

CHAPTER ONE

Natural History

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Crickets are among the insects that impose upon human consciousness without biting, stinging, or destroying. Because their songs are generally perceived as pleasant, they rank with butterflies and fireflies as insects to enjoy. The acoustic conspicuousness of crickets has also been important in their enjoyment by researchers in field and laboratory biology. Taxonomic, ecological, and behavioral studies of crickets have been prompted and made easier by the persistent, locatable, identifiable calls of the males. It is not surprising that most chapters in this volume present studies made possible or facilitated by the acoustic behavior of crickets.

Although crickets have long been known to biologists, the literature dealing with their natural history is varied and diffuse. Fragments are included in faunal works such as those of Chopard (1969), Matsuura (1976–83), and Otte and Alexander (1983). Life cycles have been reviewed by Alexander (1968a) and by Masaki and Walker (1987). B. B. Fulton (1915) wrote and beautifully illustrated a bulletin on the tree crickets (*Oecanthinae*) of New York. More recently, Walker (1984) produced a 54-page bulletin on Florida mole crickets (*Gryllotalpinae*). Furthermore, one-third of Gwynne and Morris's (1983) *Orthopteran Mating Systems* concerns crickets. These noteworthy concentrations of cricket lore do not alter the fact that most accumulated knowledge of cricket natural history is scattered thinly through entomological and biological journals.

This chapter presents aspects of the natural history of crickets that are not dealt with in later chapters and yet are important as background for all studies of crickets. Aspects of taxonomic and ecological diversity, zoogeography, and especially life cycles are included, together with aspects of dispersal and migration. Crickets are confronted with the tasks of finding food, partners, and oviposition sites. They have natural enemies, pathogens, and parasites to avoid or overcome. The ways that crickets cope with these problems are described. Finally, the cultural and eco-

nomic aspects of cricket natural history are considered. We begin by considering the diversity of crickets.

Diversity

Phylogeny

The more than 2,600 modern species of crickets are apparently descended from a common ancestral species that lived ca. 300 million years ago (Fig. 1.1). Sharov (1971) proposed that crickets originated when their immediate ancestors adapted to hiding under shelters; the posterior portions of the forewings became flattened over the somewhat flattened body, with the anterior portions retaining their primitive lateral positions. Because the lateral (anterior) portions of the forewings of the flattened protocricket were necessarily modest, the dorsal (posterior) portions (including the stridulatory areas) were dominant. The stridulatory areas of male forewings expanded, and the forewings themselves became shorter, exposing the tips of the folded hindwings in species that fly. Male forewings eventually became principally acoustic devices—as attested by the contrast in male and female forewings in all calling species and by the retention of forewings by males in many flightless species that have wingless females. The specializations of the male cricket's forewings permit them to vibrate in one principal mode at a time and at relatively low

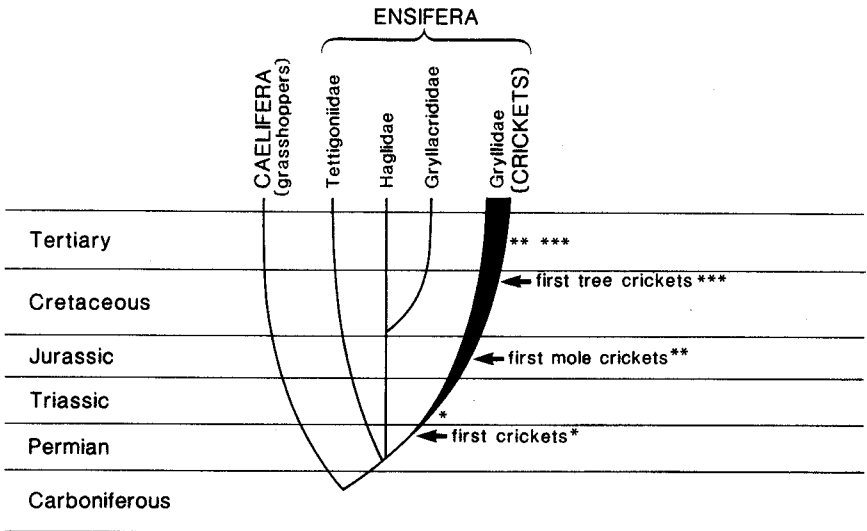


Fig. 1.1 Phylogenetic relationships of crickets and other Orthoptera. Arrows indicate probable times of origin based on fossils of presumptive ancestors; asterisks indicate the earliest fossils of crickets, mole crickets, and tree crickets. (Modified from Sharov 1971.)

frequencies (see chapter 8), making the songs of crickets more pleasing to human ears than the noisier or higher-pitched songs of their close relatives, the Tettigoniidae and Haglidae (Fig. 1.1).

Major Taxonomic Divisions

Cricket fossils are too few and too fragmentary to be of much help in understanding the diversification of crickets from their Permian beginnings, and no one has reconstructed cricket phylogeny on the basis of a thorough comparative study of modern species. Modern cricket species are traditionally placed in 12–14 major groups. Each of these groups is presumed to be monophyletic or paraphyletic (i.e., all included species are thought to have descended from a common ancestral species that was itself a member of the group), but some groups may be based on convergent similarities and hence be polyphyletic. The groups have been assigned to taxonomic categories ranging from tribes to superfamilies, and recent authors do not agree on what ranks the various groups should be assigned (and may not even use the same classification in successive publications) (e.g., Chopard 1967, 1968, 1969; Vickery 1977; Otte and Alexander 1983; Otte et al. 1987). The classification used here places all crickets in the family Gryllidae and divides them among 13 subfamilies (Fig. 1.2), varying in distinctness from Gryllotalpinae (mole crickets, often given family rank) to Nemobiinae (ground crickets, sometimes treated as a tribe of Gryllinae). This treatment has the advantage of making all major groups of crickets coordinate. When morphologically divergent groups are given family rank (e.g., Myrmecophilidae and Oecanthidae), it obscures the fact that they have their closest ties to particular groups not split off from the

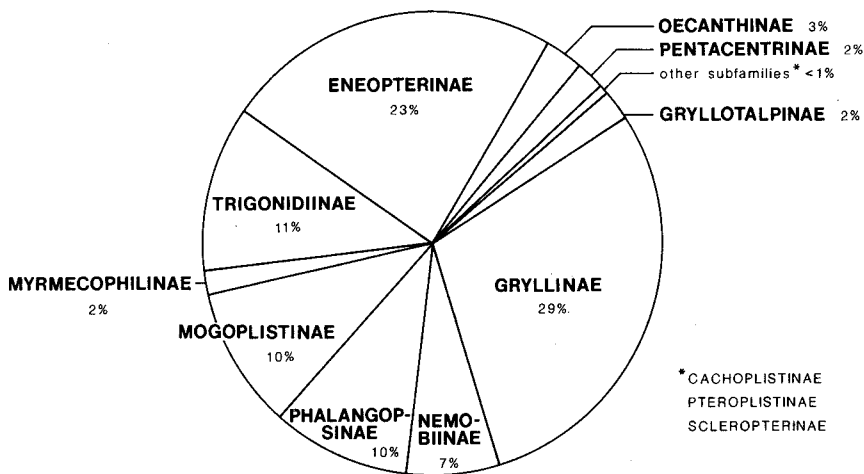


Fig. 1.2 Subfamilies of Gryllidae and relative numbers of species in each. (Based on 2,586 species listed in Chopard 1967, 1968; and Otte and Alexander 1983.)

parent family (in these two cases, Mogoplistinae and Eneopterinae, respectively).

