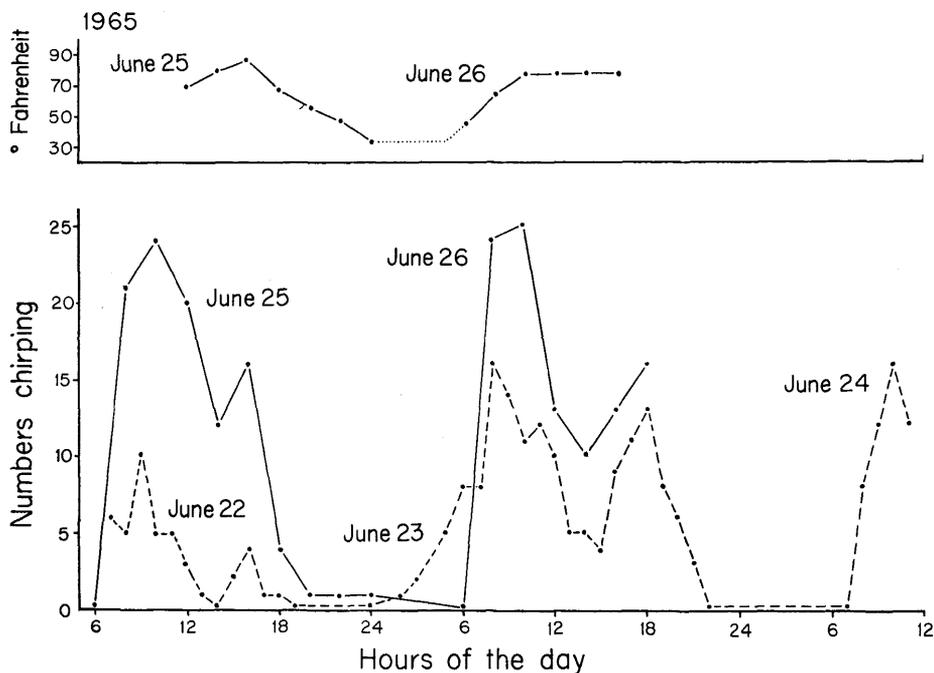


FIGURE 4. Daily changes in number of chirping males of *Gryllus veletis* during a 1965 period when the nights were too cold for chirping between shortly after sunset and shortly after sunrise, and when no part of the day was too hot for chirping. Temperature was not recorded June 22-24, but the nights were cold, and there was rain the night of June 22.

American species of Trigonidiinae, *Phyllopalpus pulchellus* (Uhler), which lives on various kinds of bushes and tall weeds, has unusually large convex eyes and calls at least as much during the day as it does at night. Several Oecanthinae that live on low, herbaceous vegetation, as well as practically all of the surface and burrowing crickets, call mostly at night, but at least a few individuals in any large population can be heard calling at nearly any time of the day. Field and ground crickets that live in the woods are usually more nocturnal in calling than their closest relatives in grasslands and open fields (RDA: unpublished observations).

Lutz (1932) used a treadle arrangement in the laboratory to demonstrate that juveniles and adult males of both *Acheta domesticus* and a *Gryllus* species (almost certainly *pennsylvanicus* because the only other cricket that occurs in New York City is *veletis*, which is much less common) are much more active, in terms of

locomotion, at night than in the daytime when temperature and humidity are relatively constant, and that they continue their 24-hour cycle for at least several days in continuous darkness. When light-dark cycles were reversed, new peaks of activity appeared during the new dark period and eventually replaced the old peaks. Continuous darkness after reversal led to partial resumption of the original cycle in two males that had been reversed four and five days.

Nowosielski and Patton (1963, 1964) and Nowosielski, Patton, and Naegele (1964) conducted further studies on *Acheta domesticus*, confirming nocturnal peaks of locomotory activity in both juveniles and adults, but indicating late afternoon peaks of feeding, drinking, and courting behavior, with high levels of these activities

