LIFE CYCLE ORIGINS, SPECIATION, AND RELATED PHENOMENA IN CRICKETS

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ABSTRACT

Seven general kinds of life cycles are known among crickets; they differ chiefly in overwintering (diapause) stage and number of generations per season, or diapauses per generation. Some species with broad north-south ranges vary in these respects, spanning wholly or in part certain of the gaps between cycles and suggesting how some of the differences originated. Species with a particular cycle have predictable responses to photoperiod and temperature regimes that affect behavior, development time, wing length, body size, and other characteristics. Some polymorphic tendencies also correlate with habitat permanence, and some are influenced by population density. Genera and subfamilies with several kinds of life cycles usually have proportionately more species in temperate regions than those with but one or two cycles, although numbers of species in all widely distributed groups diminish toward the higher latitudes. The tendency of various field cricket species to become double-cycled at certain latitudes appears to have resulted in speciation without geographic isolation in at least one case. Intermediate steps in this allochronic speciation process are illustrated by North American and Japanese species; the possibility that this process has also occurred in other kinds of temperate insects is discussed.

INTRODUCTION

CRICKETS are insects of the Family Gryllidae in the Order Orthoptera, and are identifiable by their jumping hind legs, three tarsal segments, and long tactual cerci bearing clumps of knobbed hairs. They range in body length from 1 or 2 mm to over 50 mm. The family comprises some 2455 known species, presently arranged in 14 subfamilies and about 333 genera (Table 1). Fossil evidence dates the Gryllidae at least to the Jurassic Period (Zeuner, 1939), and many of the larger subfamilies and genera have spread across two or more continents.

Crickets occupy today all of the major terrestrial habitats between approximately latitudes 55° N and 55° S, or, roughly, the region between the boundaries of the northern and southern coniferous forests, or taiga (Fig. 1). In the course of achieving this broad distribution, they have evolved at least seven kinds of life cycles, most of them more than once in

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various parts of the world. These different adjustments to climatic variation involve far more than the simple synchronizing of resistant life stages with harsh seasons. Within each species studied, there are also genetically and environmentally induced variations in morphology, physiology, and behavior that are consistent with life cycle pattern, latitude, and habitat. Particularly during the past two decades, the nature of many of these phenomena, including some of their probable origins and histories, has been clarified by parallel and complementary investigations in Europe, Japan, Australia, and North America.

This paper summarizes the available information and compares variously related species in an attempt to reconstruct some of the evolutionary changes by which known combinations of characteristics have come about.

KINDS OF LIFE CYCLES

Crickets are oviparous, hemimetabolous insects. Their eggs are injected into soil, plant stems, or twigs, or laid in burrows. There are from five to twelve juvenile instars, or molt stages, and the juveniles resemble the adults, live in the same general habitats, and eat the same kinds of food. Most species studied seem to eat either plant or animal food of a wide variety; some tree crickets are believed to subsist largely on aphids, and some mole crickets on roots and earthworms.

The seven general kinds of cricket life cycles, six of which are illustrated in Figures 2 and 3, are the following:

(1) *Continuous breeding without any diapause in environments without marked seasonal changes.* Examples are *Acheta domesticus* (Linnaeus), *Gryllodes sigillatus* (Walker) (species that are found around the world near human habitations, but that otherwise occur only in tropical regions); *Gryllus assimilis* Fabricius in the West Indies, Mexico, and extreme southern United States (Florida, Texas, California); *Teleogryllus mitratus* (Burmeister) in tropical Asia (Masaki and Ohmachi, 1967); and *Tohila atelomma* Hubbell, a cave inhabitant in Yucatan (Hubbell, 1938). [When references are not given, life cycle determination is based on my studies. I have reared all species mentioned except *Tohila atelomma*, *Myrmecophila nebrascensis*, *Gryllotalpa gryllotalpa*, and those

TABLE 1

A synopsis of the subfamilies of the Gryllidae (crickets)

| SUBFAMILY | COLLOQUIAL NAME | APPROXIMATE NOS. | | GENERAL HABITATS | GENERAL DISTRIBUTION | SOME CHARACTERISTICS |
		GENERA	SPECIES			
*Oecanthinae	Tree Crickets	3	60	trees, brushes, herbs	World-wide	medium-sized, narrow heads, soft-bodied, ♂ with 1 metanotal gland
*Eneopterinae	Bush Crickets	100	600	trees, bushes, herbs, leaf litter	World-wide (except Europe)	generally similar to above, but with more highly pigmented wings and heavier bodies
*Pentacentrinae	Five-Spined Crickets	11	40	soil surface, leaf litter, caves	Neotropic, Ethiopian, Oriental, Australian	large, long-legged, some wingless; some ♂♂ with dorsal abdominal glands
Phalangopsinae	Long-Legged Crickets	63	250	soil surface, leaf litter	Ethiopian, Oriental. Australian, Neotropic	mostly large, long-legged, some wingless

TABLE 1—Continued

| Scleropterinae	Stiff-Winged Crickets	3	16	soil surface, leaf litter	Palearctic, Ethiopian, Oriental, Australian	medium to large; wings hard, horny, and opaque
Pteroplistinae	Feather-Winged Crickets	1	3	low herbs and water surface	Oriental, Australian	tiny, soft-bodied
*Trigonidiinae	Sword-Tailed Crickets	28	380	trees, bushes, herbs, leaf litter	World-wide	small or tiny, delicate, usually pale brown in color
Cachoplistinae	None	1	4	soil surface?	Ethiopian, Oriental, Australian	tiny, soft-bodied
*Mogoplistinae	Short-Winged Crickets	14	200	bushes, herbs, ground litter	World-wide	small or tiny, short forewings, enlarged pronotum, body with scales
*Myrmecophilinae	Ant-Loving Crickets	5	45	ant nests	World-wide	tiny, wingless, hump-backed, no auditory organs, short antennae, reduced eyes.
*Nemobiinae	Ground Crickets	16	200	soil surface	World-wide	small, ♂ with tibial or tegminal gland
*Gryllinae	Field and House Crickets	70	550	soil surface and shallow burrows	World-wide	large size, yellow to black, ♀ with long ovipositor
*Brachytrupinae	Short-Tailed Crickets	12	42	soil surface and deep burrows	World-wide (except Europe)	resemble Gryllinae except with short or no external ovipositor
*Gryllotalpinae	Mole Crickets	6	65	subterranean	World-wide	mostly large, heavy bodied; shovelling forelegs, pointed head, cylindrical body, dense body setae
Totals	14	333	2455			

* Subfamilies discussed in this paper.
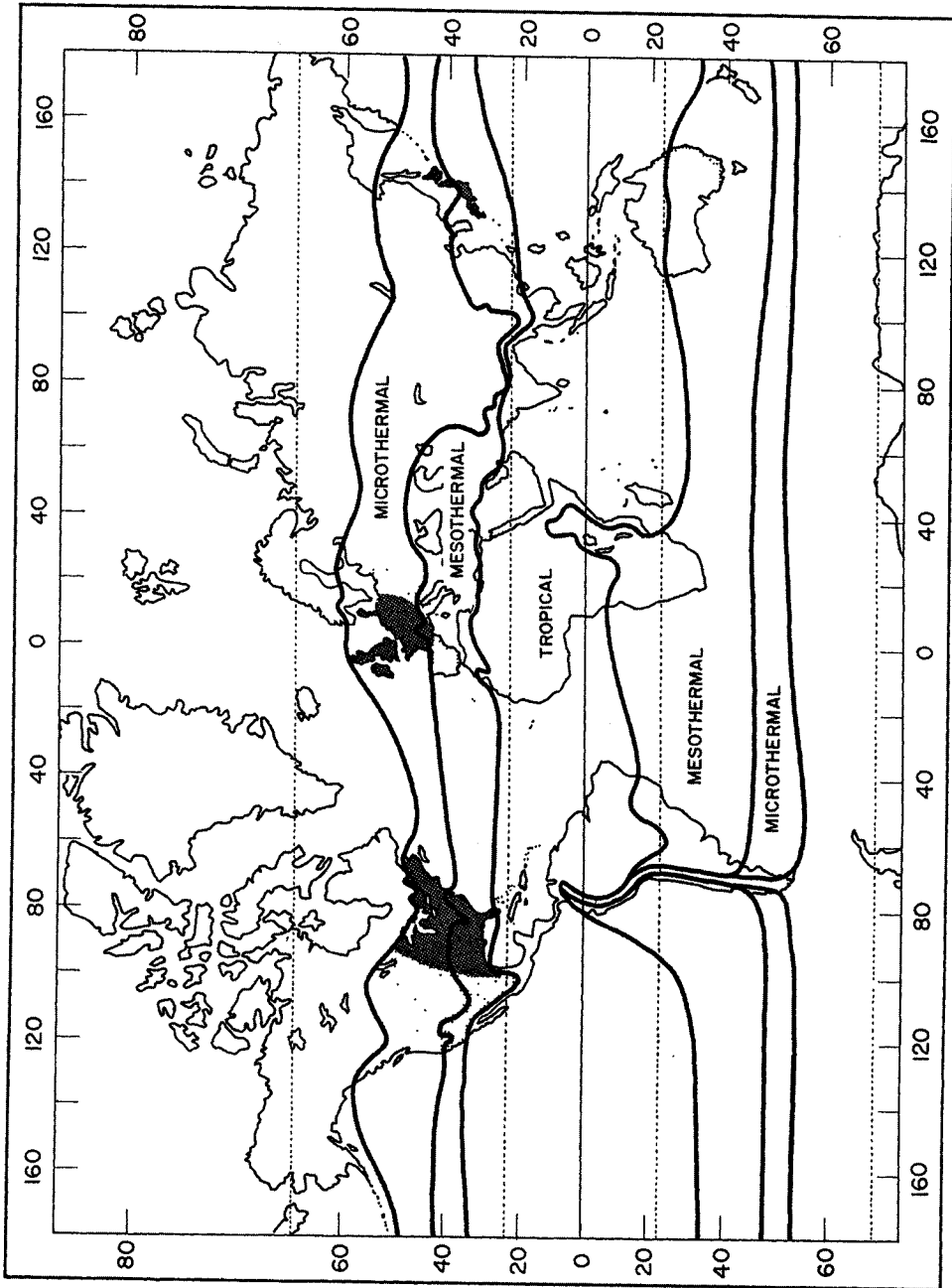
FIG. 1. WORLD MAP SHOWING THE FIVE CLIMATIC REGIONS CONTAINING CRICKETS

Tropical localities generally have the most species, microthermal localities the least. Proportions of surface and sub-terranean species, which have more kinds of life cycles than vegetation-inhabiting species, increase toward the higher latitudes. Dark stippled regions are those where life histories are known for essentially the entire cricket fauna; in light stippled areas one or a few species have been studied.

from Asia and Africa, and I have studied vir-tually all North American species.] This kind of cycle is rarer than might be supposed. Many tropical and sub-tropical crickets are evidently cyclic in association with dry and wet seasons. Wheeler (1900) even implies seasonality in the ant nest inhabitant, *Myrmecophila nebrascen-*sis Luggar, in Austin, Texas: "During April and May the testes, in active spermatogenesis. . ." and "At this same period of the year the abdomen of the female *Myrmecophila* is found to contain a few very large elliptical white eggs. . ."

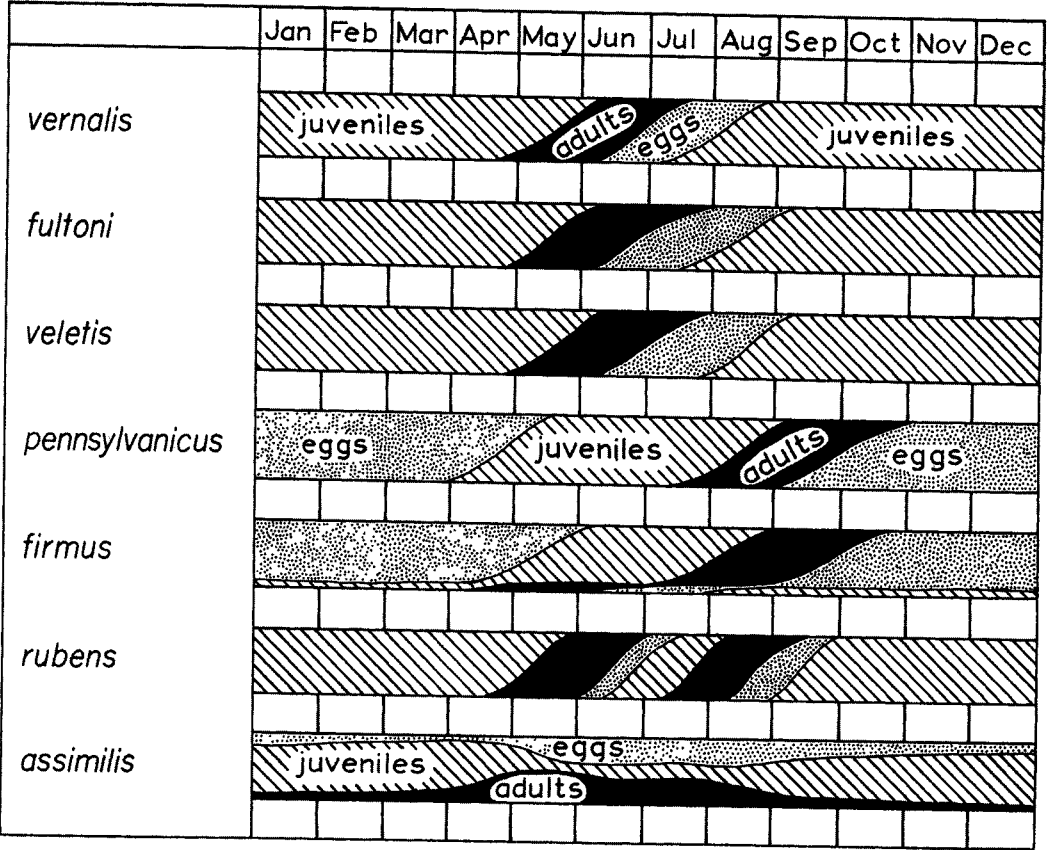2. *One generation each year with egg dia-*

FIG. 2. DIAGRAMS OF THE LIFE CYCLES OF THE SEVEN FIELD CRICKETS (*Gryllus* spp.) IN EASTERN NORTH AMERICA, ILLUSTRATING FOUR OF THE SEVEN GENERAL KINDS OF LIFE CYCLES KNOWN IN CRICKETS
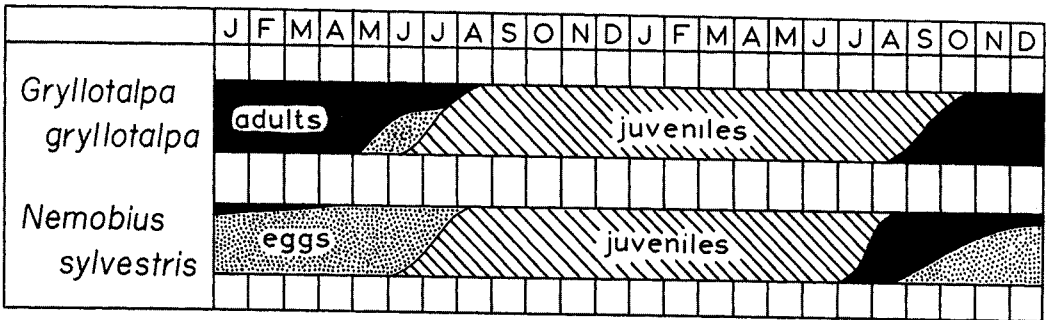

FIG. 3. DIAGRAMS OF THE TWO-YEAR LIFE CYCLES REPORTED FOR *Gryllotalpa gryllotalpa* IN SPAIN (Morales, 1940) AND *Nemobius sylvestris* IN ENGLAND (Gabbutt, 1959)

pause during winters or dry seasons. Examples are *Gryllus pennsylvanicus* (Burmeister), *Miogryllus verticalis* (Serville), *Valerifictorus micado* (Saussure) (introduced) in North America; all North American Nemobiinae north of about the 30th parallel; most temperate, vegetation-inhabiting Gryllidae (involving three subfamilies: Oecanthinae, Trigonidiinae, and Eneopterinae); *Teleogryllus commodus* (Walker) in Australia (Hogan, 1960), *T. emma* (Ohmachi and Matsumura) and *T. yezoemma* (Ohmachi and Matsumura) in Japan (Masaki, 1966).

(3) *One generation each year with juvenile diapause during winter.* The diapause usually occurs two molts from adulthood. Examples are *Gryllus veletis* (Alexander and Bigelow), *G. fultoni* (Alexander), *G. vernalis* Blatchley, *Anurogryllus muticus* (De Geer), *Nemobius ambitiosus* Scudder, *Falcicula hebardi* Rehn, *Scapteriscus vicinus* Scudder (Hayslip, 1943), and *S. acletus* Rehn and Hebard (Hayslip, 1943), in North America; *Gryllus campestris* Linnaeus in Europe (Sellier, 1954); *Nemobius yezoensis* Shiraki in Japan (Masaki and Oyama, 1963) *Melanogryllus desertus* (Pallas) in southern Russia (Megalov, 1924), *Brachytrupes megacephalus* Lefèvre in Tunisia (Valdeyron-Fabre, 1955), and *B. portentosus* Lichtenstein in Formosa (Sonan, 1931). In North America, juvenile diapause is unknown in other Ensifera, and adult diapause occurs only in two species of Tettigoniidae (Copiphorinae), the cone-headed grasshoppers, *Neoconocephalus triops* (Linnaeus) and *Pyrgocorypha uncinata* Stal. Although both species molt to adulthood in the fall, neither is actually sexually mature until spring, at least in the northern parts of their ranges (ca. 37° and 39° north latitude, respectively). In the far south, some individuals of *N. triops* mature and sing in fall and evidently overwinter as eggs (Walker, 1964).