Ecological Diversity

To an important degree, the subfamilies of crickets reflect an early radiation into a variety of habitats. Gryllotalpinae (mole crickets; Figs. 1.3 D, 1.15) are marvelously adapted to tunneling through soil. Gryllinae (field crickets and their relatives; Figs. 1.3 A, 1.10 A, D) live on the ground and amid rocks and often inhabit burrows or natural crevices. Nemobiinae (ground crickets; Fig. 1.3 E, F) are less robust than field crickets and generally are found on the ground, in surface litter, or along shorelines. Phalangopsinae (long-legged crickets; Fig. 1.3 B) sometimes congregate in crevices and caves and may forage on tree trunks and rock faces as well as on the ground. Some Mogoplistinae (scaly crickets; Figs. 1.3 K, 1.10 I) live on the ground or in leaf litter; others dwell on vegetation, traveling along leaves, stems, and vines; all are small and flightless. Myrmecophilinae (ant crickets; Figs. 1.3 L, 1.14) are inquilines with ants and termites. Trigoniidiinae (sword-tailed crickets; Figs. 1.3 G, 1.10 F–H) are small, vegetation-inhabiting crickets that have sword-shaped ovipositors for inserting eggs into plant tissue and adhesive tarsal pads for running upside down on leaves (see chapter 2, Fig. 2.10). Eneopterinae (bush crickets; Figs. 1.3 H, I, 1.10 L) also have noteworthy tarsal pads and mostly inhabit vegetation or leaf litter on the forest floor; they are more robust than the previous subfamily. Oecanthinae (tree crickets; Figs. 1.3 J, 1.4, 1.10 J, K) are slender, prognathous, somewhat predaceous, and inhabit herbaceous as well as woody vegetation. Habits of species in the remaining four subfamilies (Fig. 1.2) have seldom been reported. For example, the Cachoplistinae are large, hemipteranlike crickets (Fig. 1.3 C) known from northern India and perhaps Australia, but whether they live on the ground or high above it can only be guessed (Otte and Alexander 1983). One member of the Scleropterinae, *Scleropterus coriaceus*, lives on the ground or under litter in shrubby areas and deposits eggs in fallen dead stems of herbaceous plants (Yukinari Ban, personal communication, 1986).

Crickets are most diverse in the moist tropics; their range reaches its northern and southern limits at approximately 55° N and S latitudes (Alexander 1968a). They occur from more than a meter underground to the tops of the tallest trees. Some live in deserts. Many are associated with ponds and streams, where most live along the margins; others dwell on emergent rocks or aquatic plants, and some even skate gerridlike on the surface (Chopard 1938). Those that live near water may dive beneath the surface and remain hidden there for several minutes (Chopard 1938; Furukawa 1970). Mole crickets have a hydrofuge pile that enables them to survive in submerged soil for at least several hours and to swim on the surface for about 24 hours.

The largest crickets are thumb-sized mole crickets of the genus *Gryllotalpa* (up to 53 mm: Chopard 1969); the smallest adults are speck-sized, ant crickets (*Myrmecophilus*, as small as 1.47 mm: Hebard 1920) (see Fig. 1.14).

Zoogeography

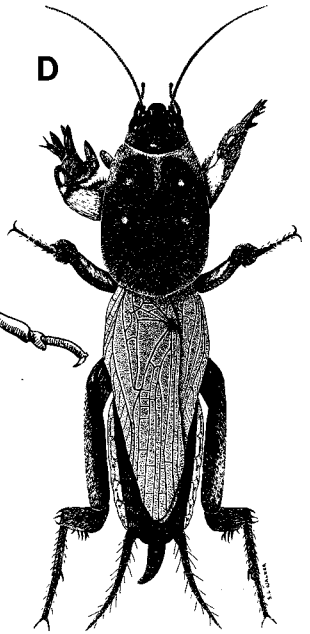
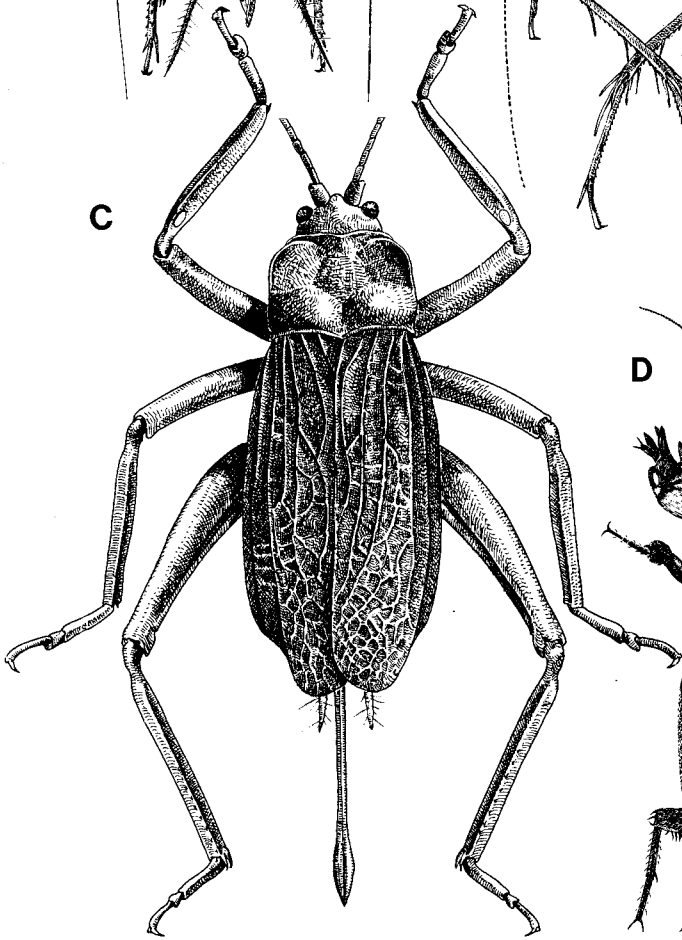
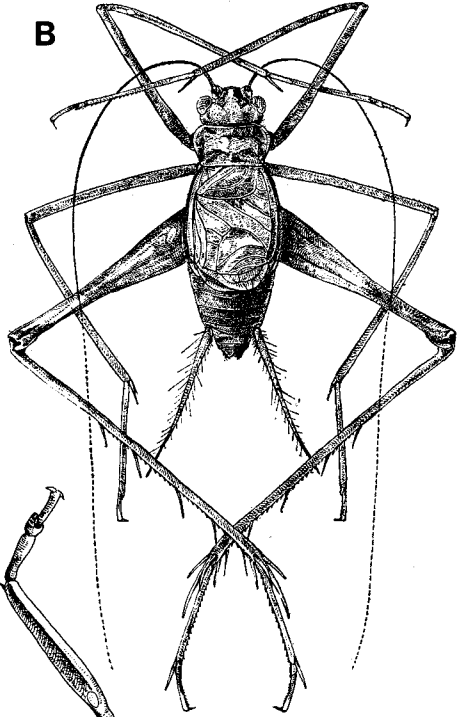
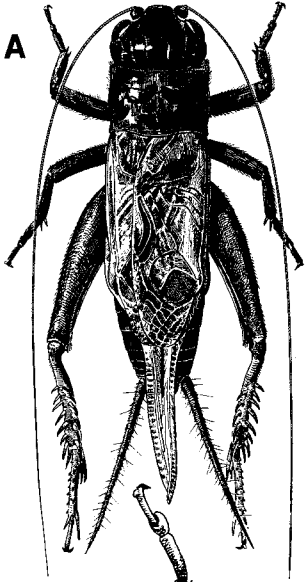
The early radiation of crickets is witnessed by their major groups being well represented in all tropical faunal regions (Neotropical and Australian as well as Oriental and Ethiopian). Indeed, the only exceptions to the generalization that all the larger subfamilies occur in every zoogeographical region are that the phalangopsines are missing from the Holarctic and that no pentacentrines are in the Palearctic.