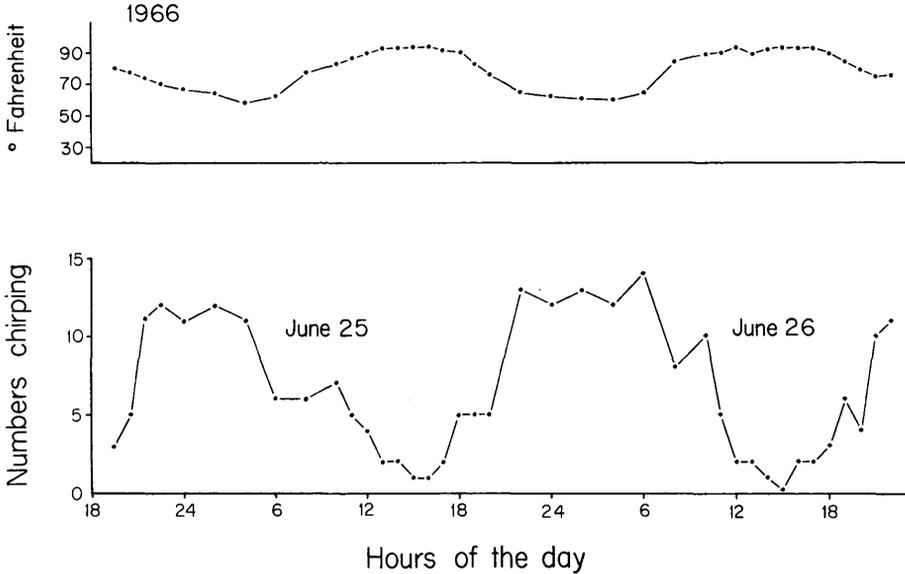


FIGURE 5. Daily changes in number of chirping males of *Gryllus veletis* during a 1966 period when the nights were never too cold for chirping, and when most locations were too hot for chirping during several hours of mid-day.

continued through most of the night. Rhythms of locomotory activity persisted in continuous light or dark, or could be reset by changing the phase of the light-dark cycle; the "free-running" period was a little over 23 hours in continuous light, just under 25 hours in continuous darkness.

Cloudsley-Thompson (1958) studied the daily activity patterns of three adult females of *Gryllus campestris* L., a juvenile-overwintering species that he collected in August as pre-diapause nymphs and reared in the laboratory. He found them to be most active in the daytime, with a peak of activity about 3 P.M. This pattern of activity persisted in continuous darkness and could be reset by (1) changing the phase of the light-dark cycle, (2) providing two-hour light periods after damping activity in continuous darkness, (3) returning the environment to 30°C. after periods at lower temperatures, or (4) supplying water after several days without water.

In this study of *G. veletis* and *P. pennsylvanicus*, the daily temperature regimes during the two *G. veletis* seasons were strikingly different, resulting in a surprising difference in the daily cycle of chirping between the two seasons (figs. 4-5). Crickets chirp only at temperatures between approximately 50°F. and 100°F. (fig. 6). In 1965, the air temperature (thermometer one-fourth inch above ground)

dropped below 50°F. shortly after sundown most evenings during the adult life of *G. veletis*, and during the day it probably rose above 100°F. in chirping locations only infrequently and for short periods. During 1966, in sharp contrast, the night temperatures did not fall below 56°F. in any singing location (thermometer at burrow entrance one-fourth inch above ground) during the 50-hour-long observations (and probably did not fall below 50°F. during any of the previous 10 or 15 nights), while during the day the air temperature rose above 90°F. on both days (and had been doing so for several previous days). At the exposed entrance of one cricket burrow, a temperature of 114°F. was recorded in the sun at 2 P.M. on