(4) *One generation each two years with diapause in both egg and juvenile stage during winters.* An example is *Nemobius sylvestris* (Bosc.) in England (Richards, 1952; Gabbutt, 1959).

(5) *One generation each two years with diapause in both juvenile and adult stage during winter.* Examples are *Gryllotalpa gryllotalpa* Linnaeus in Spain (Morales, 1940) and *Neocurtilla hexadactyla* (Perty) in North America (Fulton, 1951). Ghosh (1912) reports an unusual

life cycle in tropical India for the univoltine burrowing cricket *Brachytrupes achatinus* Stoll, which may be related to this one. Most individuals mature in June, but eggs are not laid until September or October; thus juvenile growth is retarded during winter, and the summer dry season is spent in a prolonged adult stage.

(6) *Two generations each year with juvenile diapause during winters.* Examples are *Gryllus rubens* Scudder and *G. integer* Scudder, sibling species in North America, *Teleogryllus taiwanemma* (Ohmachi and Matsumura) and *Scapsipedus parvus* Chopard in Japan (Masaki, 1966).

(7) *Two generations each year with egg diapause during winters.* Examples are *Pteronemobius fascipes* (Walker), *P. taprobanensis* Walker, and *P. ohmachii* Shiraki in southern Japan (Masaki, 1960, 1961), *Oecanthus argentinus* Saussure and *O. celerinictus* Walker in eastern United States (Walker, 1963).

[The genera discussed above are grouped into six or seven subfamilies as follows: Gryllinae (house and field crickets) = *Acheta*, *Gryllodes*, *Gryllus*, *Melanogryllus*, *Miogryllus*, *Teleogryllus*, *Valerifictorus* (and possibly *Anurogryllus* and *Brachytrupes*, although some evidence indicates that these genera belong in the subfamily Brachytrupinae instead); Nemobiinae (ground crickets) = *Nemobius*, *Pteronemobius*; Trigonidiinae (sword-bearing crickets) = *Falcicula*; Gryllotalpinae (mole crickets) = *Gryllotalpa*, *Neocurtilla*; Pentacentrinae (long-legged crickets) = *Tohila*; Myrmecophilinae (ant-loving crickets) = *Myrmecophila*.]

The species mentioned, together with those for which variable life cycles are described below, include all crickets for which this author has been able to find life cycle descriptions.

VARIABILITY IN LIFE CYCLES

All of the cricket species with broad north-south ranges in the eastern portion of North America exhibit some kind of geographic variation in life cycles. Some of these intraspecific variations, all of the known cases of which are listed below, span wholly or in part the gaps between cycles and suggest the origins of some of the differences.

(1) *Nemobius carolinus* Scudder occurs from Canada to southern Mexico and to Key West
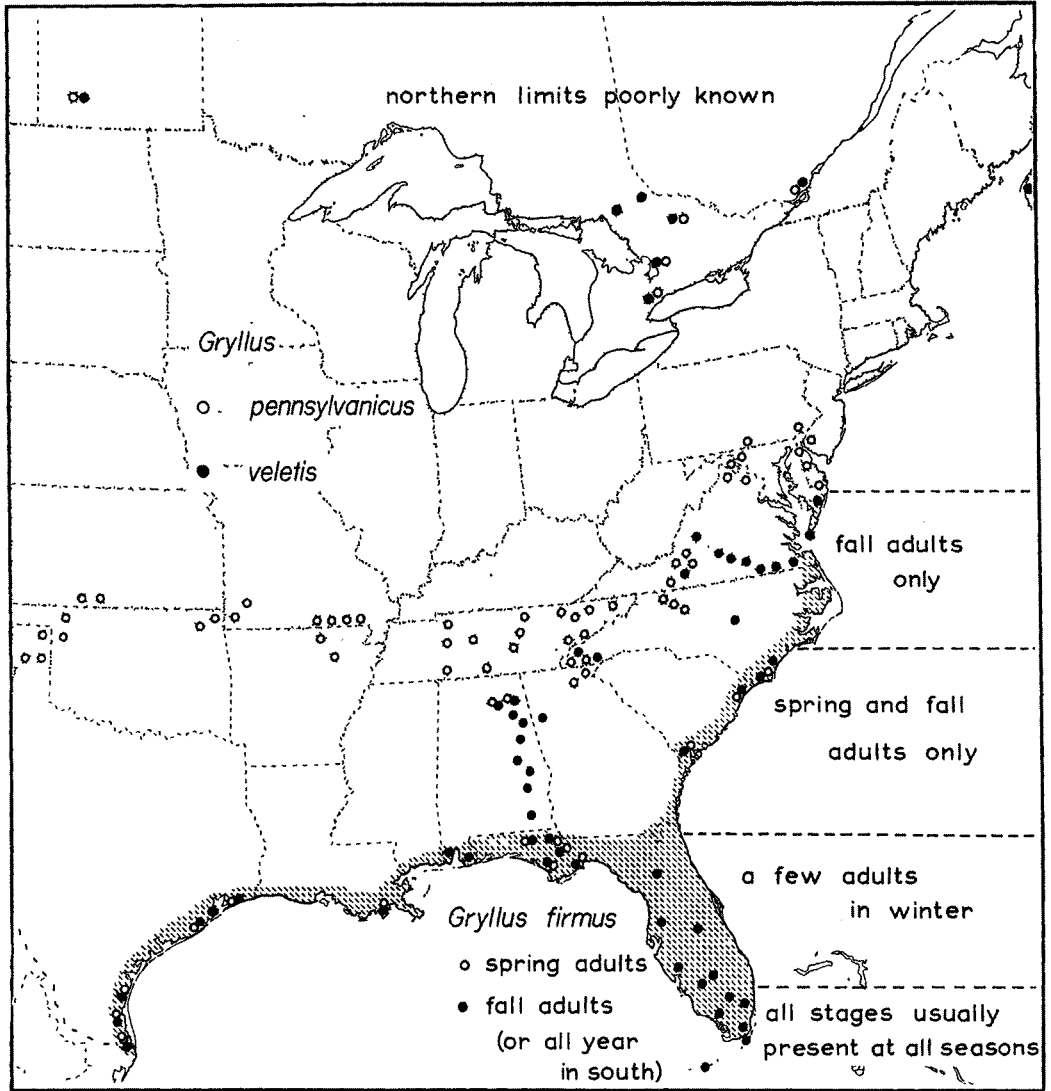
FIG. 4.   GEOGRAPHIC DISTRIBUTION OF THREE CLOSELY RELATED FIELD CRICKETS, *Gryllus veletis*, *G. pennsylvanicus*, and *G. firmus*

Hatched areas represent predicted general distributions. Symbols outside hatched areas represent known peripheral isolates; other symbols are individual collecting records, plotted one to a county. For *veletis* and *pennsylvanicus*, only the southern limital records, compiled through the author's field work, and northern limital records from the literature are shown. These two species are the most continuously distributed field crickets within the hatched area, as well as in Washington, Oregon, the Rocky Mountains, and southwestern Canada. Alabama and North Carolina records outside hatched areas are *firmus*.

in Florida. Evidently, its egg diapause is simply missing in the southern regions where adults are present continually. *Miogryllus verticalis* (Serville), extending from central Illinois and New Jersey to Key West, Florida, seems to change similarly. Neither species has any large breaks in distribution across its range; both have one restricted adult season in the North; and both have been taken as adults during all months in the South. [UMMZ: records of field observations by R. D. Alexander are preserved in the Insect Division of The University of Michigan Museum of Zoology; specimens, collected by R. D. Alexander

and others, are housed in UMMZ collection].

(2) *Nemobius fasciatus* (De Geer), with a north-south distribution almost as extensive in eastern North America as that of *N. carolinus*, is believed to produce one generation in northern states and two in southeastern states. Partial third generations may occur at some latitudes (Fulton, 1951). Restriction to egg-overwintering is retained in all but the southern limits of its distribution where it, too, evidently breeds continually, since adults are present at all times of the year (UMMZ).

(3) East of the Great Plains, *Gryllus veletis* and *G. pennsylvanicus* extend southward to New Jersey and Maryland along the Atlantic Coast, and to about 34° N in northern Georgia (Fig. 4). In the West, both species extend from Canada to central Mexico, probably with breaks in distribution, particularly in the northern parts of the Sierra Madre Oriental. Crickets thus far inseparable from these species in both morphology and song also occur around Los Angeles and San Diego, California; winter in this region is not comparable to that occurring in northern Georgia or the western mountains, or even in the central part of Mexico as far south as San Luis Potosi. The presence of many stages in southern California in June, 1963 (UMMZ), indicates continual breeding, but the relationship of the non-wintering populations there to crickets thus far indistinguishable from them in the Rockies, and eastward and southward from the Rockies, cannot be deciphered without more distributional information and further study of living material. [The broad distributions of these species in some ways resemble the distribution of some other species such as the snowy tree cricket, *Oecanthus fultoni* Walker (Walker, 1962), and the leopard frog, *Rana pipiens* Schreiber (Moore, 1944).]

(4) *Gryllus fultoni* extends southward in Florida, with an increasingly spotty distribution, to at least Key Largo (UMMZ; T. J. Walker, pers. commun.). North of Florida, this is strictly a juvenile-overwintering, spring-maturing species, but in northern Florida (Gainesville area) occasional individuals mature in fall (Fig. 5). Whether the few individuals heard chirping there every autumn (T. J. Walker, pers. commun.) represent a tiny, self-perpetuating, egg-overwintering population

or are derived each year from the juvenile-overwintering population is unknown. If, however, this species has an egg stage that is to any extent diapause-susceptible or winter-hardy, it is clear that the opportunity is being provided repeatedly for the establishment of a fall-adult, egg-diapausing population; such a derived population evidently could expand northward on its own from the southern latitude necessary for its initial separation from the parent population.

(5) *Anurogryllus muticus* also extends southward from southern Illinois (Hebard, 1934) and New Jersey (Blatchley, 1920) to at least Homestead, Florida (UMMZ). All populations of *Anurogryllus* in South and Central America, Mexico, and the West Indies currently are considered conspecific with those in North America. No intensive comparisons have been made, but the only noticeable difference in preserved material is a prevalence of macropterousness in the southern populations and virtual absence of macropterousness in those found in North America. The extent of deviations in life cycle in the southern regions, even in southern Florida, is not known. Some periodicity in the appearance of adults occurs there with the largest populations in spring as in more northern localities.

(6) *Neocurtilla hexadactyla* has an unexpectedly large range for a species restricted to marshes and stream banks. Fulton (1951) has indicated that its life cycle at Raleigh, North Carolina, is that depicted in Fig. 3 for *G. gryllotalpa*. Specimens that so far are morphologically inseparable occur through Mexico and Central America to Argentina and southern Brazil, and to the southern tip of Florida. [This is the basis of resumption of use of the name originally proposed for a Brazilian specimen by Perty (1832) rather than *borealis* used by Burmeister (1838) (see Alexander, 1964). At this point, it seems important to emphasize the similarity of specimens from Canada to Argentina in this unique case rather than the possibility that more than a single species is represented.] The two Brazilian and two U.S. specimens examined by the author even have identical numbers of file teeth on the male tegmina, usually an excellent character for separating species. It is intriguing that a similar two-diapause life cycle has been postulated
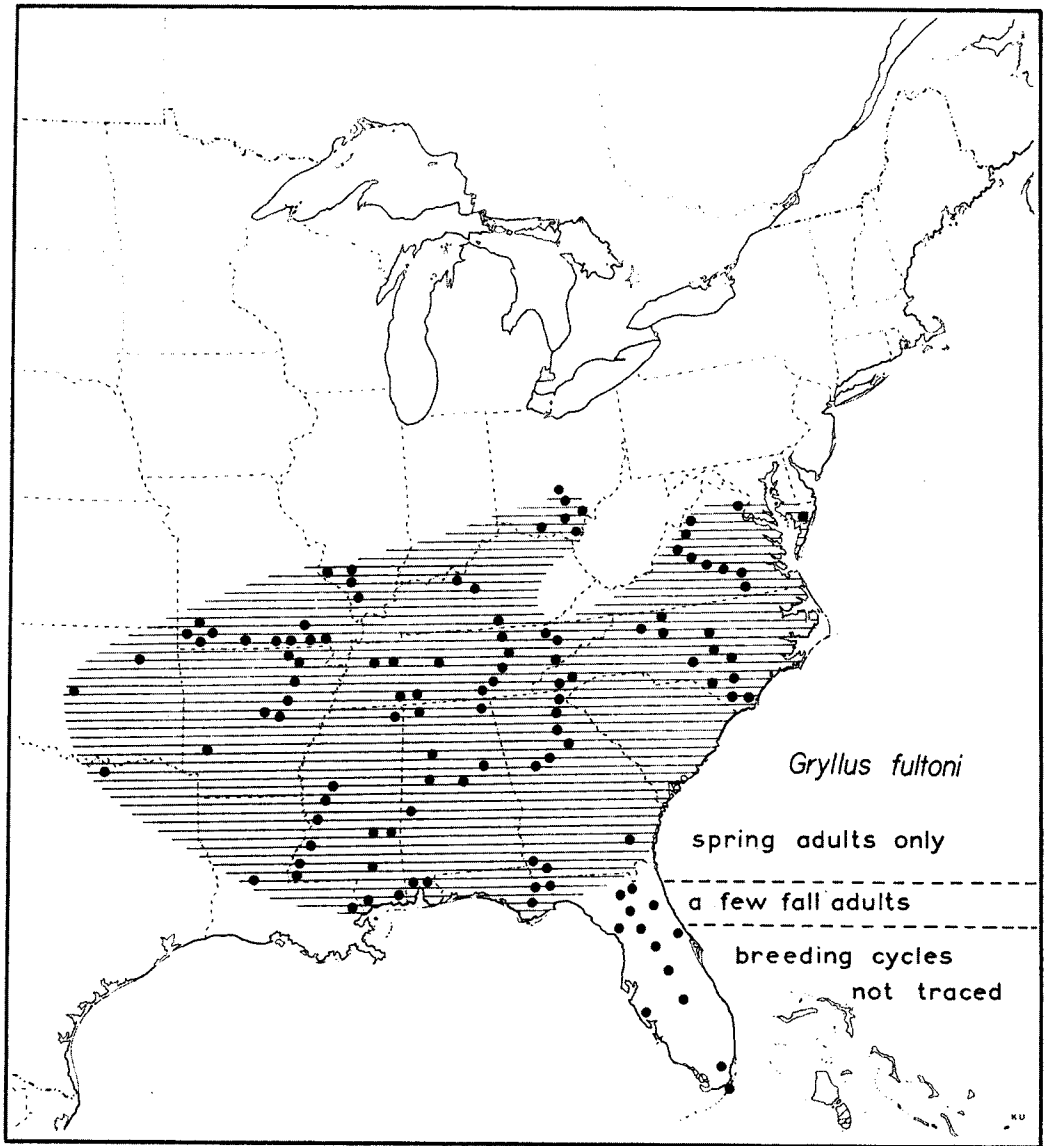
FIG. 5. GEOGRAPHIC DISTRIBUTION OF *Gryllus fultoni*

Hatched area represents predicted general distribution. Symbols outside hatched area are known peripheral isolates; other symbols are collecting records plotted one to a county.

for another distantly related mole cricket, *Gryllotalpa gryllotalpa,* in Spain (Morales, 1940). Only burrowing cricket species are known to overwinter in other than the egg stage in regions with severe winters. *G. veletis* and *N. hexadactyla* in North America, and *G. campestris, N. sylvestris,* and *G. gryllotalpa* in Europe, extend far north of any other juvenile-overwintering cricket species — in North America more than 5° latitude farther than the next juvenile-overwintering species. All of the subsocial crickets in North America — *Anurogryllus* and the various mole crickets — are either tropical in origin or evolved their life cycle tendencies in south temperate climates and retained them as they moved across the tropics to north temperate regions. Parental species are not likely to evolve egg diapause; likewise, among

temperate crickets only juvenile-diapausing or adult-diapausing species could become subsocial.

(7) *Gryllus firmus* is largely made up of a flourishing coastal population extending from Key West, Florida, north around the Gulf Coast to at least Brownsville, Texas, and north along the Atlantic Coast to the Delaware Peninsula (Fig. 4). Southern limits in Mexico are not known, but no males were heard chirping at night during searches by Alexander either along a few miles of the beach and the highway behind the beach near Nautla, Vera Cruz (7 June 1965) or in Tampico, Tamaulipas (22 October 1966). A series of inland northern populations of *G. firmus* occurs in the belt of sand hills that extends southward from North Carolina into northern Georgia and Alabama (Fulton, 1952; Alexander, 1957). This inland population is completely isolated from the coastal population in North Carolina, but in Alabama the inland and coastal populations are connected by a series of small, restricted populations. Geographic connections with *G. pennsylvanicus,* the most similar relative of *G. firmus,* occur along the North Atlantic Coast in Virginia and Maryland and in northern Alabama. In the first of these two locations there now is evidently overlapping and the possibility of interbreeding; the second case involves a series of separated local populations. File tooth counts and wingstroke rates during stridulation show some intergradation in Alabama, indicating a strong probability of past interbreeding.