Cricket faunas are generally poorly known; consequently, they do not often contribute to zoogeographical studies. Their potential, however, is great, as illustrated by what is known of the crickets of the Hawaiian Islands (Zimmerman 1948; Gurney and Rentz 1978; Otte and Rice 1989). The Hawaiian Islands are more isolated than any other archipelago. Their native birds and drosophilids are classic examples of the principle that groups of oceanic islands provide a stage for rampant adaptive radiation by the few species that manage to reach them. The native Hawaiian cricket fauna can be cited as yet another example of that principle. Otte and Rice (1989) concluded that the number of cricket species in the Hawaiian Islands is greater than in the rest of the United States combined.

The 38 species already described are placed in five genera and may have descended from as few as three founding species: an oecanthine, a trigonidiine, and a nemobiine. The oecanthine gave rise to the endemic tribe Prognathogryllini, which has 18 described species in three genera—including in addition to acoustic, foliage-dwelling species (Fig. 1.10 J, K)—13 mute species and one cavernicole that lives in lava tubes. The trigonidiine gave rise to 16 described species presently placed in the genus *Paratrigonidium* (not an endemic genus, but the Hawaiian species are atypical). Hawaiian *Paratrigonidium* are diverse, with species adapted to living on the ground, under bark, and on foliage; some are host-specific on one kind of fern, shrub, or tree. Finally, there is the endemic genus *Caconemobius*, which apparently evolved from a colonizing nemobiine (Gurney and Rentz 1978). It has two species that live on the surface and two that live underground in lava tubes. All are wingless and mute, and the cavernicolous species are pale and have reduced eyes.

Taxonomic Opportunities

Crickets are among the few insect groups that can be identified to species, meters away, in the field. Males of most cricket species advertise to females with a distinctive call, enabling cricket females to find appropriate males and biologists to learn what species occur in an area. Easy identification of species in the field makes crickets of special value to systematists (as well as to ecologists and behaviorists). By tuning in to cricket calls, a systematist can discover morphologically poorly defined species (= *sibling species*), discover rare or hard-to-collect species, and easily and accurately map geographical and ecological distributions. These advantages also accrue to those studying cicadas (Cicadidae) and katydids (Tettigoniidae), but crickets are more diverse and more tractable to rearing. The latter fact is important when controlled comparisons of