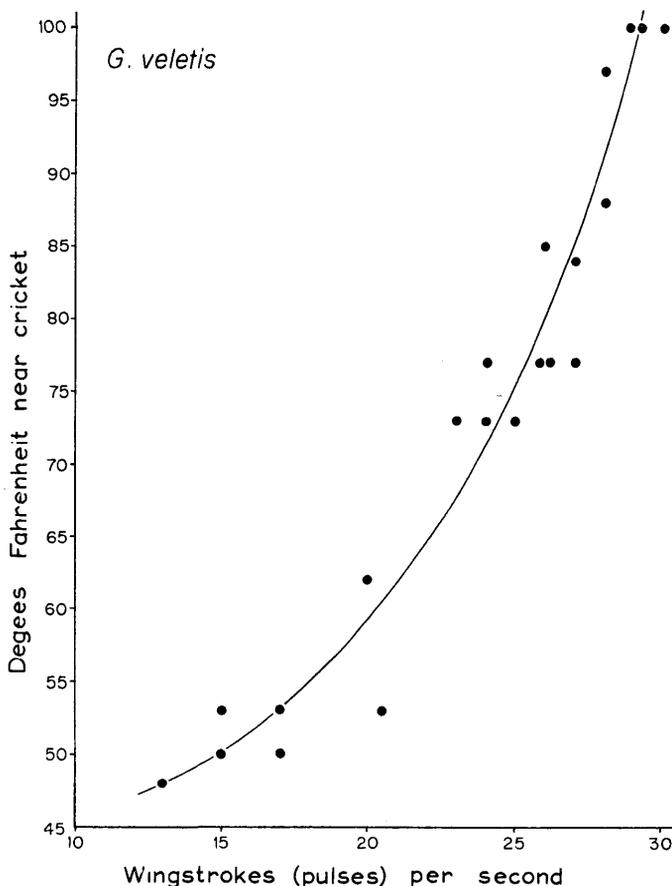


FIGURE 6. Effect of temperature on the pulse (wingstroke) rate in the chirping of a single male of *Gryllus veletis* in a refrigerator-incubator. Recording was started at 73°F. and continued as the temperature dropped slowly across two hours or more for each reading until the temperature was so low that the cricket stopped stridulating. Recording was then started again at 77°F. and continued as the temperature climbed at a similar rate until the cricket stopped stridulating again. Part of the wide variation in pulse rates in owing to the fact that pulse rates had to be taken from aggressive and mixed courtship sounds as well as from calling sounds; small variations exist between these sounds and pulse rate is often difficult to measure accurately during mixed courtship (Alexander, 1957a). Pulse rate was measured by averaging, at each temperature, several intervals from the beginning of a pulse (never the initial short pulse in a chirp) to the beginning of the next one. The curve was fitted by eye.

one day. In other words, during the 1965 observations, the days were apparently not too hot for chirping, though the nights were always too cool, while in 1966 the days were apparently always too hot (in at least some locations) and the nights were never too cool.

During 1965, scarcely any cricket was able to chirp after 8 PM or before 6 AM because of the low temperatures. During 1966, most chirping was done between 8 PM and 6 AM. During both seasons there seemed to be two peaks of chirping during the day, one about 10 AM and one at 4–6 PM; daytime chirping fell to a minimum at 2–3 PM. Some crickets (identified by location) were strictly nocturnal chirpers during 1966, while others chirped intermittently during the day and less steadily during the night, suggesting that, in spite of the temperature differences, some crickets behaved in 1966 as most or all crickets behaved in 1965.

The 1965 crickets were not simply starting their chirping earlier in late afternoon, in other words, beginning to chirp sooner as the light intensity and temperature both dropped, as the 1966 crickets did while behaving nocturnally. Instead, they started singing, for the most part, when both temperature and light intensity were rising. Because this rise in temperature always followed a dark period during which the temperature was so low the crickets could not chirp at all, one is led to believe that these crickets' chirping thresholds were being lowered by the inhibitory effect of low temperatures across long periods, so that the inhibitory effect of light on chirping was overcome. That the situation may be more complicated than this is shown by all of the low counts of chirping males in fig. 1 being obtained on cloudy and rainy days and all of the high counts on sunny days. The crickets did not chirp during rain, and they chirped considerably less when it was windy or when the vegetation was wet. But they also chirped less on dry, windless, cloudy days: compare June 9 (cloudy, 70°F.) with June 8 and 10 (clear, 68°F. and 70°F., respectively); June 16 (cloudy, 65°F.) with June 17 (clear, 64°F.). On 38 clear days during the *G. veletis* season, the air temperature averaged 69.3°F. in the shade about three feet above the ground, while on 23 cloudy and partly cloudy days, it averaged 68.2°F.; ranges were 52–88°F. and 46–80°F., respectively. These figures do not indicate how important the direct heating effect of the sun may have been in causing the dramatic rise in numbers of chirpers on sunny mornings. But, together with the other data given above, they suggest that extreme temperature fluctuations can not only change daily activity cycles of crickets in a direct fashion (by preventing, say, calling), but also alter responses to light-dark regimes at other times when temperatures are suitable for the activity involved.

Ability of these field crickets to be either nocturnal or diurnal, as conditions demand, poses interesting questions about predation, since chirping can only be effective if females are moving about. Drastic shifts in temperature regimes between seasons also raise questions about the temporal relationship between the adult populations of *G. veletis* and *G. pennsylvanicus*—both the timing of the two populations, collectively speaking, and the amount of overlap between them.

In view of these findings and those of Lutz with *G. pennsylvanicus* and Cloudsley-Thompson with *G. campestris* (the latter species having essentially the same ecology and life cycle as *veletis* and exposed to the same weather conditions), a remark by Criddle (1926) is particularly interesting (p. 82): "Both species are nocturnal to some extent but while they prefer to hide from the sun's rays during hot days, they have no hesitation in taking advantage of its warmth when the weather is cool . . . The breeding season for [*veletis*] . . . is in the height of summer and this species has, therefore, little need for extra warmth but [*pennsylvanicus*] . . . has colder days to contend with and it is consequently a common sight to see the females wandering about during the daytime, sometimes seeking the males, at others busily engaged in egg-laying."