During the past ten years I have been accumulating detailed information concerning the distribution of *G. firmus,* and the life history and morphological and song variations in different parts of its range. Adults and juveniles have been collected or sought in nearly all parts of the known range in both early and late summer, and in Florida in mid-winter. Only in southern Florida, below the region of Lake Okeechobee, is there evidence that all stages are present in fairly large numbers at all seasons. In central and northern Florida, some adults are present at most or all times of the year, but there are definite peaks in early summer and late summer. At Carolina Beach, North Carolina, fall adults are abundant, but the early summer population is tiny: in late May, 1964, I could hear fewer than six males chirping at night on the entire peninsula, whereas in August, 1954, 1956, and 1964, thousands of males were chirping, and hundreds of adults could be collected along short stretches of the highway. In the vicinity of Anniston, Alabama, there is a small population of fall adults restricted to a field of one or two acres; no early summer adults have been found. Southward from Anniston, the first small populations of spring adults occur at Marianna, Florida. In coastal regions from Carolina Beach southward through Georgia, and on Fripp, Lady, and Tybee Islands along the coast, relatively small spring adult populations and large fall adult populations are present. Inland in the sand hills of North Carolina, near Spout Springs in Wake County, the sparse fall population discovered by Fulton (1952) and confirmed by collections and tape recordings made by Alexander (1957) has evidently become extinct; the specific locality has been converted into an extensive pine plantation and I was unable to hear or locate any adults there August 14 and 15, 1964. No spring adults have ever been found there. Egg-overwintering fall adults, therefore, extend farther north than juvenile-overwintering spring adults and are more abundant where both occur.

(8) *O. quadripunctatus* Beutenmuller and *O. niveus* (De Geer) in eastern North America are univoltine egg-overwinterers in the north but bivoltine or trivoltine in the south (Walker, 1962, 1963).

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Several cases of life history variations additional to those mentioned above are known in crickets from other continents.

(1) *Gryllus campestris,* a univoltine, juvenile-diapausing species in Europe, is believed to produce fall adults rarely in southern parts of its range (Lucien Chopard, Franz Huber, pers. commun.).

(2) *Teleogryllus commodus* is a univoltine, egg-diapausing species in temperate regions in Australia, a non-diapausing species in tropical regions (Hogan, 1965).

(3) *Scapsipedus aspersus* (Walker) in Japan is a univoltine, egg-diapausing species in the north, but in certain southern prefectures facing the Pacific Ocean, an off-season, spring-

adult, juvenile-overwintering population occurs with the fall-adult, egg-overwintering population (Masaki, 1961).

(4) *Nemobius sylvestris* is believed by some European entomologists to have a univoltine life cycle with egg diapause on the European continent, contrasting with the two-year cycle that Gabbutt (1959) believes to occur in the British Isles (See Richards, 1952).

Other less spectacular variations have been indicated in various species by the investigations of Bigelow (1958, 1960, 1962) and Rakshpal (1962) in North America, Bigelow and Cochaux (1962) in Australia, Sellier (1954) and Fuzeau-Braesch (1963) in Europe, and Masaki (1960, 1961, 1963, 1965, 1966) in Japan. Many of these, particularly in Japan and Australia, involve carefully studied polygenic geographic variations in intensity and duration of diapause and are discussed later in that context.

DISTRIBUTION OF LIFE CYCLES

The geographic region occupied by crickets is approximately bounded on both north and south by taiga, the coniferous forests of the Subarctic and (much less extensively) upland South America, as delimited by Thornthwaite (1933) and others. Within the regions bounded by taiga, Thornthwaite distinguishes five general climatic belts: tropical, north and south mesothermal, and north and south microthermal (Fig. 1). His classification is useful in dealing with the distribution of crickets and their various life cycles.

Of the seven known life cycles of crickets, only one, continuous breeding, is prevalent among tropical crickets. In certain regions, dry-season diapause probably occurs, and developmental rates probably vary. Except for hints in the work of Hogan (1960, 1965) on *Teleogryllus* in Australia and Arndt (1931) on *Chremon repentinus* Rehn (Eneopterinae) in Haiti we are, however, as yet provided with no clear evidence in this regard. In Mexico near Ciudad Manté (Tamaulipas) and Guadalajara (Jalisco), I have found that with few exceptions the same species are adult in June and October, but in various localities in the arid region north of Mazatlan (Sinaloa) on the west coast, only three to five cricket species were adult in late June but 25 or more were adult in October.

With regard to variability in life histories, crickets can be divided into two categories, those that live chiefly in vegetation and those that live chiefly on or beneath the soil surface. Vegetation-inhabiting crickets do not overwinter in other than the egg stage except in the tropics and in the mildest mesothermal regions. In mesothermal and microthermal regions, egg-overwinterers are rarely multivoltine.

Four of the seven known life cycles of crickets, then, are found only in surface and subterranean species in mesothermal and microthermal regions, and a fifth occurs only rarely outside these groups. Two subfamilies, Gryllinae and Nemobiinae, have evolved six of the seven known cycles (only the peculiar two-year cycle of sub-social Gryllotalpinae is lacking).

Only one North American species outside the Nemobiinae, Gryllinae, Brachytrupinae, and Gryllotalpinae has evolved a juvenile diapause in the mesothermal region. This is *Falcicula hebardi* Rehn (Trigonidiinae), a grass-clump and leaf-litter species. Two subfamilies characteristic of leaf-litter and surface trash, Mogoplistinae and Phalangopsinae, occur rarely outside the tropics in North America, the former reaching into Ohio (one species, T. J. Walker, pers. commun.), Texas, Arizona, California, and the other into northern Mexico.

Except in the most arid regions, a given locality in the tropics generally has more cricket species than a locality of similar size in the mesothermal region; localities in mesothermal regions in turn have more species than localities in microthermal regions. South from Ontario, various regions have approximately the following numbers of cricket species: Ontario, 12; Michigan, 22; Ohio, 33; Kentucky, 34; Tennessee, 35; Georgia, 44; Florida, 67; Grand Bahama Island, 18.

As one might expect, the proportions of vegetation-inhabiting and soil-inhabiting (burrowing and surface) crickets in any given locality shift as one moves from microthermal to mesothermal and tropical regions. My field work in nearly all parts of the United States, Mexico north of Taxco (Guerrero), and on Grand Bahama Island suggests that microthermal localities have 50 to 65 per cent soil species; mesothermal localities, 35 to 50 per cent; and tropical localities, 30 to 45 per cent. A transect southward from Ontario gives the following

percentages: Ontario, 61 per cent; Michigan, 55 per cent; Ohio, 50 per cent; Kentucky, 50 per cent; Tennessee, 50 per cent; Georgia, 45 per cent; Florida, 43 per cent; Grand Bahama Island, 40 per cent. The Mogoplistinae with two species on Grand Bahama Island, 14 in Florida, two in Georgia, and one in Tennessee, Kentucky, and Ohio, are excluded because their leaf litter and surface trash habitat, coupled with the fact that they spend much time on vegetation, makes them difficult to classify. Their evident inability to overwinter outside the tropics (except for two species in eastern North America and two species in western North America, all of which overwinter as eggs) suggests that they should be classified with vegetation inhabitants. Species apparently introduced by man's activities (*Acheta domesticus, Gryllodes sigillatus, Valerifictorus micado*) also are not included in the above calculations.

Evidently the variety of life cycles available to soil-inhabiting crickets has increased the proportions of non-tropical soil-inhabiting species. One obvious way is by enabling more tropical soil species to invade non-tropical regions. Another perhaps less obvious way is through increased speciation in temperate regions, either because of longer inhabitation by more species, compared to vegetation-inhabiting species, or through speciation directly associated with life cycle changes. Evidence for both possibilities exists. In the first case, numerous soil species have evidently penetrated into the mesothermal region more or less recently from the tropics (*Anurogryllus muticus, Neocurtilla hexadactyla, Scapteriscus acletus* Rehn and Hebard, *S. vicinus* Scudder, *S. abbreviatus* Scudder, and others). In the second case, there are temperate sibling species such as *Gryllus veletis* and *G. pennsylvanicus*, with different life cycles, and some temperate species are divided into populations with different life cycles and temporally isolated adults (*Gryllus firmus, G. fultoni, Scapsipedus aspersus*, and others).

ORIGINS OF LIFE CYCLE DIFFERENCES

How have differences in the life cycles of non-tropical crickets arisen? Evidently both egg and juvenile diapause have evolved independently several times, since species with each type of diapause occur in three or more different subfamilies along with non-diapausing species. Adult diapause, even though it seems restricted to almost entirely subterranean mole crickets, may also have evolved more than once, for it occurs in European and American species in different genera.

A simple hypothesis is that continuously breeding tropical crickets expanding their ranges into temperate regions would have the number of generations between winters (and consequently the number of eventual diapauses per generation) determined by their existing developmental rates and the growing season length at the latitude where winter survival began to be affected. Some species could get in two full generations, others but a single one, while still others might have time to move only from one diapause-susceptible (or "winter-hardy") stage to another. The last group would require more than a year, and eventually (as they were able to penetrate far enough north, or south, and the necessary genetic alterations occurred), more than one diapause to mature. Reverse changes, it would seem, could produce continually breeding tropical crickets from temperate species having any kind of life cycle involving diapause.

This hypothesis probably accounts for many of the differences among the life cycles of temperate species, particularly those existing between species that are not closely related and seem obviously to be derived recently from tropical stock. It does not explain, however, why certain stages are evidently more susceptible to diapause than others throughout diverse groups of crickets, and it does not approach the question of whether or not life cycle differences ever arise between species restricted to temperate climates, and if so how. It does not, therefore, answer the important question of how it is that juvenile diapause and egg diapause occur as variations among the species within a single genus — a question made more interesting by the case of *Gryllus veletis* and *G. pennsylvanicus*, sibling species with this particular difference in their life cycles (Alexander and Bigelow, 1960) (Fig. 16).

Two univoltine life cycles are prominent among north temperate crickets: (1) egg-overwintering with fall adults and (2) juvenile-overwintering with spring adults. Both are represented in most or all temperate regions,

and repeatedly involve congeneric species. The most difficult questions about origins of differences in cricket life cycles seem chiefly to involve these two cycles and the kinds of crickets that have them — namely, field and ground crickets (Gryllinae and Nemobiinae) that live on the surface of the soil and excavate shallow burrows. The other four temperate life cycles are less common, and evidently are restricted to species derived directly from tropical species or at least lacking close temperate relatives with different life cycles.

Comparing various species of *Gryllus, Teleogryllus* (Masaki, 1961), and *Nemobius* seems to suggest only two possibilities additional to those already given for the origin of life cycle differences. First, tropical species moving north or south, or otherwise being subjected to increasingly severe winters, might give rise to both of the two prominent kinds of univoltine temperate life cycles, rather than just one, as winter begins to restrict the number of successful overwintering stages. Second, in certain locations or under certain circumstances, temperate crickets with established life cycles might produce off-season or off-year populations that would remain in isolation (temporal, geographic, or both) and eventually become new species.

Both of these changes require that certain stages be more diapause-susceptible or winter-hardy than others. The repeated, independent evolution of diapause in the egg stage and the penultimate juvenile stage in different groups of crickets and on different continents already makes this a certainty.

The development of two life cycles from one stock, or one overwintering stage, seems most likely to occur in the colder part of the range of a mesothermal species and in the warmer part of the range of a microthermal species. These would be the places where in the first case winter would be severe enough to cycle the population, and in the second case winter would least likely be so severe as to annihilate off-season individuals.

Before considering in detail the relationship of life cycle differences to speciation, it is appropriate to review the available information on several other phenomena associated with life cycle variations: the nature and intensity of diapause and its geographic variations, the na-ture and extent of polymorphisms correlated with habitat permanence and population density, and the effect of weather fluctuations on daily cycles of activity.

THE NATURE OF DIAPAUSE IN CRICKETS

William Morton Wheeler (1893) introduced the term diapause to describe a stage in the morphogenesis of an egg-overwintering meadow grasshopper, *Conocephalus brevipennis* (Scudder) (Tettigoniidae: Conocephalinae). Henneguy (1904) applied the term to the condition of arrested growth represented by the stage described by Wheeler, and it has since been used in this broader sense to refer to any period of arrested development regardless of life-stage and whether associated with winter hibernation or summer or dry season aestivation (Lees, 1955).

In crickets, non-diapause eggs usually hatch in 15 to 25 days at 25° C and with a high degree of synchrony (Masaki, 1961; Rakshpal, 1962; Bigelow, 1962). Diapause eggs characteristically (1) require a few days to reach the diapause stage of morphogenesis; (2) hatch after delay and over a long period of time if not subjected to a cold period; (3) hatch with less delay and more synchronously if subjected to a brief cold period, and (4) hatch without delay (in about 15 days at 25° C.) and over a very brief period of time after a long cold period. Diapause adults have not been studied in crickets. Diapause juveniles characteristically reduce their activity and their metabolic rate during the three immediately pre-adult instars, and mature in ways similar to the hatching performances of diapause eggs when subjected to similar conditions. In non-diapause juveniles the later stages are similar in length to the earlier stages (Bigelow, 1960; Rakshpal, 1964; Ohmachi and Masaki, 1964; Fuzeau-Braesch, 1965).

DIAPAUSE SUSCEPTIBILITY OF DIFFERENT LIFE STAGES

Numerous aspects of potential winter-hardiness may be cryptically involved in the developmental physiology of all crickets, even those living in tropical regions, but as yet we have no direct knowledge of any such characteristics.

Some other possible explanations of restrictions in over-wintering stages, however, are evident.

Overwintering in other than the egg stage occurs only in surface and subterranean species. Three stages in such species — eggs, late juveniles, and (to some extent) adults — are protected from climatic extremes by being underground, just as eggs of vegetation-inhabiting species are somewhat protected by injection into plant stems. Eggs are buried by the ovipositing females, and the two other stages ensconce themselves in burrows. These are the only three stages that overwinter in northern climates. But the same three stages are largely subterranean in the same kinds of crickets in tropical climates, indicating that the selection occurred in other contexts and constituted a pre-adaptation as far as winter survival is concerned, rather than an *a posteriori* response to winter conditions based on some kind of physiological cold-hardiness restricted to certain stages. In other words, any physiological specializations presently making these stages unusually winter-hardy seem, on the basis of available evidence, appropriately viewed as adjuncts to behavioral characteristics originally responsible for the restriction of selection for physiological winter-hardiness to these particular stages. The only alternative is the exceedingly remote possibility that all burrowing by late juveniles evolved in temperate regions in juvenile-overwintering species.

Nearly all crickets "bury" their eggs, either in the soil or in plant stems; the known exceptions are a few sub-social species that drop their eggs in their burrows without injecting them into the soil (West and Alexander, 1963). Oviposition into the soil is ancient in the Orthoptera, apparently extending to Paleozoic cockroaches, some of which evidently had long, tubular ovipositors (Laurentiaux, 1951). Long ovipositors may never have been lost in some of the phyletic lines leading to the various groups of modern surface-dwelling crickets.

Adult male field crickets characteristically burrow more extensively than females, evidently in association with attracting the more "roving" females by long-continued, stationary stridulation. Mate attraction by stridulation is ancient in the Suborder Ensifera, pre-dating the family Gryllidae, and probably beginning sometime in the Triassic Period (Alexander, 1962). Burrowing by late juveniles and females is prominent only in species with burrowing males and may be restricted to them. Burrowing by the late juvenile stages could have been selected as an overwintering advantage, and also in the same context as that of the adult male, if newly emerged males with burrows already excavated have an advantage over males that have to begin excavation after maturing. The burrow of a stridulating male may also be important in protecting him from predators responsive to his stridulation. This idea is substantiated by the close association of calling males with burrows or crevices and their rapid and direct retreat into their burrows upon disturbance.

In some field crickets, one often finds up to three adult females in the bottom of a stridulating male's burrow, and West and Alexander (1963) suggest that females of the burrowing, sub-social species, *Anurogryllus muticus,* may often take over a male's burrow for the brood chamber. It would seem that burrowing by adult males has to some extent pre-adapted field crickets both for increasingly subterranean life involving both sexes — as now exemplified by Gryllotalpinae and Brachytrupinae — and for overwintering in the late juvenile stages. The early and intermediate juvenile stages are in many species the only stages that are not more or less continually associated with a burrow.

In northern climates, only mole crickets overwinter as adults. They seem to have been assisted toward this condition by two specializations: their elaborate subterranean life, including feeding on such things as earthworms and roots, and the lengthened life of adult females, a feature that in arthropods is commonly associated with parental attention to eggs and young.

GEOGRAPHIC VARIATION IN DIAPAUSE

Some of the cases of life history variation described above undoubtedly involve geographic variation of a genetic nature. As examples, a genetic basis for variations in both egg-hatching time and post-hatching development time has been demonstrated by Masaki (1961, 1965) in a Japanese egg-over-wintering *Teleogryllus* species; and Hogan (1965) has shown experimentally that the tropical, non-diapausing

populations of *T. commodus* in Australia differ genetically from the temperate, egg-diapausing populations. But photoperiod regimes have also been shown to be instrumental in initiating or by-passing diapause or altering developmental time in juvenile-overwintering crickets (Fuzeau-Braesch, 1963; Masaki and Ohmachi, 1967; Fig. 6). Accordingly some geographic variation in diapause expression could exist — in fact, must exist in any cricket widely distributed in a north-south direction — independent of genetic variation and owing solely to the larger shift in day lengths during the season at higher latitudes. Among other things, such information places stringent requirements upon experimenters that they might not have considered. Many of the numerous rearing tests on crickets do not report photoperiod data, an omission that often renders the results useless.