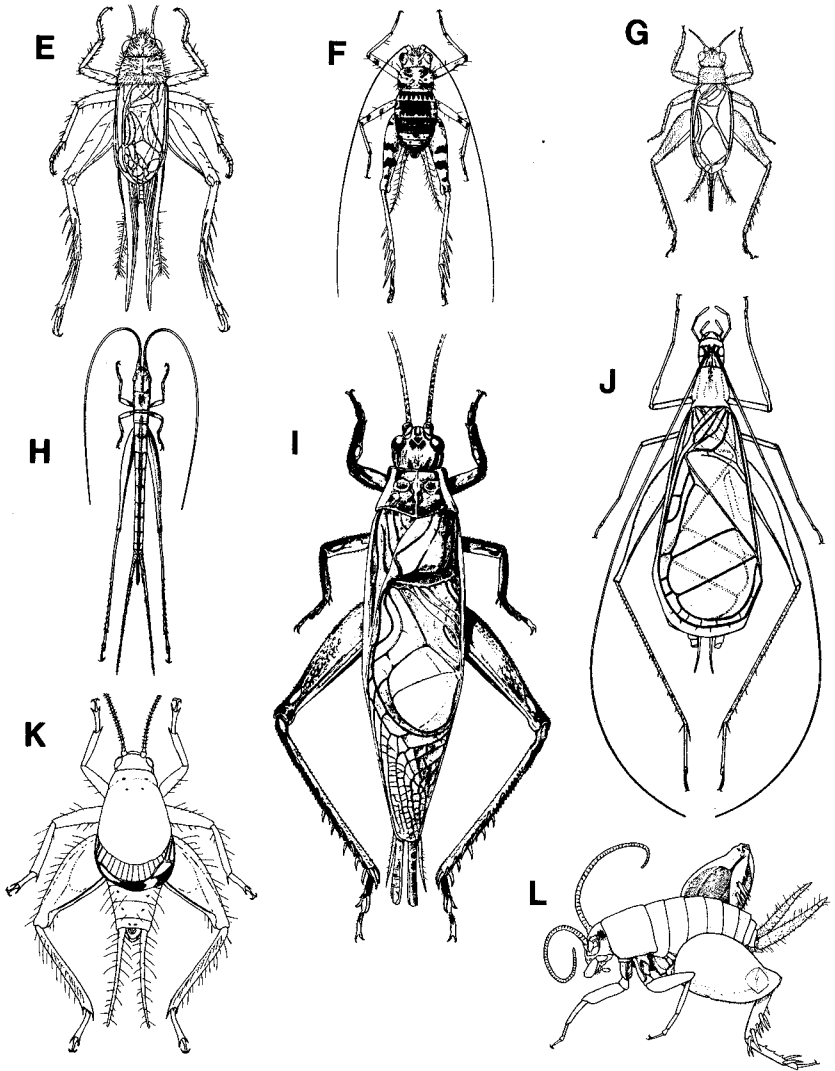


Fig. 1.3 Morphological diversity among crickets. A, *Teleogryllus commodus* male (Gryllinae). B, *Parendacustes pictipes* male (Phalangopsinae). C, *Cachoplistus brunnerianus* female (Cachoplistinae). D, *Scapteriscus acletus* male (Gryllotalpinae). E, *Allonemobius allardi* male (Nemobiinae). F, *Apteronemobius darwini* male (Nemobiinae). G, *Cyrtoxipha columbiana* male (Trigonidiinae). H, *Burrianus pachyceros* male (Eneopterinae). I, *Madasumma affinis* male (Eneopterinae). J, *Oecanthus latipennis* male (Oecanthinae). K, *Cycloptilum bidens* male (Mogoplistinae). L, *Myrmecophilus pergandei* male (Myrmecophilinae). A–J, $\times 2$; K, $\times 4$; L, $\times 8$. (A, C, F, and I from Otte and Alexander 1983; B from Chopard 1969; D courtesy of S. L. Walker; E from Alexander et al. 1972, courtesy of *Great Lakes Entomologist*; H from Chopard 1961; J from Fulton 1915.)

geographically or seasonally isolated populations are desired or when studies of genetics or physiology are needed to test taxonomic hypotheses.

Sibling species. B. B. Fulton (1932) was the first to use cricket songs extensively in distinguishing species, and he found numerous instances of a supposed species producing more than one calling song. For example, he recognized four songs of "*Gryllus assimilis*" in North Carolina and showed that populations producing the four songs had different seasonal life cycles, occurred in different (though overlapping) habitats, and were reproductively incompatible in laboratory crosses (Fulton 1952). Subsequent studies of "*G. assimilis*" in the eastern United States proved the existence of at least eight cryptic species—including two that have indistinguishable songs but are seasonally separated (Alexander and Bigelow 1960) and one that has no calling song (Walker 1974). (The latter two cases illustrate that acoustic studies do not identify all sibling species of crickets.) Once the species of *Gryllus* in the eastern United States were recognized on the basis of song or life cycle, most proved identifiable by conventional morphological features or by the number and spacing of teeth in the stridulatory file (Alexander 1957; Alexander and Walker 1962, Nickle and Walker 1974). The species had not been distinguished in earlier studies of museum specimens because distinguishing species within a group of specimens containing an unknown number of species is far more difficult than finding differences between groups of specimens already known to represent species. A similar series of events occurred with "*Teleogryllus mitratus*," which are *Gryllus*-like Japanese field crickets. Differences in calling songs led Ohmachi and Matsuura (1951) to distinguish three species that subsequently proved different in color pattern, ovipositor length, and karyotype.

Modern recording and analyzing devices have made it much easier to study cricket calls, and sibling species have been recognized by song in practically every group of crickets in which the acoustics have been studied—for example, field crickets in Australia (Leroy 1965), field crickets in Japan (Matsuura 1977, 1978a, 1978b), mole crickets in France (Bennet-Clark 1970a), and ground crickets and scaly crickets in the United States (Alexander and Thomas 1959, Love and Walker 1979).

Sibling species seem unusually numerous in crickets, but they may be no more frequent than in other insects—just easier to detect (Walker 1964b). As Henry (1985) proposed, acoustic signaling to form sexual pairs may be conducive to speciation because once populations diverge in calling song they can remain reproductively isolated even if, in other respects, they are remarkably similar. However, the fact that some sibling species of crickets lack distinctive songs and have been recognized through studies of life cycles or allozymes strengthens the notion that sibling cricket species would be frequent even if crickets were mute (e.g., Alexander and Bigelow 1960, Howard 1983, Masaki 1983).

Faunal studies. Otte and Alexander's (1983) monograph on Australian crickets amply illustrates the effectiveness of using cricket songs to facilitate a faunal study. Of the 376 species not recognized previously, about 250 were first recognized by song during a single year of fieldwork. On a lesser scale, but perhaps as impressive because the cricket fauna already had been studied intensively, the number of species known in the eastern United States increased from 55 to 91 during 1957 to 1987—largely as a result of using acoustic clues to find new species. Other species already identified but not yet described will bring the number of species to 103, nearly twice the 55 known in 1956 (T. J. Walker, unpublished). Otte and Cade's (1984) studies of African Gryllinae, and the study of New Caledonian crickets (Otte et al. 1987) are other examples of how cricket calls make fieldwork more profitable and the recognition of species easier.

Hybrid zones. Much of the special lure of crickets as exemplars for systematics, ecology, and biogeography flows from the fact that species can generally be recognized in the field by the songs of the males. Hybrids between cricket species generally have calling songs intermediate between the songs of the parent species (Alexander 1968b, Doherty and Hoy 1985, Inagaki and Matsuura 1985). Since these intermediate songs are usually unique, they offer the opportunity of acoustically detecting hybridization in the field even though adult hybrid males are extremely rare. Surprisingly, the only hybrid zones yet described for crickets were discovered and mapped by electrophoretic analyses, and the acoustic concomitants have not been reported (*Gryllus firmus* and *pennsylvanicus*: Harrison and Arnold 1982, Harrison 1985; *Allonemobius fasciatus* and *socius*: Howard 1986). In contrast, intermediate calling songs have been used to detect and study hybrid zones in katydids (Alexander 1968b), cicadas (Lane 1984), and frogs (Littlejohn and Watson 1985).

Development and Life Cycles

Crickets are nearly as diverse in their life cycles as they are in their external appearance, but the two types of diversity are largely independent. Similar suites of life cycles occur in different phyletic lines both between and within subfamilies, making crickets of special value in studying the evolution of life cycles (Masaki and Walker 1987).

Egg Stage

Although development within the egg involves more morphological change than does subsequent metamorphosis, it requires no material input other than water and oxygen. The water that cricket eggs must absorb before completing their development amounts to 60–120% of the weight of newly laid eggs. This requirement places an important restraint on where crickets can lay their eggs, because the site must provide moisture to the eggs at some stage of their development. The stage at which the

eggs absorb water ranges from yolk cleavage to postdiapause embryological stages (Masaki and Walker 1987).

Metamorphosis

Crickets, like other insects with gradual metamorphosis, develop from hatchlings to adults via a series of instars that are progressively more like the adult (Fig. 1.4). The number of molts (i.e., number of instars, since each instar ends with a molt) has been reported for only about 30 species in six subfamilies (Masaki and Walker 1987), making generalization risky.

The number of molts in crickets ranges from 5 to 14. Nineteen of the species studied belong to two subfamilies of thickset, ground-dwelling crickets that have an indeterminate number of molts. Among nemobiines (5 species) 6–12 molts have been reported and among gryllines (14 species), 5–14. Number of molts may vary from 5 to 13 within a single species (*Gryllus* sp.) (Fuzeau-Braesch 1975). The only other subfamily in which several species have been studied is Oecanthinae, which are slender, plant-dwelling crickets. Fulton (1915) investigated six species and found all to have five molts (e.g., *Oecanthus fultoni*; Fig. 1.4).