It would be most interesting to see if a group of crickets can be changed, under

experimental conditions, from the 1965 behavior to that of 1966 and, if so, precisely how the shift occurs.

BEHAVIOR OF INDIVIDUALS

Few observations were made on individual crickets, since marking would usually cause gross disturbance, and in most cases would require at least partial destruction of the cricket's burrow or niche. Considerable moving about by individual males was revealed by staking, though some males, particularly late in the season, remained in burrows that had been located. One male in 1966 was identified (by general size and color and a broken antenna) calling at his burrow entrance on eight successive nights. In 1965, a chirping male was watched for 50 minutes as he walked about an area approximately eight feet by four feet, travelling a total distance of more than 40 feet and returning three times to the same spot from distances of more than four feet.

During 1965 and 1966 combined, three crickets sang at spots located three feet from one another, and two others sang from about two feet from one another; all the rest were farther apart. One fight was heard in 1965 in which both males chirped vigorously, and one of the combatants was later located in a hollowed-out niche in heavy grass.

Four of the five most persistent chirpers in 1966 were located in stone walls; the fifth chirped from a burrow on top of a mound of bare soil. These five crickets averaged almost 10 hours of continual chirping per day (based on five 2-hour checks), ranging between 8 and 12 hours. No other cricket chirped during four or more successive check periods two hours apart. These five persistent chirpers were almost solely nocturnal.

During the hottest part of the day in 1966, the crickets that chirped were always in the shadiest spots. Several located in stone walls chirped from deep inside the wall during mid-day so that their chirps seemed very soft. The chirps of crickets in this same location, singing in exposed locations, carried farthest at night because of the effect of the wall behind them. Movement in and out of the wall must have been chiefly in response to temperature changes, for at mid-morning, when the sun was brightest against an east-facing stone wall, the crickets chirped in more exposed positions than during mid-day and early afternoon when the temperature was higher, but the sun less direct against the wall.

Crickets with burrows, or ensconced in stone walls, seemed to chirp more continuously and for longer periods, and to move about less than crickets with less impressive retreats. Furthermore, the percentage of males singing in new locations steadily decreased toward the end of the season, and the last few males were always permanently located. These findings suggest that burrows or elaborate retreats of other kinds increase the life expectancy of a male cricket.

Although copulation in field crickets requires less than a minute when both individuals are responsive, a pair does not mate and separate immediately; instead, the male "corners" the female and prevents movement by her, or her departure, until he has formed another spermatophore (Alexander, 1961). A pair may copulate repeatedly at intervals of 15 minutes or more throughout a period of several hours. When a female was introduced into the burrow of the most persistent nocturnal chirper in 1966, he began to court inside the burrow, became silent within a few minutes (evidently copulating), and did not sing again during the next three hours. The next evening, however, he began calling at dusk as usual. Another probable advantage of a burrow is seen here: it would not only facilitate the "holding" of the female by the male, but would also allow a pair to continue copulating through part or all the day relatively free from possible interruptions or predation. Acquisition of females probably explains many of the nights of silence from chirping locations which became active again on subsequent nights.

SUMMARY AND CONCLUSIONS

In a field in southeastern Michigan containing both *Gryllus veletis* and *G. pennsylvanicus* (adult in spring and in fall, respectively), sampling by counting chirping males indicated a total adult season of six months, population peaks about 80 days apart, and very nearly a complete break between adult populations of the two species in mid-season. The *G. pennsylvanicus* population, which was larger than that of *G. veletis*, persisted past heavy frosts into late autumn when all nights were below freezing and most days were not warm enough for chirping.

In 1965, when most nights were too cold for chirping, *G. veletis* males chirped almost entirely in the daytime, with peaks in mid-morning and later afternoon; in 1966, when nearly all nights were warm, they chirped mostly at night. A comparison of these results with those of other investigators studying daily activity cycles in crickets indicates that the different activities of crickets may be cycled differently and that even closely related species may differ in their responses to daily cycles of light and dark. Perhaps most important, these data suggest that a considerable flexibility must exist, so that (1) prior experience of individuals (in terms of temperature and light regimes) may have unsuspected significance, and (2) it may be difficult or impossible to gain a reasonable understanding of daily activity cycles without considerable insight into the kinds of variations occurring in the climate regimes in which the crickets have evolved (Alexander, in press).

ACKNOWLEDGMENTS

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