Two kinds of geographic trends in diapause variation have been demonstrated in crickets. Among species restricted to cold temperate regions, diapause intensity and duration increase in the direction of milder winters (Bigelow, 1960; Masaki, 1961, 1965). Species which extend from the subtropics into warm temperate regions show a reversed trend, with populations in the subtropical regions lacking diapause and those at higher latitudes having progressively more intense diapauses in the direction of more severe winters (Hogan, 1965). Clinal variation and intermediacy in hybrids indicates polygenic control of such variation in the cases studied (Masaki, 1965). Hogan (1965, 1966) and Bigelow and Cochaux (1962) found that the proportion of diapause eggs of *T. com-*
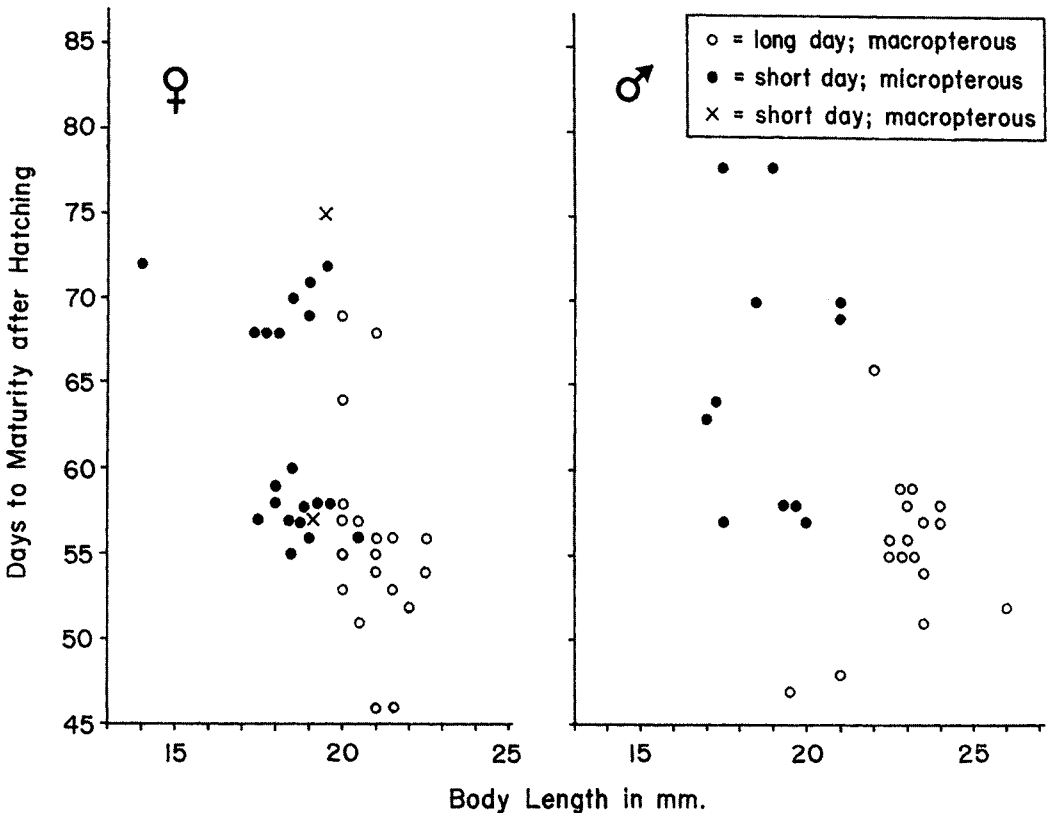

FIG. 6. EFFECT OF PHOTOPERIOD ON DEVELOPMENT TIME, WING LENGTH, AND BODY LENGTH IN *Gryllus integer*, A BIVOLTINE, JUVENILE-DIAPAUSING CRICKET

Photoperiod was 12 hours each 24 hours until 18 days after hatching; then 14 hours for long-day, 12 for short-day, with 15 minute increases and decreases, respectively, each five days until the tests ended. Temperature was 82°F in both incubators, with six one-degree deviations downward in the long-day incubator, and three one-degree deviations upward and two downward in the short-day incubator.

modus gradually increases toward the south in Australia. Hogan (1966) believes that the capacity to diapause may be monogenic in this species, but that the intensity of diapause may be polygenic or cytoplasmic. Tendency not to diapause seems to be dominant, and Hogan suggests that mass introduction of non-diapausing tropical individuals into temperate regions might be an appropriate control. He refers to crickets from different regions as different "races," however, and he and Bigelow and Cochaux (1962) found some inter-sterility between these "races." Hogan (1967) found evidence in the laboratory of differential mating that reduced hybridization between diapausing and non-diapausing populations, and was apparently eliminated by silencing the males. How these findings relate to field conditions is still unknown.

The selective bases for the various geographic trends in the presence or absence, intensity, or duration of diapause are not difficult to imagine. At high latitudes in the temperate region, winter temperatures do not rise above the developmental threshold for crickets, and the autumn temperature-drop and spring temperature-rise probably occur across shorter time periods and with fewer fluctuations than in the milder temperate regions. Winters that are more fickle and are associated with longer summers, yet remain sufficiently severe to be annihilatory to all but the diapause stage, favor a more positive diapause. On the other hand, gradual penetration of a subtropical cricket into a region with winters annihilatory to all but one or two stages would necessarily be accompanied by selection producing not only a higher proportion of diapausing individuals but an increasingly intense diapause.

These facts yield an interesting situation. Diapause intensity and duration, at least in species that are not recent immigrants, tend to decrease in both directions from a region of mild winters that seems to fall around 33° N to 37° N. Northern Florida and the southern tip of the Appalachians are regions where changes in life cycle are associated with changes in morphology and behavior in numerous Gryllidae and Tettigoniidae. One is led to believe that these are somehow "fragile" connections between northern and southern components of widely ranging species, where changes in the direction of selection may make the slightest break in geographic continuity highly significant. Fulton (1951) suggests that in the widely distributed species, *Nemobius fasciatus,* multiple generations also first appear at about these latitudes.

It would seem from this evidence that some species, particularly those that have occupied their present ranges relatively recently, would reveal their origins (whether northern or southern) by the nature of geographic trends in the intensity and duration of diapause. A re-examination of species distributions leads one to divide the crickets of the world into six general categories: (1) strictly tropical and sub-tropical species, (2) chiefly microthermal species (with more intense diapauses toward the lower latitudes), (3) species extending from tropical or subtropical regions into warm temperate (mesothermal) regions (with more intense diapauses toward the higher latitudes), (4) chiefly mesothermal species, (5) species extending broadly across both mesothermal and microthermal regions, and (6) species extending from tropical or sub-tropical regions into microthermal regions. In crickets, geographic trends in diapause intensity have not been investigated in the last three kinds of species.

POLYMORPHISMS, LIFE CYCLES, AND HABITAT
PERMANENCE

Hatching time and development time are only two of many characteristics that vary in ways significant to the understanding of adaptations by crickets to different climatic conditions. As illustrated in Table 2 and Figs. 6–11, body size, wing length, body form, pigmentation, aggressiveness, and propensity to burrow also vary, not only between species, but within species as well. Interspecific differences must in most cases reflect genetic variation, one way or another, particularly when the species involved are sympatric and synchronic and when the differences persist in laboratory cultures. Except for Masaki's findings (1967) concerning size variations in *Teleogryllus emma,* however, the observed intraspecific differences seem rarely to be related to genetic variation. Instead, they can be produced by adjusting one or more of various natural and artificial stimuli (Figs. 10, 11).

TABLE 2

Habitat, life cycle, and proportion of macropterous individuals in 13 field and ground crickets from North America, Europe, and Asia

SPECIES	HABITAT	OVERWINTERING STAGE	GENERATIONS PER YEAR	APPROXIMATE % MACROPTER-OUSNESS IN FIELD	NUMBER OF SPECIMENS EXAMINED
Gryllus vernalis [1]	woods	juvenile	1	0	ca. 200
" *fultoni* [1]	"	"	1	0	ca. 300
Nemobius sylvestris	"	"	½	0	?(Sellier, 1954)
" *tinnulus* [2]	"	egg	1	0	ca. 600
" *yezoensis*	"in and around paddy fields"	juvenile	1	0	100
Gryllus campestris	grasslands	"	1	1	?(Sellier, 1954)
Miogryllus verticalis	"	"	1	1	ca. 1000
Gryllus veletis [3]	"	"	1	4	314
" *pennsylvanicus* [3]	"	egg	1	4	1000
Nemobius fasciatus	"	"	1-2	10	ca. 1000
" *allardi* [2]	"	"	1	25	ca. 1000
Gryllus rubens	"	juvenile	2	8 & 75	50 & 150
" *firmus* (spring)	"	"	1	14	107
" *firmus* (fall)	"	egg	1	18	116

Superscripts indicate three pairs of sibling species.

Pigmentation

Variations in pigmentation extending from almost completely yellow individuals to completely black ones are geographic in *G. firmus* and correlate with soil color; similar variations can be induced by different amounts of crowding in *G. bimaculatus*. Fuzeau-Braesch (1960, 1961, 1962) and Levita (1962) reported that, in the second case, tactual, visual, and olfactory stimuli all seem to be implicated, according to the following evidence:

(1) Crickets reared in isolation are darker than crickets reared in groups. (2) Crickets reared in isolation in the dark are darker than those reared in groups in the dark. (3) Crickets reared in groups in the dark are darker than those reared in groups in the light. (4) Crickets reared in isolation in a cage with walls made of mirrors are lighter than those reared in isolation in cages with plain walls. (5) Crickets reared in groups with their antennae and cerci severed are darker than normal crickets reared in groups. (6) Crickets reared in cages with other insects (such as grasshoppers) are like crickets reared in isolation unless the cage is especially rigged to transmit vibrations made by the movements of the other species.

Wing Length

Wing length variation is probably the easiest characteristic on which to base a discussion of polymorphism in crickets because its general significance is clear (Alexander, 1961), and it correlates closely on an interspecific basis with variations in habitat and life cycle. Furthermore, with the exception of pigmentation, all of the other polymorphisms seem to be related in some fashion, either directly or indirectly, to wing length variations.

[As used here, the term *macropterous* means that the hind (under) wings extend beyond the forewings or tegmina; some individuals are more macropterous than others (Figs. 7–9) and fly easily, some can fly only a few feet or yards. *Micropterous* means the hind wings are completely hidden beneath the tegmina; these individuals cannot fly, and usually do not open their
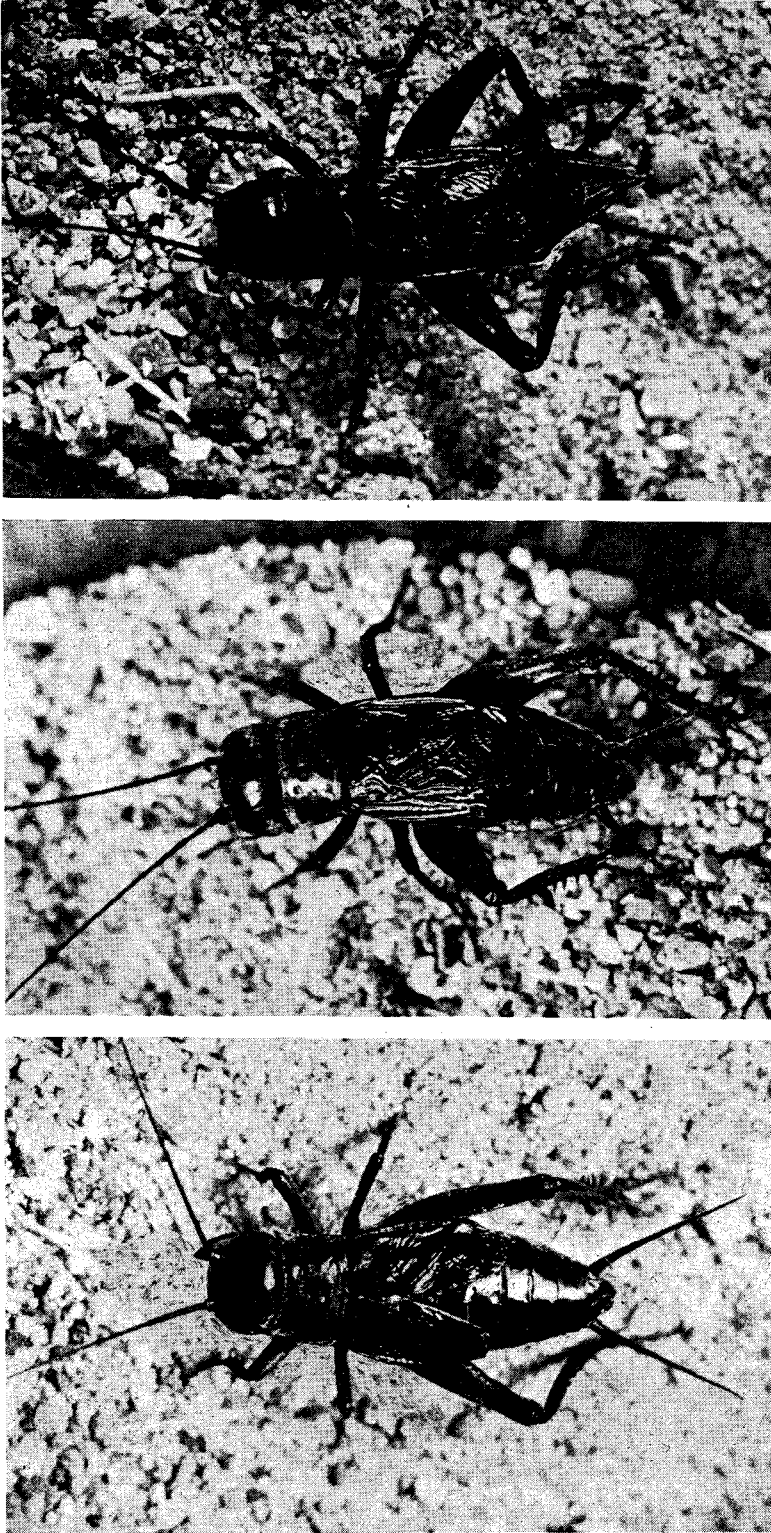
FIG. 7. MICROPTEROUSNESS AND MACROPTEROUSNESS IN *Gryllus veletis*

Left, a very short-winged adult male, unable to stridulate, found in a laboratory population; center, the usual micropterous male with normal tegmina; right, a macropterous male (note tips of long underwings), produced in the laboratory. Only the last two are known in field populations.
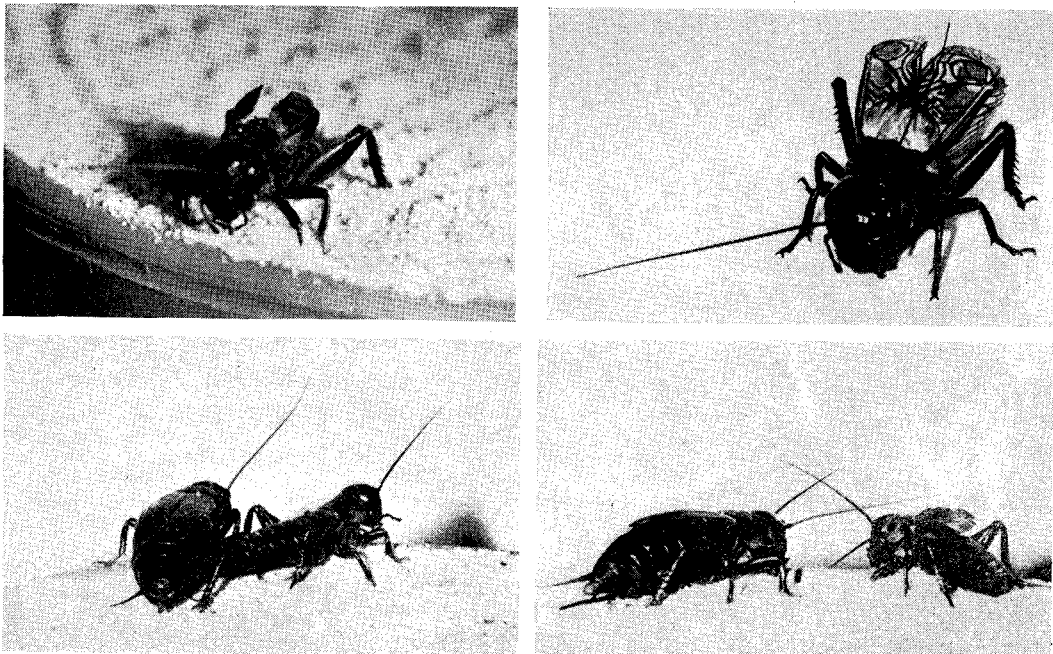
FIG. 8. MICROPTEROUSNESS AND MACROPTEROUSNESS IN *Gryllus campestris*

Upper left and lower right, a very short-winged male, unable to stridulate, produced in the laboratory; lower left, a neotenic male, produced in the laboratory, with tiny wings and no spermatophore, making copulatory movements near a female; upper right, normal micropterous male stridulating with fully developed tegmina. (Photographs by Franz Huber.)

hind wings at all, or lift their tegmina except prior to stridulation. Some variation in tegminal length is associated with these drastic variations in length of the hind wings, but individuals with greatly reduced tegmina are usually referred to as *neotenic* (Fig. 8); again, two degrees of neoteny are known, insofar as tegminal size is concerned. In some crickets, the general body shape, particularly head and pronotal conformation, is changed rather strikingly by differences in wing length in ways that resemble genetically-based differences among species (Alexander and Thomas, 1959).]

All of the four woods-inhabiting species listed in Table 2 are totally micropterous in the field, regardless of overwintering stage and number of generations per year; all of the grassland species, on the other hand, produce some macropterous individuals. In eastern North America, this general relationship extends, with exceptions, to Tettigoniidae and Caelifera as well. Perhaps this relationship could be predicted on the basis that woodlands are more permanent habitats, at least in North America, than the kinds

of grasslands that occur over the same area — now chiefly lawns, pastures, and old fields, all of which are man-made situations that possibly represent pioneer associations in the pre-agricultural landscape in these regions. Certain kinds of marshes and prairies in North America also represent permanent habitats and contain wholly micropterous species, such as *Nemobius melodius* (Thomas and Alexander, 1957); this may explain the presence of the micropterous species, *N. yezoensis*, in rice paddies in Japan.