For those crickets that have a variable number of molts, the realized number is usually less when development is faster. For example, *Gryllus bimaculatus* required an average of 117 days and 10 instars to reach adulthood on a low-protein diet and 55 days and 8 instars on a high-protein diet (29°C day, 11°C night; 16:8 LD photoperiod) (Merkel 1977). The mean number of days between molts, another index of speed of development, was 12 for the low- and 7 for the high-protein diet. For a given diet the number of instars (as well as number of days per instar) was less at higher temperatures. Tanaka (1979) counted instars of *Pteronemobius nitidus*, a cricket that, before reaching the diapause instar, develops faster in short than in long photoperiods (within an ecologically realistic range). At 28°C, the median number of instars was 8 at 12:12 LD and 10 at 15:9 LD (Fig. 1.5).

In most crickets the last two instars can be recognized by their conspicuous, dorsally visible, posteriorly directed wing pads. (In the preceding instar the pads are tiny, cannot be seen from above, and point downward.) In the penultimate instar the mesothoracic pads are usually well separated dorsally, while in the ultimate instar they are nearly touching. Rarely three molts (instead of two) follow the reversion of the wing pads. The sexes commonly can be distinguished as early as the middle instars, when developing ovipositor values of females become apparent (Fig. 1.4).

In all crickets except mole crickets, the tibial tympana become evident only at the final molt (see chapter 13). In mole crickets the tympana are well developed by the second instar (of nine or more) (B. Lenczewski, personal communication, 1987).

Voltinism and Diapause

Seasonal versus aseasonal life cycles. Theory and available evidence support the generalization that species living in aseasonal habitats, such

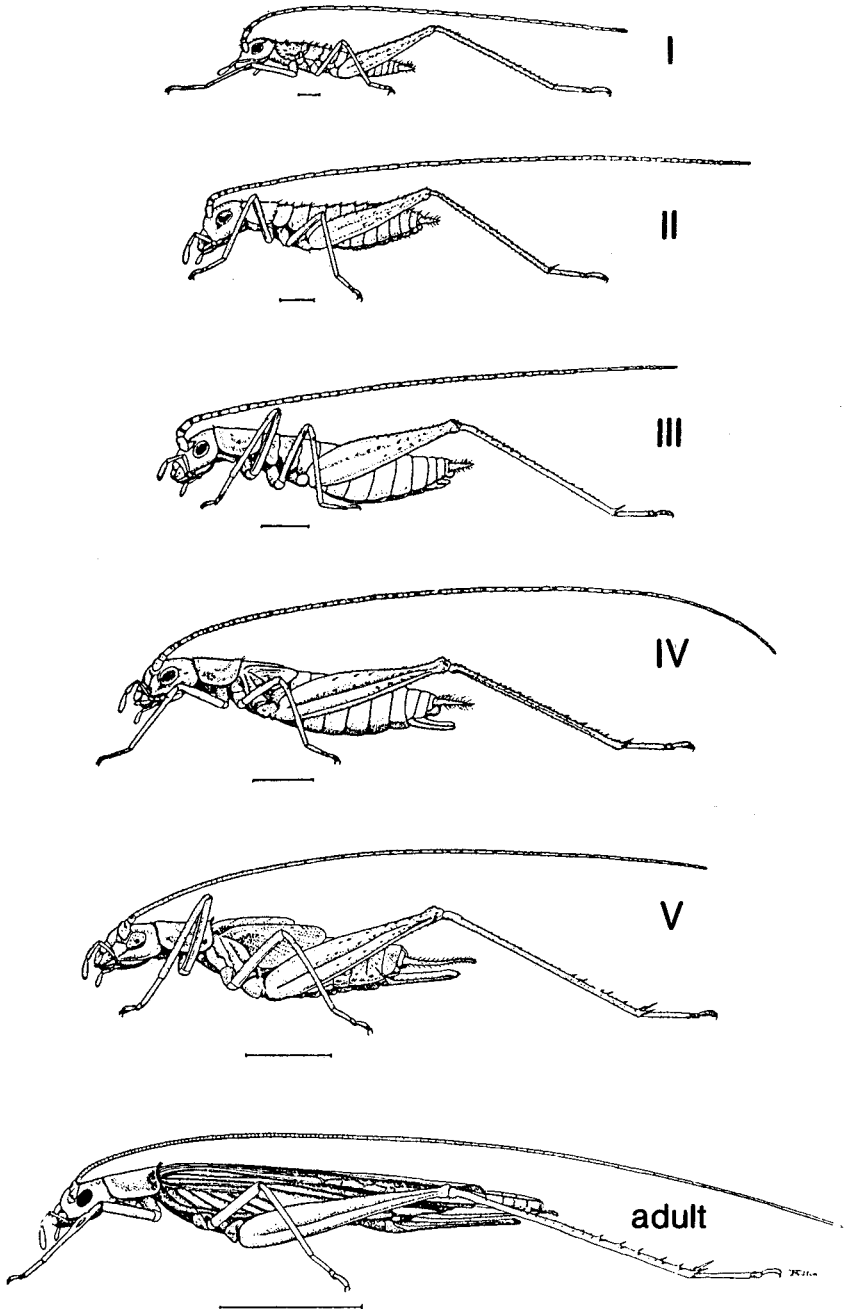


Fig. 1.4 Metamorphosis in *Oecanthus fultoni*. Instars I–V and adult female. Line beneath each drawing is proportional to body length. Line for instar I equals 3 mm; for adult, 19 mm. (From Fulton 1915.)

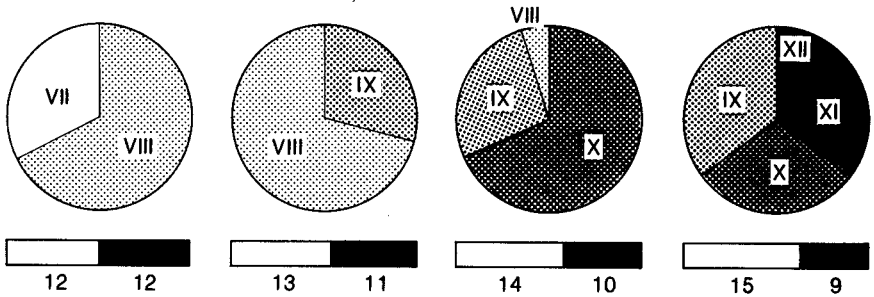


Fig. 1.5 Effect of photoperiod on how many instars occur in *Pteronemobius fasciatus* reared at 28°C. Each circle shows the relative frequency of different numbers of instars required to reach adulthood (among the approximately 30 individuals reared in the photoperiod indicated by the bar beneath). Numbers of instars range from 7 to 12; photoperiods from 12:12LD to 15:9LD. (Modified from Tanaka 1979.)

as caves and the moist tropics, reproduce and develop continuously or nearly so. All life stages occur at all times of year, and there is no synchrony of generations. In seasonal habitats, on the other hand, life cycles take advantage of seasons favorable for development and reproduction and accommodate to unfavorable ones. For example, in temperate climates, each species has one or a very few life stages specialized for surviving the cold season, and life cycles adjust to assure that these stages are the ones likely to be present when winter comes. Winters and, presumably, tropical dry seasons have a synchronizing effect on cricket life cycles, resulting in generations that are discrete enough to count.