But variations in habitat permanence are not sufficient in themselves to explain the observed variations in macropterousness. There is also a relationship with the kind of life cycle that is evidently even more fundamental. Thus, the seven strictly juvenile-overwintering species in Table 2 average less than 1 per cent macropterous, while the four strictly egg-overwinterers average nearly 10 per cent macropterous. Among the seven grassland species (excluding *N. yezoensis*), the three univoltine juvenile-overwintering species average only two per cent
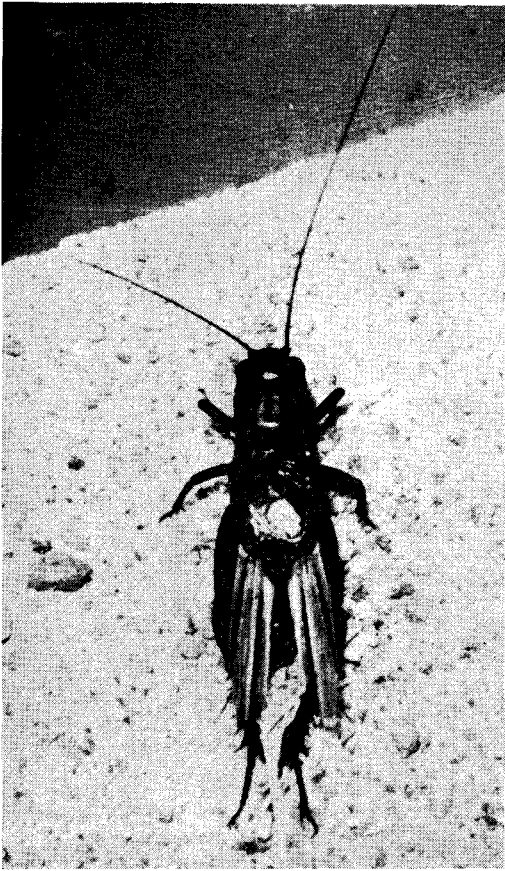
FIG. 9. A FULLY MACROPTEROUS MALE OF *Gryllus rubens* WHIRRING HIS LONG UNDERWINGS JUST PRIOR TO FLIGHT

macropterousness in the field, while the three egg-overwintering species average 13 per cent. Further, in the single bivoltine species, *G. rubens,* the overwintering juveniles are 8 per cent macropterous, while the directly maturing generation is 75 per cent macropterous. A comparison of 107 pre-July adults and 116 post-July adults of *Gryllus firmus,* representing the two seasonally separated populations of this species that overwinter as juveniles and eggs, respectively, gives figures of 15 macropterous individuals among juvenile-overwinterers and 21 macropterous individuals among egg-overwinterers, or approximately 14 and 18 per cent respectively. Thus, even within species, there may be more macropterous individuals among juvenile-overwinterers than among egg-overwinterers. Masaki and Oyama (1963) note that

N. yezoensis is the only ground cricket in Japan that overwinters as a juvenile, and also the only one in which only micropterous individuals are known in the field: ". . . both long-winged and short-winged specimens are usually found in the related species." Long photoperiods, either with or without cold treatment, produced rapidly developing individuals, up to 50 per cent of them macropterous in the laboratory.

Gryllus veletis and *G. pennsylvanicus* represent an apparent exception to the rule that differences in wing length occur between similar juvenile-overwintering and egg-overwintering species, since about 4 per cent are macropterous in both cases (Table 2). It would be interesting to compare northern and southern samples of these species, as well as early and late-maturing individuals. Of seven individuals of *veletis* collected 27 May 1965, only the last two to mature were macropterous; presumably they were subjected to longer day lengths at comparable developmental stages than the early-maturing individuals. Under continuous light in the laboratory, nearly all individuals of *veletis* develop directly, without evident diapause delay, and in contrast to crickets reared under ordinary day lengths most (13 of 19 in the only test) are macropterous. Further, there is a concentration of micropterousness among the latest of such individuals to mature. Juveniles of *pennsylvanicus* were collected 28 August 1966, and reared in three groups at 75° F.: (1) six-hour days, (2) normal day lengths, and (3) continuous light. All matured at the same times and all were micropterous. Evidently, day length has its principal effect on younger individuals of this species. Two possible influences on the correlation between wing length and overwintering stage are evident. First, juvenile-overwintering populations are characteristically less dense, and Fuzeau-Braesch (1961) and Saeki (1966a) have shown this can be a factor in some species. More significantly, long days have been shown to produce long wings in both univoltine and bivoltine species, while short days produce short wings (Saeki, 1966b; Masaki, 1966; Masaki and Oyama, 1963; Fig. 6).

Wing polymorphism in crickets has been shown to be related to other phenomena which affect or correlate with development time, al-
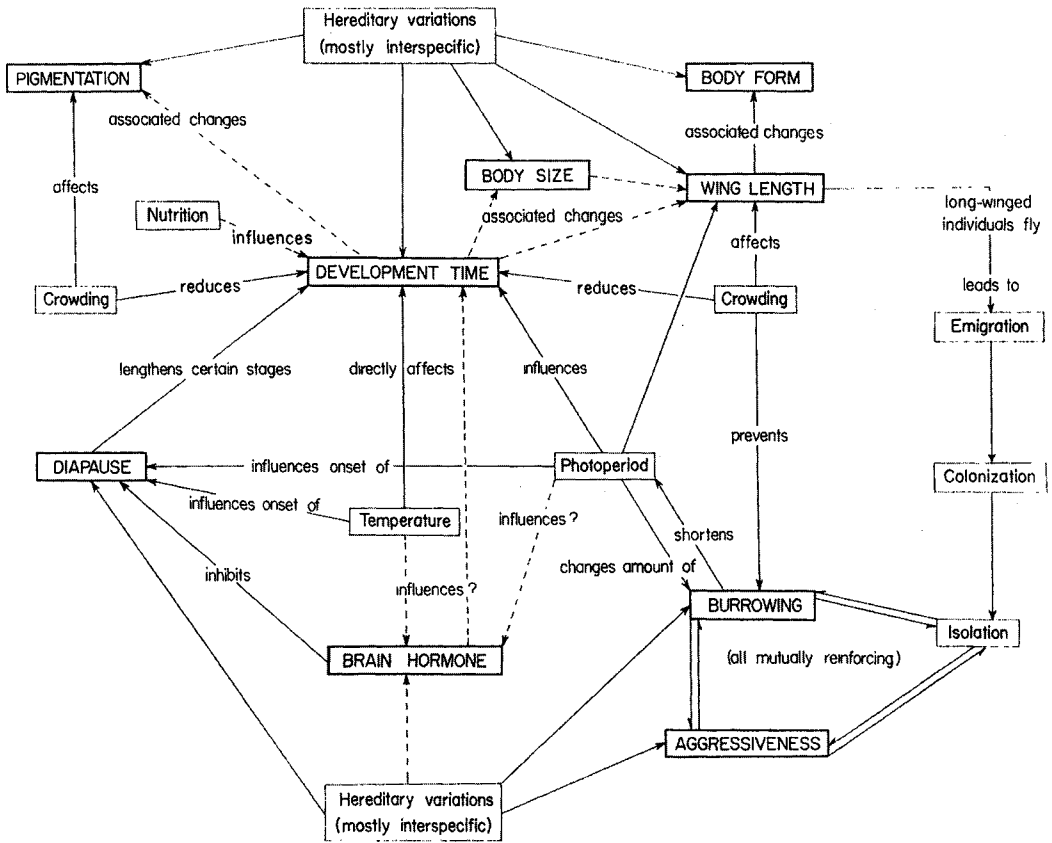
FIG. 10. A SUMMARY OF THE INTER-RELATIONSHIPS OF DIFFERENT MORPHOLOGICAL, PHYSIOLOGICAL, AND BEHAVIORAL VARIATIONS IN CRICKETS

The nine characteristics enclosed in heavy-lined rectangles vary interspecifically, presumably at least in part because of hereditary differences. They are also adjusted intraspecifically in the ways indicated, by differences in crowding, nutrition, temperature, and photoperiod. Sources of evidence are given in the text. Dashed lines indicate probable relationships.

though all of the reported results do not seem to agree. Thus, Sellier (1954) found with various European species that neither adjustments of temperature, light, and humidity, nor castration produced macropterous individuals. On the other hand, acceleration of development by preventing the onset of diapause in the ninth instar did cause macropterousness. This was done by massive injections of brain tissue from younger (not yet diapausing) juveniles of *G. campestris,* or from juveniles of *G. bimaculatus* (which does not have a juvenile diapause). Sellier concluded that the brain produces a non-specific "morphogenic" substance (presumably the "brain-hormone" of other authors) which prevents diapause and induces

wing growth; that with respect to wing growth the threshold to stimulation from the brain is higher in some species than in others; and that the sporadic appearance of macropterous individuals in *G. campestris* can be attributed to an abnormal functioning of the brain. Sellier also reported that *Acheta burdigalensis* Latreille produces a higher percentage of macropterous individuals under high, even temperatures than under low, fluctuating temperatures.

In a test conducted by the author with *G. integer,* in which all photoperiods were ten hours each 24 hours, at 33° C, 87 females matured 35 to 59 days after egg-laying and were 98.8 per cent macropterous; 79 males matured in 38 to 56 days and were 85 per cent mac-
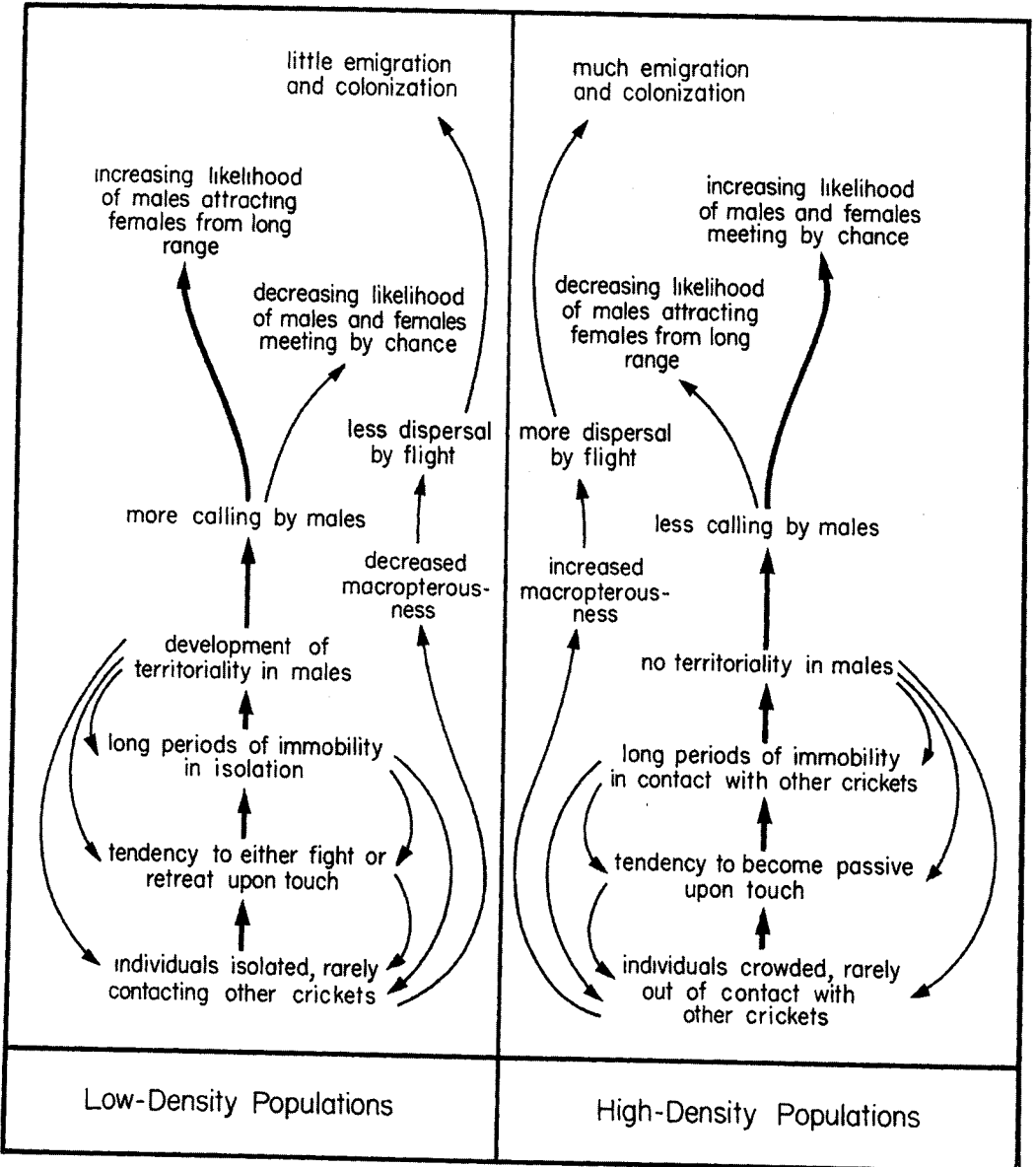
FIG. 11. SOME EFFECTS OF POPULATION DENSITY ON BEHAVIOR AND MORPHOLOGY OF FIELD CRICKETS AND HOW THEY ARE REFLECTED IN THE PERFORMANCE OF THE POPULATION

ropterous. At 25° C and the same photoperiod, 24 females matured in 91 to 243 days and were 87.5 per cent macropterous; 21 males matured in 101 to 235 days and were 85.7 per cent macropterous. Seventeen females reared at 25° C until 59 to 97 days after egg-laying, then changed to 33° C, matured 78 to 128 days after egg-laying and were all macropterous; 19 males reared under the same conditions matured in 82 to 129 days and were 84.2 per cent macropterous. Mortality in the three tests (sexes combined) was 52.8, 76.3, and 72.5 per cents, respectively. These results indicate that in the laboratory, low even temperatures (1) retard development, (2) cause maturation to be less synchronized, (3) cause higher mortality, and (4) increase micropterousness, at least in females. A shorter photoperiod might have exag-

gerated the last effect. The selective basis for lower macropterousness in males may be that most emigrating females are inseminated, reducing the relative reproductive chances of emigrating males.

Evidently, *Gryllus desertus* is the only case in which genetic variation is believed to account for an intraspecific variation in proportions of macropterousness in crickets (Sellier, 1954), and it seems reasonable, based on the paucity of evidence of a taxonomic nature, to question whether the southern populations that are macropterous are conspecific with the northern micropterous populations. Only two other cases of geographic variation in proportions of macropterous individuals seem to have been described in insects. Lindroth (1949) believes that such variations in ground beetles (Carabidae) reflect genetic variation and cites laboratory tests and the prevalence of long-winged individuals at the periphery of the ranges of polymorphic species as evidence for this view. He does not provide evidence, however, that photoperiod was controlled in the laboratory test, and he does not discuss the possibility that peripheral populations produce more long-winged individuals solely because of the triggering effects of more rapid fluctuations in habitat. Thomas and Alexander (1962) demonstrate geographic variation in proportions of long-winged individuals of three meadow grasshopper species in the *Orchelimum concinnum* group. Only micropterous individuals are produced in relict areas, while the flourishing populations in other regions produce many macropterous individuals. No evidence is available to test the question whether this variation is owing to one or the other of two apparent possibilities: (1) genetic change resulting in loss of the ability to produce macropterous individuals in the relict area; or (2) failure of relict populations to reach densities necessary to trigger macropterousness.

Alexander (1961) noted the close correlation between wing length, flying ability, and habitat permanence among different species, wondered if behavioral events such as might result from crowding could affect wing length, and speculated that anything which accelerates development, such as highly nutritious diets, high even temperatures, breaking of diapause, and tactual stimulation from crowding, might have essen-tially the same effect on wing length. All of the necessary experiments to test this hypothesis have not yet been carried out, but the data reported above seem to support the likelihood that it is true in at least some cases. Particularly pertinent are the findings of Fuzeau-Braesch (1961) that in two of six species she tested, rearing in groups, as contrasted with rearing in isolation, caused significant increases in the proportion of macropterous individuals. Saeki (1966a) obtained similar results with *Scapsipedus aspersus*.

Chauvin (1958) discovered that raising house crickets (*A. domesticus*) in pairs or groups accelerates development, an effect erased by removing the cerci and antennae, suggesting a tactual stimulus such as Ellis (1959) found in migratory locusts. Fuzeau-Braesch (1965) obtained similar results with *G. campestris*. McFarlane (1966) has summarized his results, similar to the above, obtained with *Gryllodes sigillatus* (Walker), and has indicated that a fundamental and pervasive relationship between developmental rate and wing length exists through many or all groups of crickets.

Body Size

Variations in the body size of crickets have been reported by various authors to be associated with (1) differences in latitude and altitude (Alexander and Bigelow, 1960; Masaki, 1966, 1967); and (2) variations in development time caused by photoperiod or temperature differences (see Fig. 6, and Masaki and Oyama, 1963). Masaki (1966, 1967) has made an intensive study of altitudinal and latitudinal size variation in two Japanese crickets, *Teleogryllus emma* and *T. yezoemma*. He discovered that size differences persist when strains from different regions are reared under identical conditions in the laboratory. Short photoperiods caused faster development and smaller adults in these egg-diapausing species; faster development and larger adults, on the other hand, result from the effect of long days on juvenile-diapausing species (Fig. 6; Masaki and Oyama, 1963). Fuzeau-Braesch (1966) found that diapausing individuals of *G. campestris* are larger whether they mature before or after non-diapausing individuals retarded by low tempera-

tures during early juvenile stages. Because egg size seems always the same, Masaki believes that in *T. emma* larger females lay more eggs, and that, omitting other possibilities such as predation, selection favors larger size except when maturing time causes eggs to be laid so late that they fail to reach the diapause state before the onset of winter. Likewise, small females maturing and laying eggs too soon in southern climates run the risk that the eggs will hatch before winter. There are additional compensating factors: high temperatures intensify egg diapause, thus reducing likelihood of premature hatching in early-laid eggs; diapause is more intense in southern populations; and the photoperiod effect adjusts maturation times of the juveniles. In at least some cases, longer development time and larger size are associated with an extra molt (Saeki, 1966b).