Temperate life cycles. In temperate climates, life cycles of crickets may be conveniently classified by overwintering stage and number of generations per year (Masaki and Walker 1987) (Fig. 1.6 A–F). Most temperate species of crickets overwinter as eggs, some overwinter as mid to late juveniles, and a few overwinter as adults. Most have one generation annually (i.e., are univoltine); but some are bivoltine, and a very few are semivoltine. Semivoltine species overwinter one winter as juveniles and the other as either adults or eggs. North of 30° latitude in Japan and eastern North America, approximately 75% of cricket species are univoltine, 22% are bivoltine, and 3% are semivoltine. Of 87 bivoltine and univoltine species studied, about 80% overwinter as eggs and 20% as juveniles. The percentage of species that overwinter as nymphs decreases poleward (Masaki and Walker 1987).

Environmental cues. As in other insects (Tauber et al. 1986), seasonality in crickets is controlled by physiological mechanisms that take their principal cues from seasonal changes in photoperiod and temperature. In egg-overwintering species, there is generally a physiological block at some

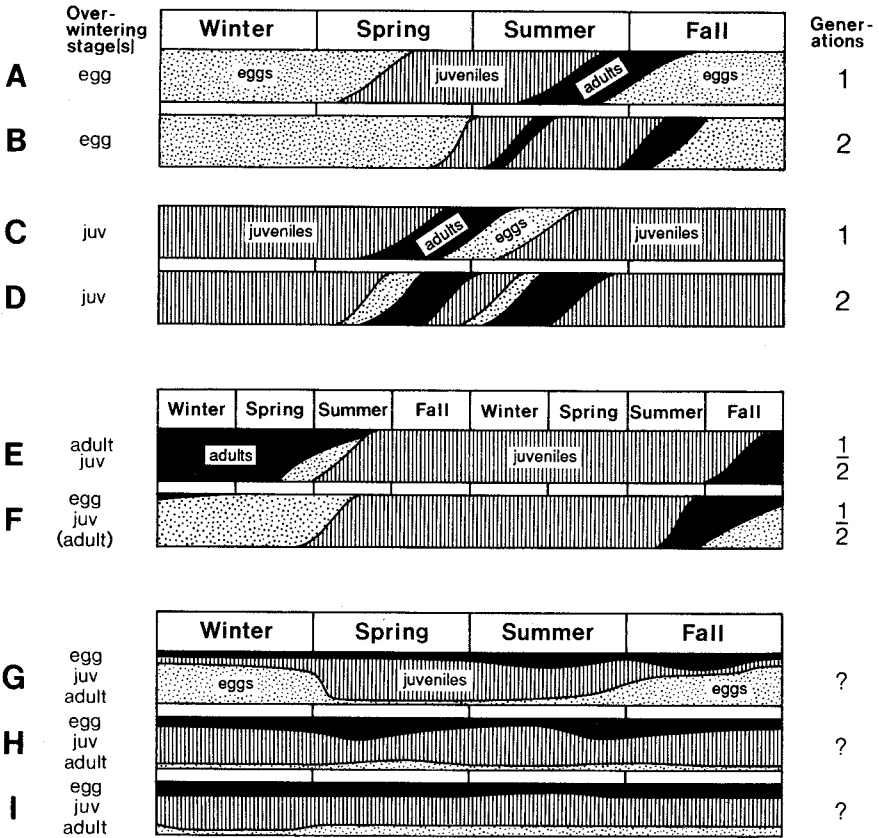


Fig. 1.6 Life cycles of crickets. A–D, Common cycles in temperate latitudes classified by overwintering stage and voltinism. E, F, Semivoltine cycles. G–I, Cycles in subtropical and tropical climates. Exemplars (references in Masaki and Walker 1987 unless otherwise indicated): A, *Gryllus pennsylvanicus*, *Oecanthus nigricornis*; B, *Dianemobius mikado* (southern), *Oecanthus celerinctus*; C, *Gryllus campestris*, *Pteronemobius nitidus*; D, *Gryllus rubens*, *Teleogryllus occipitalis*; E, *Gryllotalpa africana*, *Neocurtilla hexadactyla* (South Carolina: Semlitsch 1986); F, *Nemobius sylvestris* (England); G, *Gryllus firmus* (Florida: T. J. Walker, unpublished); H, *Gryllus rubens* (Florida: T. J. Walker, unpublished); I, *Scapteriscus abbreviatus* (Florida: K. O. Lawrence and J. L. Castner, personal communication, 1986).

specific embryological stage which prevents the eggs from hatching during warm spells in fall. These eggs are said to be in *diapause*, and they do not resume development until diapause has been eliminated by time and/or exposure to certain temperatures (Fig. 1.7). In univoltine egg-overwintering species, all eggs undergo diapause; but in bivoltine species, summer eggs that produce fall adults hatch without delay. For summer and fall eggs to have different developmental programs requires a sen-