Length of Adult Life

Winter may be a cause of high mortality in northern crickets, but it is also a convenient synchronizer of adulthood. In species in which adults tend their young, or those in which there is little competition between adults and juveniles (for example, holometabolous insects), long-lived adults may by more prevalent than in species in which the adults compete with their own offspring. Temperate crickets which do not tend their young evidently all have short-lived adults (Figs. 2, 11). In contrast, adults of tropical species seem, on the basis of preliminary observations in the laboratory, to live many times as long as temperate adults; and most tropical and sub-tropical species seem to be represented by at least a few adults, often simultaneously with juveniles of many ages, at all or nearly all times of the year.

A given area habitat unit cannot produce as dense an adult population of a continuously breeding species in which adults and offspring compete as it can of a seasonally cyclic species in which they do not. There can never be as many adults around in the former case. Three possible selective trends in the tropics may be considered in this general context: (1) selection for synchronized adulthood may be based on some regular seasonal change such as dry and wet seasons (both temperature and photoperiod

changes ought to be less effective in tropical regions); (2) the method of pair formation may be adjusted, in some fashion compensating for the lower density of adults in populations; and (3) longer adult life may be advantageous, on the basis that longer-lived adults in a sparse (adult) population will have a better chance to reproduce maximally, and also because successful offspring can be produced during a greater part of the year (than in a temperate region where overwintering stages and developmental habitat are restricted). Pace (1967) suggests that long-lived adults may generally be more prevalent in temperate species that overwinter in several stages and live in habitats continuously suitable for development.

Gryllus campestris

Fuzeau-Braesch (1963) studied the role of photoperiod in adjusting the life cycle of this univoltine, juvenile-overwintering species. She found that juveniles burrowed more when isolated, and more when photoperiods were long (up to about 20 hours). Eight-hour photoperiods speeded up the molting from the eighth instar into the ninth diapause instar; 16-hour days retarded it; and continuous light gave intermediate results. Short photoperiods during egg laying also seemed to delay molt of the offspring to the diapause stage. She suggested that burrow inhabitation effectively shortens the cricket's photoperiod, thereby hastening the onset of diapause. This would mean that individual crickets which had excavated suitable overwintering burrows would enter diapause more quickly, thus probably reducing their activity, their nutritional requirements, and their likelihood of losing contact with the burrow while locating food. In contrast, molt and diapause would be delayed among crickets without suitable burrows. The synchrony of adults that is so evident within cricket populations (Fig. 12) thus seems, in spring-maturing species, to have a significant beginning during the previous summer.

As already mentioned, *G. campestris* produces macropterous individuals extremely rarely, evidently only when diapause is by-passed for one reason or another. Whether this capability is being maintained by selection or is a vestigial
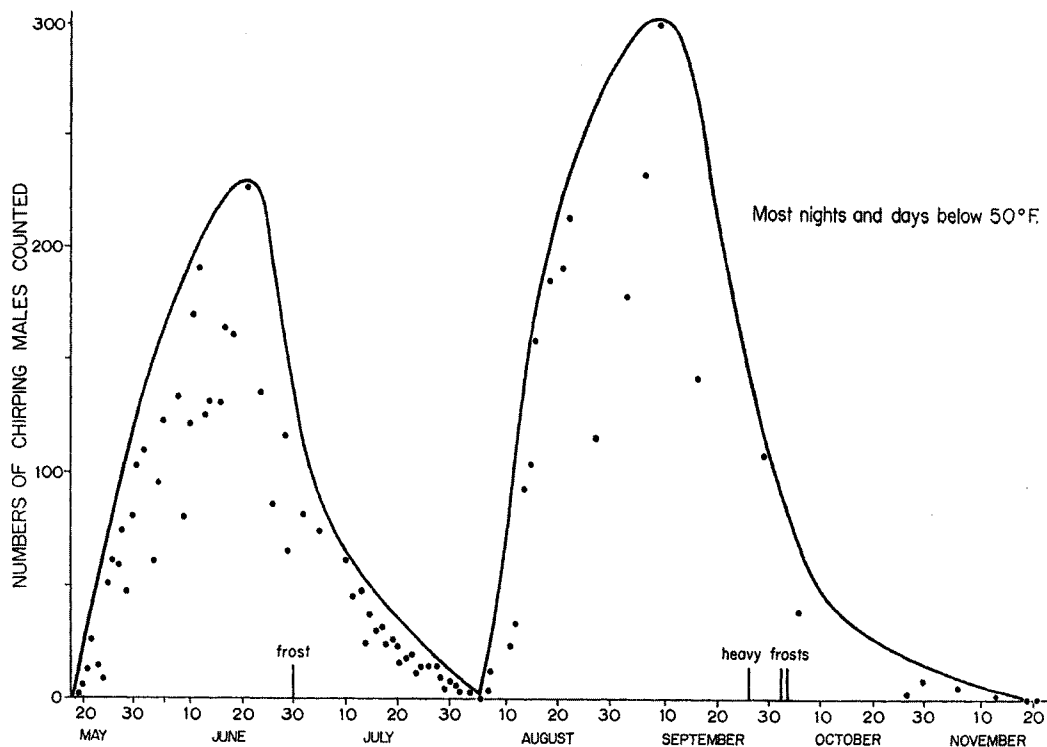
FIG. 12. SEASONAL RELATIONSHIPS OF ADULT POPULATIONS OF *Gryllus veletis* (LEFT) AND *G. pennsylvanicus* (RIGHT) IN A BRUSHY PASTURE IN SOUTHEASTERN MICHIGAN, AS MEASURED BY COUNTS OF CHIRPING MALES

High counts were on warm, sunny days; low counts were on cold, cloudy or rainy days.

characteristic is unknown, but the same rare macropterousness occurs in two other univoltine, juvenile-overwintering species, *Miogryllus verticalis* and *Nemobius yezoensis*. In all these cases, females are more likely to be macropterous than males.

Gryllus rubens and G. integer

Alexander (1961) has noted that, based on collections, proportions of macropterous and micropterous individuals are almost exactly reversed in the spring and fall adults of the bivoltine, juvenile-overwintering cricket, *Gryllus rubens*. It was suggested that development time might be involved, since one generation (8 per cent macropterous) is composed of diapausing, overwintering individuals, while the other (75 per cent macropterous) matures without such delay.

I have since tested the effect of photoperiod on developmental time in *G. integer*, a sibling to *G. rubens* which has the same bivoltine life cycle (Fig. 2) and was available when *rubens* was not. Long increasing photoperiods caused more rapid development and 100 per cent macropterousness, while short decreasing photoperiods retarded development and caused almost 100 per cent micropterousness (Fig. 6). A serious shortcoming of previously published results was failure to provide adequate temperature data, particularly since most lights produce heat, and higher temperatures and long days have similar effects. Temperatures were controlled by automatic thermostats throughout these tests, and adjusted so that the slight overall temperature difference between cages would tend to favor the crickets kept under short days.

The results of these tests are like those of Masaki and Oyama (1963) and Masaki (1966) with *Nemobius yezoensis* and *Teleogryllus yezoemma*, univoltine species, in that individuals

reared in short days were also smaller than those reared under long days.

G. *rubens* and G. *integer* live in lawns, pastures, roadsides, and old fields, suggesting that their pre-civilization habitats were relatively unstable. Retention of flight and emigrating (colonizing) capacity will in the long run be favored in such nomadic species if habitats deteriorate and disappear. Even though emigrating individuals may not be reproductively favored at the time of emigration or during the generations immediately following it, the fact remains that if the original habitat eventually disappears, only the descendants of migrants are left.

These species also have to contend with fairly severe winters, at least in the northern parts of their ranges. The significance of their complex phenotypic variations may be summarized as follows: most late summer juveniles are better off ensconcing in a burrow and diapausing, and subsequently remaining in the same spot as an adult; most early summer juveniles are better off maturing directly and emigrating; and every individual is therefore best off, because of the bivoltine life cycle, if it has the potential for both capabilities and has their expression adjusted by day length.

G. *veletis* and G. *pennsylvanicus*

Post-diapause juveniles of *veletis* and early juveniles of *pennsylvanicus*, present together in early summer, are both subjected to sharply increasing and long day lengths (14 hours in mid-April to 16 + hours in mid-June at 45°–50° N). On the other hand, early (pre-diapause) juveniles of *veletis* and late juveniles of *pennsylvanicus*, present together in late summer, are both subjected to sharply decreasing and short day lengths (16 + hours at July 1 to 10 hours in late October at 45°–50° N). If these species behave as do those others which have been tested (Masaki and Oyama, 1963; Fuzeau-Braesch, 1963, 1966), presumably the conditions to which the above stages are subjected should accelerate development in all cases but one: shortening days, while accelerating development of pre-diapause *veletis* juveniles, should decelerate or stop development of diapause-age *veletis* juveniles. Photoperiod may

also affect embryonic development in the egg, either directly or via the mother, but no evidence is available regarding crickets. In egg-diapausing crickets photoperiod thus far seems only to time the period of egg-laying by adjusting maturation time (Masaki and Ohmachi, 1967).

POLYMORPHISMS, POPULATION DENSITY, AND COLONIZATION

Some phenotypic variations in insects are density-dependent. Migratory locusts are an especially well-known example. Contrary to the conclusions of some biologists discussing this general topic, I think the evidence suggests that density-dependent polymorphisms tend to increase the reproductive capacity of the individuals possessing them except in cases when insufficient time has elapsed for mutation and selection to bring about genetic alterations that compensate very recent changes in the environment. The available evidence regarding cricket polymorphisms supports this generalization. Thus, I do not find reasons to support the frequently stated idea that (1) emigration or (2) suppression of reproductive tendencies have the evolved function of relieving population pressure—i.e., they are suicidal in nature. Instead, the evidence indicates that, except for incidental effects such as pathological conditions arising from overcrowding, individuals suppress their reproductive tendencies or migrate during times of high population density or habitat deterioration—in other words when such behavior is most likely to lead to increases in the realized reproduction of the individuals doing the suppressing.

The following quotations from the writings of contemporary biologists illustrate the contrary viewpoint: "The transformation of grasshoppers into phase *gregaria* is a classical reaction of the sort referred to as 'density-dependent' in population ecology. Its function is clearly to produce emigration that will relieve pressure on the *solitaria* foci, which are the most favorable breeding areas for the species" [Wilson, 1963]. "The major purpose of the emigration [of locusts] at this stage appears to be the relief of congestion, though, as a minor or secondary advantage, it no doubt helps the species to disseminate itself and colonize new habitats as these become available" [p. 273, Wynne-Edwards, 1962].

Fig. 11 summarizes the effects of several dimorphic or polymorphic tendencies known to be related to population density in crickets. In general, high density populations result in (1) higher tolerance of crowding, and (2) increased emigration (dispersal). Both effects have clear probable advantages to individuals possessing the dual potential. In a crowded situation, hyperaggressiveness except just following mating is likely to diminish an individual's mating success, and territorial behavior is futile. Thus, pair formation occurs more frequently by chance, and, as this tendency increases, mating success becomes more closely linked with tolerating the presence of other individuals, and joining groups of tolerant individuals. Such toleration by males should be minimized chiefly in connection with monopolization of a female, which is the one circumstance during which aggressiveness remains high in crowded situations: a male is always hyperaggressive during a bout of copulations, driving other males from the vicinity (Alexander, 1961).

In contrast, during periods of low density, aggressiveness and territoriality increase a male's chances of attracting and monopolizing females, since an increased proportion of matings depend upon attraction of the females to individual calling males. A male with a burrow is a more persistent, stationary caller, and an aggressive male is more likely to retain his burrow. In turn, possession of the burrow enhances dominance (Alexander, 1961).

A given individual's contribution to subsequent generations will be minimized as population size increases. This shift reduces the relative risk taken by an emigrant, assuming that colonization or the joining of other, less dense populations is possible. Emigration during times of high population density may indeed increase the reproductive possibilities of individuals staying at home, but it is difficult to view such an outcome as anything other than an incidental effect of the selective advantage accruing to emigrants under such conditions; further, there seems to be no reason for so considering it.

In various Orthoptera, the close correlation between habitat permanence, absence or scarcity of invadable habitat, and loss of flying ability indicates that repeated loss of emigrants

consistently results in disappearance of the ability to emigrate. Presumably, proportions of emigrating individuals should decrease, at a rate influenced by the amount of immigration, for the duration of each habitat-deme relationship. Each deme established by macropterous emigrants should initially have a high proportion of emigrants, and each disappearance of a habitat and extinction of its non-emigrant population would raise the proportion of emigrants in the species. Density-related emigration can be advantageous even where habitats do not disappear if differences in probability of breeding success correlate closely with density, and population densities fluctuate sufficiently among demes to give emigrants a high probability of entering low density demes. Otherwise, low proportions of emigrants or deleterious emigration may persist because further loss of emigrating ability is retarded by immigration, habitat impermanence involving relatively long cycles, or some combination of these events.

Loss of emigrating ability in permanent habitats can occur whether or not the difference between flying and non-flying individuals is genetic to begin with; when it is not genetic, any mutation eliminating the plasticity that leads to production of some fliers under some conditions, or reducing it, will be favored. On the other hand, if emigration were suicidal as an evolved function, or at least had its chief effects on the individuals staying at home ("relieving population pressure"), we should expect dimorphism in regard to it to be retained not only in normally nomadic species (sometimes called "fugitive" species), but also in non-nomadic species living in permanent habitats in regions where a new invadable habitat does not appear and successful colonization cannot occur.

The close relationship between photoperiod changes and flying ability in bivoltine crickets such as *Gryllus rubens* and *G. integer*, discussed in a previous section, is particularly interesting in these connections. Late summer is evidently a better time for this nomadic species to colonize than is early summer. A correlation with season as such may exist, for example, in availability of food for developing young. Another possibility is that a genetic factor has been incorporated which enables individuals to predict the consistently much higher population density of

late summer, using photoperiod as the cue. In other words, selection may have favored a wing length response based on photoperiod because photoperiod is a reliable indicator of other seasonal changes that result in the second adult population of the summer being much larger than the first one. Individuals are accordingly able to emigrate when emigration is the favored alternative because of changes in population density, but they use photoperiod and not population density as the cue. Mortality during winter is undoubtedly one of the reasons for the smaller early summer population, but additional factors may be involved.

EFFECTS OF WEATHER ON
DAILY CYCLES OF ACTIVITY

Most crickets, tropical or temperate, are nocturnal, calling only or chiefly at night. Characteristically, species that live only in trees are more strictly nocturnal than their close relatives living in weeds and grasses: for example, *Oecanthus pini* Beutenmuller and *O. laricis* Walker (*Oecanthinae*) living on pine and tamarack trees, respectively, rarely call during daylight hours, while the four other North American members of the *Oecanthus nigricornis* group live on herbaceous vegetation and sing in large numbers most of the day as well as at night. Variations in diurnal cycle also occur among surface dwelling crickets. For instance, ground and field crickets (Nemobiinae and Gryllinae) that live in the woods are usually more nocturnal than their relatives living in grasslands or open fields.

Some of these variations seem most likely to be correlated with intensity of predation by birds, but a few are not easily explained on that basis. *Gryllus veletis* and *G. pennsylvanicus*, for example, call both day and night east of the Rocky Mountains and can be heard at any time of day continuously along hundreds of miles of grassy roadsides in the Great Plains. Farther west the same species rarely chirp except at night.

Daily activity cycles have been studied experimentally in four crickets. Lutz (1932) used a treadle arrangement to demonstrate that juveniles and adult males of *Acheta domesticus* and *Gryllus pennsylvanicus* locomote more at night than during the day 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) studied the house cricket further, 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 continued through most of the night. Rhythms of locomotory activity persisted in continuous light or dark and 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 dark.

Cloudsley-Thompson (1958) reported that three adult females of the northern European field cricket, *Gryllus campestris*, were most active in the daytime in the laboratory, with a peak of activity about 3 pm. 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 the rhythm had been damped by continuous darkness; (3) returning the environment to 30°C after periods at lower temperatures; and (4) supplying water after several days without water.

Alexander and Meral (1967) recorded the daily cycles of chirping of another northern cricket, *Gryllus veletis*, in southeastern Michigan by counting numbers of chirping males and found a striking difference on different years, evidently owing to differences in the general temperature regimes of the two years (Figs. 13-14). In 1965, during the recording period and for some days before, the air temperature dropped too low for chirping (about 50°F) shortly after sundown and rarely was too high (about 100°F) in chirping locations during the day; during the same period in 1966, the night temperature did not fall below 50°F and the day temperature was higher, probably too high for chirping in many or most chirping locations. As a result, in 1965
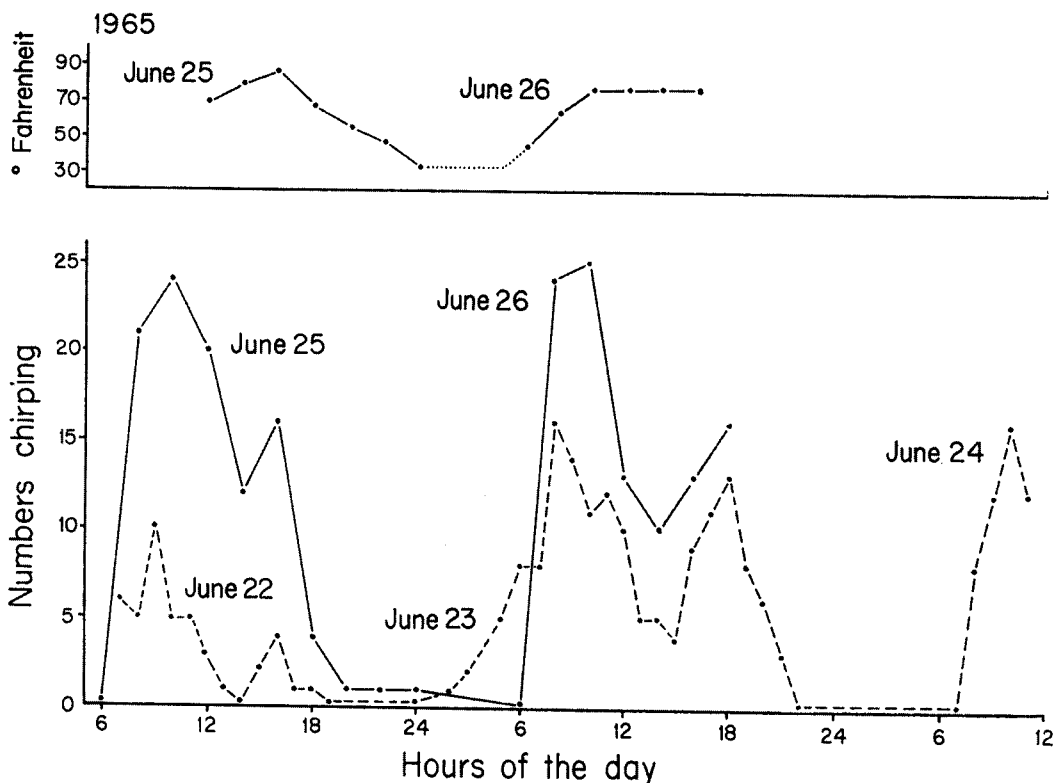
FIG. 13.   DAILY CHANGES IN NUMBER OF CHIRPING MALES OF *Gryllus veletis* DURING A 1965 PERIOD WHEN THE NIGHTS WERE TOO COLD FOR CHIRPING BETWEEN SHORTLY AFTER SUNSET AND SHORTLY AFTER SUNRISE, AND WHEN NO PART OF THE DAY WAS TOO HOT FOR CHIRPING

Temperature was not recorded June 22–24, but the nights were cold, and there was rain on the night of June 22.

veletis was strictly a daytime chirper, at least during the periods of observation, with the principal chirping peaks in mid-morning and a lesser one in mid-afternoon. In 1966, the same species in the same field chirped chiefly at night, though there were small daytime peaks at almost the same times of day as in 1965.

These observations indicate that *Gryllus veletis,* and perhaps other field crickets living at extreme latitudes, can be either nocturnal or diurnal, depending upon the prevailing weather conditions in any given year in the variable climates where they occur. How quickly such reversals can take place, precisely how they occur, and whether or not weather conditions during juvenile life affect the daily activity cycles of adults are questions that remain to be answered.

LIFE CYCLE CHANGES AND SPECIATION

Bigelow (1958) and Alexander and Bigelow (1960) postulated that *Gryllus veletis* and *G. pennsylvanicus* may have originated when a tropical species developed both egg-overwintering and juvenile-overwintering populations along its northern border. Masaki (1961) described a juvenile-overwintering population in the southern part of the range of the otherwise egg-diapausing species, *Scapsipedus aspersus,* sympatric with the parental population but with the adults of the two populations seasonally separated. Earlier in this paper, I described a temporally isolated, fall-adult population in the southern part of the range of *G. fultoni,* a species which farther north overwinters only in the juvenile stage and is adult only in the spring. Fulton (1951) and Alexander (1957) described
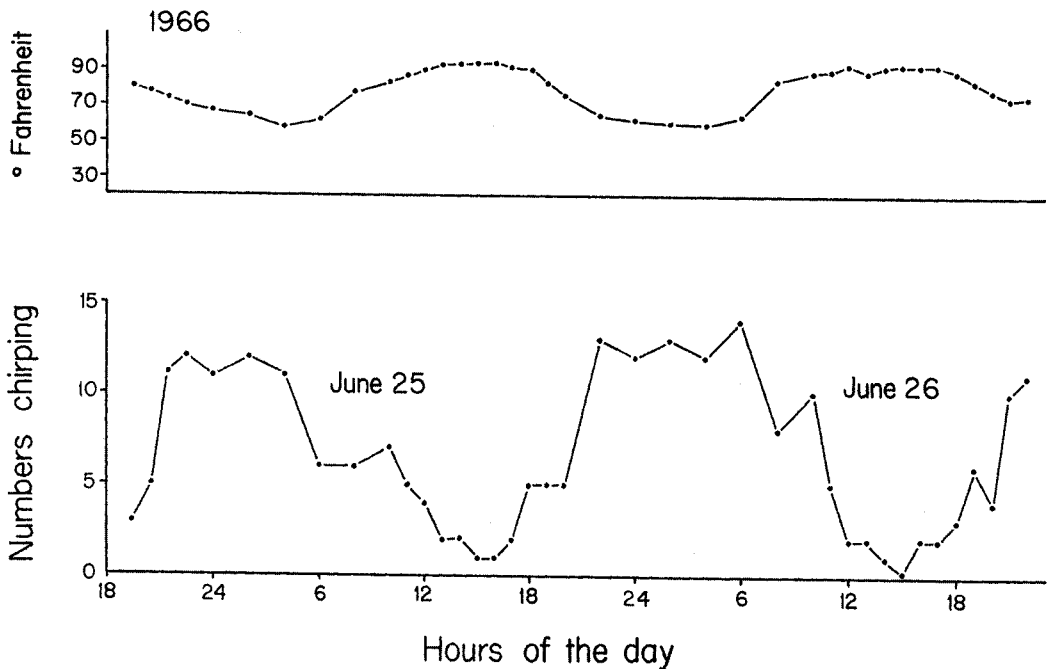
FIG. 14. DAILY CHANGES IN NUMBER OF CHIRPING MALES OF *Gryllus veletis* DURING A 1966 PERIOD WHEN THE NIGHTS WERE NEVER TOO COLD FOR CHIRPING, AND WHEN MOST LOCATIONS WERE TOO HOT FOR CHIRPING DURING SEVERAL HOURS OF MIDDAY

temporally isolated, spring-adult populations in the northern part of the range of G. *firmus.* None of these temporally isolated populations is geographically isolated from the rest of the species.

These four cases, and the hypotheses given earlier that relate to them, all imply a connection between the appearance of a new life cycle and the multiplication of species. In fact, the presence of sibling species with radically different life cycles, such as G. *veletis* and G. *pennsylvanicus,* is enough to raise the question of whether the life cycle change contributed to the speciation process or was merely incidental to it. This question is particularly interesting with crickets and their relatives (1) because both of the common temperate life cycles discussed earlier occur within species as well as between siblings; (2) because no genetic difference is necessary for essentially complete temporal isolation of the relatively short-lived adults (Figs. 2, 11); and (3) because no case is known of spatial isolates with the two different life cycles, either sibling species or conspecific populations.

The next question seems to be: to what extent

is it necessary or reasonable to postulate that geographic isolation was in some way involved in the development of life cycle differences between closely related species or populations of the same species? Alexander and Bigelow (1960), in referring to G. *veletis* and G. *pennsylvanicus,* maintain (p. 344): "It is doubtful that the possibility of allopatric speciation could ever be completely ruled out, but the evidence suggests that geographic isolation is both unlikely and unnecessary in this particular case." There is a remarkable similarity between this statement and the following one made by Ghent and Wallace (1958) (and not seen by me until 1965) in trying to explain a similar case of egg and pre-pupal overwintering with seasonal separation of adults in *Neodiprion* sawflies: "The change in overwintering habit effects temporal isolation of breeding adults with complete efficiency, and as a pathway of speciation, it calls more urgently for a premise of geographical continuity than for one of geographical isolation" p. 271. Mayr (1963a), on the other hand, believed (p. 477): "It would be altogether unlikely for a population to adapt itself simultaneously to

two different breeding cycles. Where a species evolves two such cycles it does so in different, geographically segregated, populations . . ." [and] "It is rather probable that the difference in breeding cycle of [G.] *pennsylvanicus* and [G.] *veletis* was not yet complete, when they first met, after emerging from their geographic isolation. If so, competition eliminated any tendencies for spring breeding in *pennsylvanicus* and of fall breeding in *veletis.*" Alexander (1963) discounted the likelihood of Mayr's interpretation, pointing out that certain species have in fact evolved two cycles in one locality, but Mayr (1963b) responded (p. 206): "To me, at least, it would be far simpler to have the ancestral species of the *veletis-pennsylvanicus* group split into at least two border populations, one let us say east and another one west of the Appalachians, furthermore, to assume that in one of these egg-overwintering was more advantageous, in the other one, juvenile-overwintering, and that with the post-Pleistocene improvement of the climate, the two populations could overlap and coexist, owing to their previously established seasonal separation." Mayr concluded by repeating his earlier conclusion that "in not a single case is the sympatric model superior to an explanation of the same natural phenomenon through geographic speciation."

Mayr's (1963a) postulate that seasonal separation was completed because of competition following establishment of sympatry brings up some points evidently requiring clarification. Two kinds of competition could be meant: (1) between adults at mid season, particularly in connection with reproductive activities, and (2) between juveniles of the two populations, or between juveniles of one and adults of the other, particularly in connection with food. It is difficult to imagine how either of these kinds of competition could be eliminated by shifts in life cycle. First, adult and juvenile crickets (possibly excepting very tiny juveniles) live in the same places and eat the same things. Competition of the second kind, therefore, probably still exists between G. *veletis* and G. *pennsylvanicus,* and seemingly could not be changed by any possible shift in their life cycle. Second, competition (or interference) between adults of the two species also could not easily be construed to

shift the life cycle, though it might adjust slightly the timing of the adult periods. The cycle itself is evidently restricted by possible overwintering stages; there are no known intermediate overwintering stages between eggs and late juveniles and, therefore, no seasonally intermediate periods of adulthood. The only possible "intermediacy" is represented by late adults of *veletis* or early adults of *pennsylvanicus;* but *veletis* and *pennsylvanicus* currently have about the same adult periods as other univoltine crickets that overwinter respectively as juveniles and eggs and lack seasonally different sympatric siblings (Figs. 2, 11). No evidence exists, therefore, that competition between *veletis* and *pennsylvanicus* has materially affected their life cycles.

Because of the history of the discussion about the significance of seasonal isolation in speciation, and the general attitude among biologists toward the possibility of speciation without geographic separation, it seems useful to account for other disagreements between Mayr (1963a, 1963b) and Alexander and Bigelow (1960) and Alexander (1963).

Mayr (1963b) (1) says that it is not stated how the northern and southern populations of a species such as the ancestor of G. *firmus* might have been geographically separated so that a process of allochronic speciation could occur within the northern segment; (2) believes that not one but a series of peripheral isolates would have been involved; (3) suggests that there may have been an east-west split between two such border populations (contrasting this with a north-south split); and (4) believes that one isolate became solely juvenile-overwintering and the other solely egg-overwintering, and that speciation occurred allopatrically between them.

Concerning the first point, geographically isolated populations of G. *firmus* in the inland sand hills of North Carolina were first described by Fulton (1952), and later discussed by Alexander (1957), who noted that they hybridized with coastal populations (unpubl. tests by Fulton) and had the same song. Additional inland populations in Alabama have been found since then (Fig. 4), some of which contain individuals with different life cycles. The example

of a north-south split is, therefore, already before us in the proper species group, the right geographic locations, and (at least today) the right climate.

Secondly, the number of successful peripheral isolates does not seem to be important in assessing the significance of seasonal isolation in causing speciation. Actually, the more isolates there are, the more likely it is that allochrony was involved in this case, and the less likely that allopatry was more than incidental to the speciation process. The reason for this assertion is the following: if a species tends to produce populations with two kinds of life cycles, as, for example, *G. firmus* does, then an increased number of isolates will mean it is less likely that none contains both life cycles. The universal success of breeding tests among related *Gryllus* species that overwinter in the same stage (Table 3), and the absence today of song or ecological (habitat) differences between *veletis* and *pennsylvanicus*, indicate that any persistent, double-cycled, ancestral population would have contributed genes to both incipient species. Accordingly, the significant isolation would still have been temporal from the start, and whatever geographic isolation occurred would have been incidental. Thus, speciation would have occurred in the north even if *every* isolate had been double-cycled. Furthermore, unless the temporal isolation were effective as an extrinsic separator (in fact, capable of causing speciation), double-cycled populations would tend to destroy the effects of prior geographic separation when they became sympatric with geographic isolates (incipient species) that had developed different, single cycles while living in different places. In other words, even if there were evidence that geographic isolates sometimes develop different cycles (and there is none), we are not free to consider the fact by itself until we can eliminate the likelihood that double-cycled populations will also persist.

Thirdly, whether the split, or separation of double-cycled northern populations from southern non-cycled populations, is "east-west" or "north-south" does not matter as long as it took place somewhere in the northern part of the range of the species — or in the region where there are mild winters, as there are today in the sand hill region of North Carolina where an

TABLE 3

Successes and failures in 16 attempts to hybridize field cricket (Gryllus) *species with known diapause stages**

MATING	OFFSPRING
A. Non-diapausers × non-diapausers	
1. *assimilis* × *bermudensis*	+
B. Non-diapausers × juvenile-diapausers	
1. *bimaculatus* × *campestris*	+
2. *bermudensis* × *campestris*	+
3. *assimilis* × *rubens*	+
4. *assimilis* × *integer*	+
5. *assimilis* × *veletis*	—
C. Non-diapausers × egg-diapausers	
1. *assimilis* × *pennsylvanicus*	+
D. Juvenile-diapausers × juvenile-diapausers	
1. *veletis* × *veletis*	+
2. *veletis* × *rubens*	+
3. *veletis* × *fultoni*	+
4. *veletis* × *vernalis*	+
5. *vernalis* × *fultoni*	+
E. Egg-diapausers × egg-diapausers	
1. *firmus* × *pennsylvanicus*	+
F. Egg-diapausers × juvenile-diapausers	
1. *pennsylvanicus* × *veletis*	—
2. *pennsylvanicus* × *rubens*	—
** 3. *firmus* × *veletis*	—
4. *firmus* × *rubens*	—

*, summarizing Fulton (1951), Alexander (1957, and unpublished 1967), Bigelow (1958, 1962), and Cousin (1961).

+, offspring obtained in at least some attempts.
—, no offspring obtained.
**, from Alexander, 1967 (unpublished).
Only species for which diapause seems well understood are included. The most extensive attempts have been carried out between *veletis* and *pennsylvanicus* and between *veletis* and *firmus*.

"east-west" split is known to have occurred in *G. firmus* (Fig. 4). Mayr's postulate of an east-west split on either side of the Appalachians is not unreasonable, but it somewhat confuses the issue since the only important point is that the populations involved must be separated in some fashion from the continuously breeding populations farther south in Florida; otherwise the latter would provide a means of indirect gene exchange between sympatric northern spring-maturing and fall-maturing populations. This required break has no relevance to the question of geographic isolation between the two northern populations, which need never be allopatric during their speciation; three species,

not two, would result from the one geographic discontinuity. Likewise, the particular timing of the geographic break relative to the genetic divergence of the sympatric northern populations from one another is of no relevance.

Mayr's fourth point of concern — whether life cycle differences now existing between sibling species arose during allopatry or during sympatry — is evidently the critical one.

First we should check natural populations for evidence. The four cases I have already mentioned are pertinent: *Gryllus firmus, G. fultoni, G. campestris,* and *Scapsipedus aspersus.* In all four cases populations with the two kinds of life cycles coexist in the same regions, in the southern part of the range of the three more or less northern species and in the northern part of the range of *G. firmus,* the only southern species. Recourse to natural situations, therefore, does not support Mayr's argument, for in no cricket, and to my knowledge in no other arthropod, are there allopatric populations with seasonally staggered life cycles correlated with different overwintering stages.

This finding is no surprise. The kind of life cycle shift it would involve can occur in three possible ways: (1) a continuously breeding population moving north in two or more locations could develop one kind of life cycle in one place and a second kind in another place; (2) one or more populations already having a single life cycle could make a complete shift in one generation to the other cycle, or (3) one or more single-cycled populations could develop a double life cycle and then lose the original cycle through extinction (shift slowly from one cycle to the other).

No case is known of the first of these three possibilities, which has already been discussed. But if it is used to account for the origin of species such as *G. veletis* and *G. pennsylvanicus,* two problems are introduced. First, if a third (southern) derived species is involved, such as *G. firmus* in this case, then the near-identity of *veletis* and *pennsylvanicus* in a variety of regards in which they differ from *firmus,* such as chirp rate and pulse rate in calling, number of file teeth on the tegmina, and general size and body form, must be accounted for by parallel evolution or divergence only by *firmus* from the common ancestor of all three species. Second,

we must wonder why, in species like *firmus* and *fultoni,* populations with one of the two possible cycles are inevitably small, sympatric portions of a large population with the other cycle; likewise *veletis* has never been found without *pennsylvanicus,* though *pennsylvanicus* occurs without *veletis* in Nova Scotia.

The second possibility above, a sudden shift in one generation of an entire population from one life cycle to another, seems too far-fetched to consider seriously. Only slightly more likely is the third possibility that some individuals would shift cycles and those with the old cycle would subsequently disappear leaving only the new cycle. But if we must involve allopatry this third possibility seems to be the only one. To propose allopatric development of life cycle differences when sympatric duality in life cycles is known is to require a more complex hypothesis than is necessary to take account of the facts.

Suppose allopatry is not required. Can the pairs of seasonally different populations that persist today in a completely sympatric relationship with members of the larger (parent) population that still possesses the original cycle, fail to diverge, since they overwinter in different stages and are subjected to different temperature and photoperiod regimes during the various parts of their life cycle? I suggest that selection would strongly favor divergence between such populations from the start, particularly in regard to overwintering behavior and physiology. We have already seen (Table 2) what striking effects alterations of life cycle timing can have, in the absence of any genetic alteration, in the field performance of species such as *Gryllus rubens, G. integer,* and *G. firmus,* and in laboratory populations of *G. campestris, Nemobius yezoensis,* and others. Even if some gene flow occurred at mid-season between sympatric, differently cycled populations, or because of repeated shifting back and forth between the two life cycles, divergence would surely continue if only because of the selective advantage in the acquisition of different kinds of special overwintering characteristics, owing to the difference in the life stage that repeatedly enters winter.