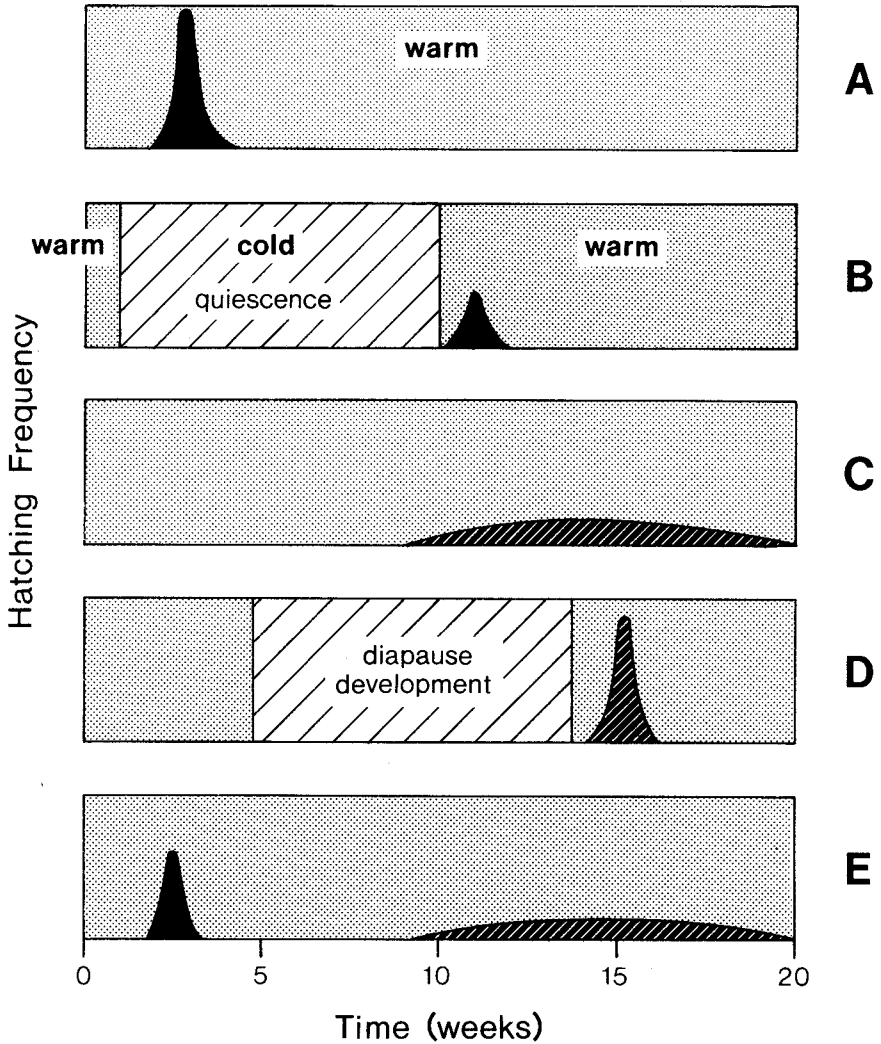


Fig. 1.7 Hatching patterns of cricket eggs. A, Nondiapaue eggs, continually warm. B, Nondiapaue eggs, hatching delayed by cold weather (as long as 14 weeks in *Gryllus rubens*). In most cases nondiapaue eggs probably cannot survive prolonged cold-arrested development. C, Diapause eggs, continually warm (as in laboratory). D, Diapause eggs, first warm, then cold, then warm (as in fall-laid eggs in temperate climates). E, Mixture of diapause and nondiapaue eggs, continually warm (as laid by most *Gryllus firmus* females in Gainesville, Florida, at most times of the year). Exemplars: C, D, Masaki et al. 1979; A, C, E, Walker 1980a; B, T. J. Walker, unpublished.

sitivity to environmental cues. In *Dianemobius nigrofasciatus*, one of the few species in which bivoltine egg-overwintering populations have been investigated, females exposed to long days (summer photoperiods) lay nondiapauses eggs, and those exposed to short days (fall photoperiods) lay diapause eggs. If temperatures are high (e.g., 30°C), even fall eggs may avert diapause—both because the female developing the eggs responds in that manner and because the eggs (embryos) themselves switch to a non-diapause state (Kidokoro and Masaki 1978).

Egg diapause in *Allonemobius fasciatus* is unusually complex and gives clues to how crickets in warm climates may survive unfavorably hot, dry seasons. Tanaka (1984) studied a population of *A. fasciatus* that was univoltine and egg-overwintering but that occurred at a latitude low enough for adults to mature as early as late July. Eggs of early-maturing adults had a summer diapause at an early embryological stage and developed to a later, winter diapause stage when temperatures decreased. Eggs of late-maturing (fall) adults developed directly to the winter diapause stage. Alternative paths of egg development were, to some extent, controlled by temperature: high temperatures (27° or 30°C) promoted summer diapause, and low temperatures (20°C) promoted development directly to winter diapause. However, eggs laid later in the season were increasingly unsusceptible to high-temperature-induced delay in early embryological development. Furthermore, the later the eggs were laid, the less intense was winter diapause. Each of these varied responses is appropriate to maintaining a univoltine, egg-overwintering life cycle.

In univoltine egg-overwintering species summer photoperiods may delay and fall photoperiods may speed maturation of juveniles, resulting in adults emerging nearly synchronously in the fall and in all eggs needing to maintain diapause through only a relatively short period prior to winter.

Juvenile-overwintering species have juvenile diapause. As in embryonic diapause, species generally undergo diapause at a particular stage. For juvenile overwinterers, this stage is always a mid or late instar and is often the penultimate instar. The mechanisms that synchronize the life cycles with the seasons are similar to those for egg overwinterers. For example, in univoltine juvenile-overwintering species such as *Gryllus campestris* and *Pteronemobius nitidus* long days prolong, and short days speed, development to the diapause instar. Once the diapause stage has been reached, however, the response is reversed: long days terminate and short days maintain diapause (Tanaka 1978).

Natural photoperiods are always changing, and increasing or decreasing photoperiods may be more effective in averting or promoting diapause than constant ones. Such effects have been demonstrated in crickets, but interpretation is made difficult by the exclusive use of unnatural photoperiodic and thermal regimes (e.g., Beck 1983).

Latitudinal transitions in voltinism. Within the temperate zones, the time available for development (roughly equivalent to the frost-free or