One question that might be raised, and perhaps was involved in Mayr's objections,

concerns the problem of survival of newly off-cycle individuals in the face of competition from the established population. Lewis (1966), for example, raises this question in attempting to describe how chromosomal reorganization may result in speciation without geographic isolation. That this problem is probably not pertinent to allochronic speciation in crickets is indicated by the coexistence of seasonally different populations within species.

If no gene flow at all occurs between seasonally cycled populations, then speciation would occur almost exactly as if the separation were geographic. If gene flow persists, however, then divergent selective action (roughly equivalent to a combination of disruptive selection and partial extrinsic separation) will result in speciation only if overwintering differences in some way eventually become linked to incompatibility.

Here an unexplained phenomenon enters the picture, at least with regard to *veletis* and *pennsylvanicus.* Among some 40 attempts to hybridize different cricket species, of which about half have been really intensive efforts, four of the five complete failures known to me have involved northern crickets with different over-wintering (diapause) stages (Table 3). No hybrids have even been produced between species with different diapause stages, even though three investigators in North America (Fulton, 1952; Bigelow, 1958, 1960; Alexander, 1957, and unpubl.) have tried several cases.

> The closest case is Masaki and Ohmachi's (1967) success in hybridizing an egg-diapauser with what they call a "facultative" juvenile-diapauser (dependent upon photoperiod). Their results are rather complex and interesting: for example, some female F_1 hybrids took longer to mature without any delay in egg hatching time than even the facultatively juvenile-diapausing parent, and the reciprocal crosses gave quite different results.

This failure of hybridization between species with different diapause stages is almost the only generalization about incompatibility between *Gryllus* species that can be presented at this time. Both copulation and oviposition (less frequent in the interspecific matings) occurred in all such crosses tried by me, but no eggs hatched. Since populations of crickets consistently entering winter in different stages ought to develop

appropriate diapause rather quickly, any strong reduction of gene flow between populations with different over-wintering stages could, therefore, cause an irrevocable shift toward total inter-sterility. This kind of divergence seems appropriately described in crickets as a "short route" to speciation, for total sterility is actually rare among sibling species of most or all kinds of animals. But early inter-sterility is not a *required* part of the process of speciation by seasonal separation as outlined here.

Both spring and fall adults of *firmus* have repeatedly produced hybrids in matings with *pennsylvanicus,* but neither has hybridized with *veletis.* This may be an indication of ancestral northern affinities in *firmus,* and along with the more northward extension and greater northern abundance of egg-overwintering populations of *firmus* (Fig. 4), suggests a close relationship with *pennsylvanicus.* Because of this information, the possibility cannot be eliminated that *firmus* is a derivative of a *pennsylvanicus*-like ancestor, rather than vice versa. This would mean that, if present distribution and sterility barriers are taken into consideration, spring-adult *firmus* may be independently derived (Figs. 15, 16). It could also mean that *veletis* and *pennsylvanicus* may have diverged by production of a double-cycled population in the southern part of the range of a northern species rather than vice versa. This question affects the relative probability of the two models for allochronic speciation illustrated in Fig. 15 explaining the origin of *veletis* and *pennsylvanicus,* but it does not reduce the likelihood that seasonal separation was the cause of speciation.

In summary, it would seem difficult to prevent genetic divergence between persisting seasonally different populations, even if they were sympatric, even if some gene flow persisted, and even if hybrids were not adult at the wrong season and did not enter winter during other than the two winter-hardy stages. The eventual result of such divergence would be two species that overwintered in different stages and were adult at different seasons, but had essentially the same habitats and occupied, at least initially, the southern portion of the parental range in the case of a northern species and the northern portion of the parental range in the case of a southern species.
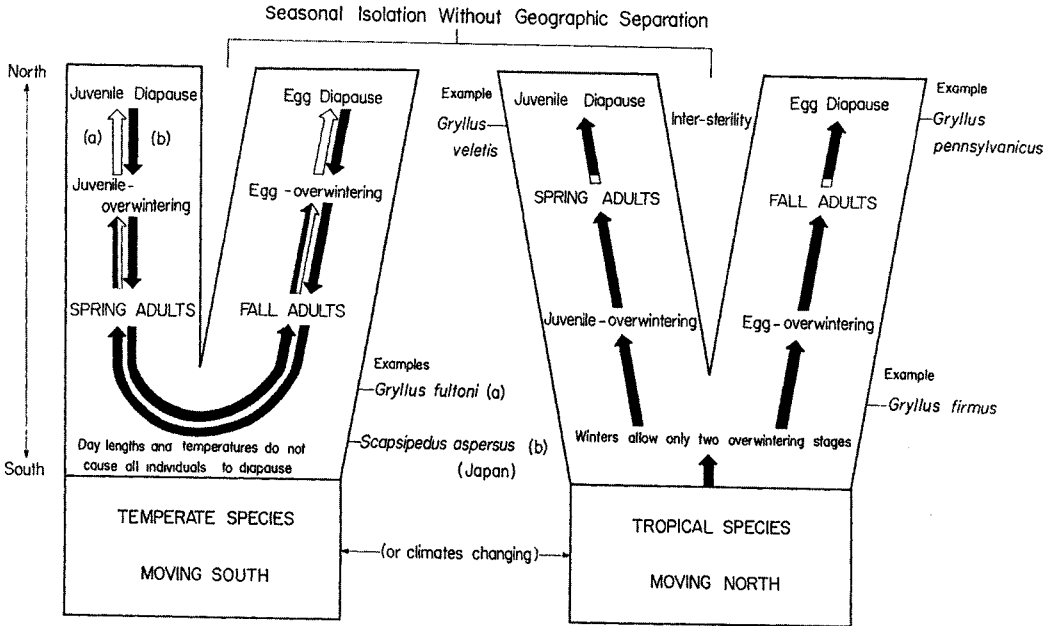
FIG. 15. ALTERNATIVE HYPOTHESES FOR THE MULTIPLICATION OF FIELD CRICKET SPECIES WITHOUT THE NECESSITY OF GEOGRAPHIC ISOLATION

Left, (a) a northern, egg-diapausing cricket producing spring populations in the southern part of its range; (b) a northern, juvenile-diapausing cricket producing fall adults in the southern part of its range. Right, a southern cricket developing both of the prevalent temperate life cycles in the northern part of its range. Black arrows represent parts of the diagrams that have been demonstrated in natural populations; partly black arrows indicate possible situations in known species; white (open) arrows indicate hypothesis.

There does not seem to be any easy way to derive *veletis* and *pennsylvanicus* except by one of the two possible variations of this scheme, which Alexander and Bigelow (1960) termed "allochronic" speciation in reference to the central role of extrinsic temporal separation. "Allohoric" speciation is a more specific term referring directly to seasonal separation.

It seems impossible even to gain an inkling concerning how frequently allochronic speciation may have occurred in various kinds of insects until intensive systematic-biological work has been carried out on a large number of temperate insect groups by investigators who are at least aware of the possibility and know how the process can work. Such studies obviously have not yet been accomplished, for the possibility had not been considered prior to presentation of this case and that of Ghent and Wallace (1958). For at least three reasons I believe a large number of additional cases may be discovered:

(1) Multiple-year life cycles and univoltine life cycles with short-lived adults are widespread among temperate insects (Pickford, 1953; Brooks, 1958; Alexander and Moore, 1962). Both involve potential temporal isolation of adults. As Walker (1964) points out, there is less expectation of rapid divergence in the case of multiple-year life cycles; geographic restriction of populations emerging in different years is also more likely, and is known in various cicadas (Alexander and Moore, 1962).

(2) Unexplained variations in overwintering stage are prevalent in all major groups of temperate insects, both within and between species as presently recognized.

[Any entomological text or periodical in which life histories are described can be used to verify this remark. Metcalf, Flint, and Metcalf (1951) is an excellent example, and their remarks on the life history of "the field cricket" in the United States, *"Acheta assimilis* Fabricius" (p. 528–529), constitute an instructive illustra-
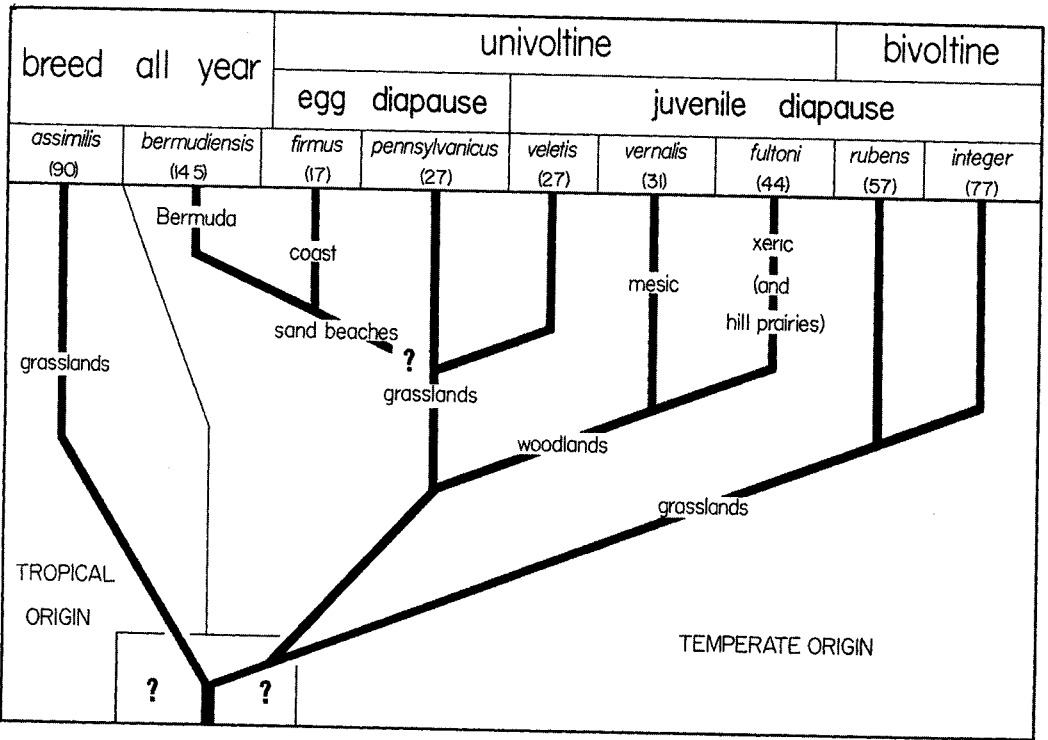
FIG. 16. A DIAGRAM OF THE PROBABLE PHYLOGENETIC RELATIONSHIPS OF THE FIELD CRICKETS OF EASTERN NORTH AMERICA, INCLUDING THEIR PROBABLE GEOGRAPHIC ORIGINS, HABITAT SHIFTS AND LIFE CYCLE CHANGES

Although *firmus* seems everywhere to have a tendency toward egg diapause, some northern populations overwinter as juveniles, with no evidence of juvenile diapause (see text for further explanation). Numbers in parentheses below species names are approximate wingstroke rates in the calling song at 80° F; *rubens* and *integer* are trillers, *assimilis* a B_2 chirper (Alexander, 1962), *fultoni* a B_3 chirper, *vernalis* intermediate between B_1 and B_3; all the rest are B_1 chirpers. All morphological characters studied support this arrangement (see Alexander, 1957; Alexander and Walker, 1962, for all species but *bermudensis* and *integer*, which are morphologically most like *firmus* and *rubens*, respectively).

tion: "The life history varies greatly throughout the range of the insect, but in the northern states the majority hibernate in the egg stage and complete a single generation in a year, while in the Imperial Valley of California and the Gulf Coast they winter as nymphs or remain more or less active the year round and may produce as many as three generations. . . . Throughout most of the northern states, adults are present from late July until heavy frosts and lay their eggs mostly in August and early September." This attempt to generalize around an impossible taxonomic situation resulted in a series of remarks in which scarcely a single clause is correct.]

Except for species with many generations per year, or long-lived adults that reproduce during successive seasons or cause overlap of generations, when such variations are intraspecific

they lead either to multiple-year life cycles or to seasonal separation of adults. As an example of the possibilities, Brooks (1958) has presented evidence that populations of a grasshopper, *Arphia conspersa* Scudder, in Alberta, Canada, contain some individuals that mature in two years, overwintering first as eggs and then as juveniles and producing spring adults, and other individuals that mature in one year, overwintering only as eggs and producing fall adults.

(3) Cryptic species are abundant in every well-studied insect group, and most insect groups (tens of thousands!) have not yet been well enough studied to detect them. Every life cycle change that occurred within a temperate region could have involved allochronic speciation, and every pair of sibling species with different adult seasons and overwintering stages may properly

be suspected of having speciated allochronically.

Even geographic speciation can only be inferred in the vast majority of cases. As a consequence there will never be a successful argument against those who insist that no alternative is possible. It does not matter whether this insistence takes the form of a flat statement or simply the rejection of all alternative hypotheses through construction of a geographic one that is continually altered and defended as more likely in the face of contrary evidence. Speciation by other than geographic isolation may justifiably be inferred whenever sibling species are not geographically related in the ways common to sibling species, and when they simultaneously exhibit a striking ecological difference (such as a host difference or a life history difference) that effectively separates their adults and does not appear to have arisen through competition or other interaction between the species. Such facts are not only inconsistent with a geographic hypothesis, they may cause the necessity of accounting for a geographic difference to become an onerous complication. If, under the above conditions, an alternative to geographic speciation exists that is reasonable in its totality, based on the characteristics of the organisms under consideration, and if intermediate steps in such a presumed alternative process are found in natural populations, geographic speciation may become an extremely unlikely possibility.

In view of the importance of explaining rates and distribution of speciation, I think it will be unfortunate if attention to extrinsic temporal isolation is delayed by lumping it with some of the more outlandish attempts to explain speciation without extrinsic isolation of any kind, or discouraged by pronouncements deriving from previous arguments over the old specter of "sympatric speciation" in the sense of no extrinsic isolation. On the other hand, even if field crickets were so peculiar that allochronic speciation turned out to be trivially infrequent, I think we would still want to understand it in this case.

CONCLUSIONS

The literature on diapause and related phenomena in arthropods is massive (see reviews by Umeya, 1950; Masaki, 1963; Browning, 1952;

and Danilevskii, 1965). Relatively few studies, however, deal with life cycle variations within narrow taxonomic groups, their significance in relation to differences in habitats and geographic ranges, and the problems in accounting for their evolutionary origins. Ohmachi and Matsuura (1951), Fulton (1952), Walker (1963), Masaki and Ohmachi (1967), Pickford (1953), and Brooks (1958) are notable exceptions, with discussions of life cycle variations among closely related species of crickets and grasshoppers. Danilevskii (1965) has reviewed other studies of interest in this regard. However, Ghent and Wallace (1958), Bigelow (1958), Alexander and Bigelow (1960), Masaki (1961), and Masaki and Ohmachi (1967) seem to be the only investigators who have seriously endeavored to account for life cycle differences between closely related species. As already indicated, the conclusions of Ghent and Wallace (1958) and Masaki (1961) are strikingly similar to those of Bigelow (1958) and Alexander and Bigelow (1960), discussed and enlarged by Alexander (1963, and in the present paper).

It would seem that, except for analyses toward understanding of certain physiological mechanisms in a relatively few cases, we have really made only the barest start toward understanding the morphological, physiological, and behavioral complexities that selection has produced in different insects that live in different climates. Reasonable progress toward generalizations concerning adaptation to climate seems possible only if we keep in mind, on a larger scale than has been the case, that appropriate comparisons always involve not one but two kinds of variables: (1) climate and habitat (environment) and (2) phylogeny. We cannot hope to understand the significance of similarities and differences between species living in the same or different climates unless we know something about the similarities and differences in the equipment and way of life with which each began.

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A LIST OF CORRECTIONS AND EXPLANATORY NOTES

for the paper:

Alexander, Richard D. 1968. Life cycle origins, speciation, and related phenomena in crickets. Quart. Rev. Biol. 43(1):1-41.

p. 1. The number of "known" cricket species is optimistic, on the basis of published descriptions and recent arrangements of old names, partly because of undescribed species known to me and partly because my experience suggests that, accidentally or not, a higher proportion of the old names represent good species. It might have been better to date the Gryllidae to the Triassic Period.

p. 3, table 1. I should have used the common name "scaly crickets" for the Mogoplistinae.

p. 6, col. 2, l. 39. Ohmachi and Matsuura (1951) list cycles for several additional species in Japan. I am indebted to Sinzo Masaki for furnishing a translation of this almost unobtainable paper.

p. 7, fig. 4 caption, l. 6. Alabama, Georgia, and North Carolina . . .

p. 10, col. 2, l. 43-46. T. commodus may indeed be non-diapausing in the north (I heard several males singing on 16 July 1968 at Rockhampton, Queensland). T. commodus and T. oceanicus, however, cannot be considered members of the same species -- the latter simply a non-diapausing northern race -- for both species were singing in the same field at Rockhampton without evidence of interbreeding.

p. 21, fig. 10. The phrase "mostly interspecific" under "Hereditary variations" refers to most of the observed variations, and is not intended to imply that intraspecific hereditary variations in these regards are largely absent.

p. 24, col. 1, l. 39. A given area or habitat unit . . .

p. 25, fig. 12. The phrase "Most days and nights below 50°F." applies only to the period following September 27.

p. 35, fig. 15. In the figure itself "(a)" should apply to Scapsipedus aspersus and "(b)" to Gryllus fultoni, as can be discerned from the text.

p. 37, col. 2, last line. Angus Hull (not Hall).