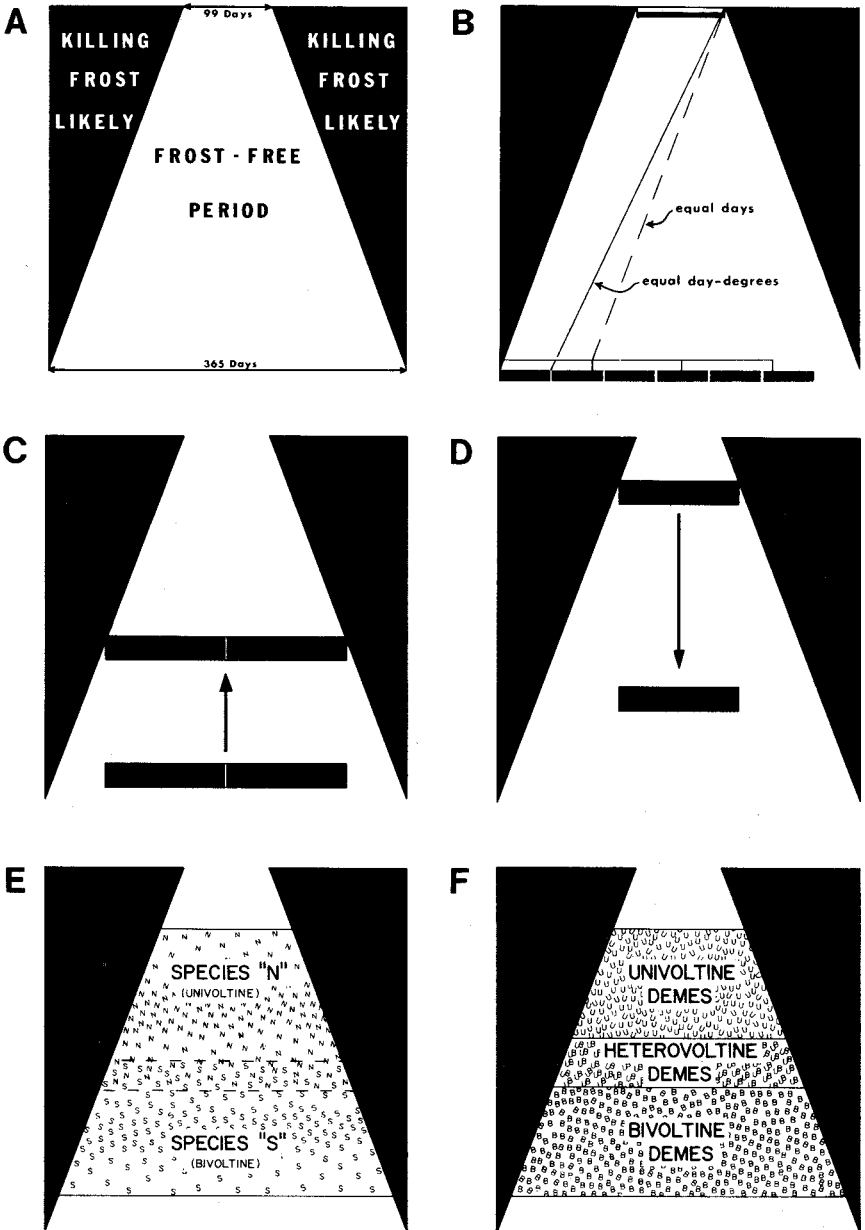


Fig. 1.8 Latitudinal effects on life cycles of temperate zone crickets. A, Increase in frost-free period across 23° latitude, from northern Minnesota (99 days) to southern Florida. B, Potential latitudinal effects on cricket voltinism, expressed as increased growing period and increased day-degrees. Frost-free time increases threefold; day-degrees increase sixfold. C, Species may be bivoltine at the poleward extreme of their latitudinal range (e.g., *Gryllus rubens*, *Velarifictorus parvus*).

“growing” period) gradually increases as the range approaches the equator (Fig. 1.8 A). In the United States, for example, the average frost-free period varies from 100 days in northern Minnesota to 365 days in the Florida Keys, a latitudinal range of 23° . A cricket species that has time for one generation in the north has twice as much time in the central states and three times as much in the southern ones. Actually the latitudinal effect on developmental opportunity is much greater than the effect on growing period. Southern growing periods are not only longer, they are hotter. If one compares day-degrees during the frost-free period in Minnesota with those in Florida, the “generation multiplier” approximates six rather than three (Fig. 1.8 B). If day-degrees were the sole determinant of voltinism in crickets, one would expect crickets with a latitudinal range of 5° or more to show a transition in voltinism—or at least to have the ecological opportunity to do so. Day-degrees are not the sole determinant, but they should be a major one. Crickets, unlike many other insects, do not generally depend on seasonally limited food for their development. Contrary to expectation, latitudinal changes in voltinism in temperate crickets are few. Of 60 species that have a latitudinal range of $5\text{--}14^\circ$ in Japan and the eastern United States, only nine change their annual number of generations (Masaki and Walker 1987). (Species that range 15° or more in latitude are more likely to change; 14 of 19 species do so.) The conservatism of cricket life cycles is well illustrated by six species that are bivoltine to the northern limits of their distributions (Fig. 1.8 C) and by five species that remain univoltine over a latitudinal range of 15° or more (Fig. 1.8 D).

Univoltine and bivoltine life cycles predominate in cricket species in temperate climates. The transition from uni- to bivoltine life cycles in a given species is interesting because it is so rare, and it warrants further study. The 17 apparent instances in Japan and the eastern United States might give clues to the causes of the rarity, but, unfortunately, no case has been exhaustively analyzed. In fact, circumstantial evidence suggests that there are actually fewer than 17 cases of transition. In two instances in the eastern United States, southern bivoltine populations that were believed conspecific with northern univoltine populations proved to be specifically distinct when more carefully studied, and what would have been considered a zone of voltinism transition proved instead to be a zone of species overlap (Fig. 1.8 E). Future studies may reveal that other presumptive cases of transition are, instead, pairs of sibling species.

Fig. 1.8 (continued)

D, Species may remain univoltine over latitudinal ranges exceeding 14° (e.g., *Anurogryllus arboreus*, *Teleogryllus emma*). E, Northern univoltine and southern bivoltine populations may belong to sibling species with overlapping ranges (e.g., *Orocharis saltator* and *O. luteolira*; *Oecanthus nigricornis* and *O. celerinictus*). F, A species that is univoltine in the north and bivoltine in the south may be heterovoltine (i.e., have a mixture of life-cycle types) in the transition zone (e.g., *Dianemobius nigrofasciatus*).

In cases where the transition is real, the zone of transition is also a zone of disruptive selection. At transitional latitudes, individuals that exhibit univoltine life cycles should benefit from developing more slowly and becoming larger, whereas those that exhibit bivoltine life cycles are in danger of not reaching the diapause stage by fall unless they develop, on average, nearly twice as fast as their univoltine conspecifics. One effect of this disruptive selection could be speciation (Masaki 1973, White 1978). This type of speciation might be a source of univoltine/bivoltine sibling pairs (Fig. 1.8 E), but such pairs could also evolve through divergence, in life cycle, of geographically isolated northern and southern (univoltine) populations.

Disruptive selection in transition zones can also lead to stable polymorphism (Fig. 1.8 F). *Dianemobius nigrofasciatus*, the only cricket whose life cycle has been studied in a zone of transition between univoltine and bivoltine life cycles, is probably stably dimorphic in photoperiodic control of development rates (Kidokoro and Masaki 1978). Laboratory studies of crickets from the transition zone, and hybridization of crickets from that zone with crickets from a univoltine area, support the conclusion that individuals from the transition zone are conspecific but respond to photoperiod in ways that lead either to two quick generations or to one prolonged one. This apparent dimorphism in life-cycle type has many parallels with the more easily documented dimorphism in wing length discussed in Dispersal and Migration, below.

A population in which members undergo variable numbers of generations in a year is *heterovoltine*, in contrast to *homovoltine* populations, which have an invariable number (Jackson and Peters 1963). Heterovoltinism has the effect of preventing some members of a population from all having the same ill-adapted life cycle in a growing period that is unusually short and cool or unusually long and warm. Possible genetic bases for risk-spreading dimorphism are discussed by Walker (1986a, 1987b).

The discussion above focused on the univoltine/bivoltine transition. Masaki (1978) and Masaki and Walker (1987) advanced similar ideas in relation to the transition from a heterovoltine subtropical, nearly aseasonal, juvenile-overwintering life cycle to a bivoltine egg-overwintering life cycle.

Latitudinal clines and seasonal trends in adult size. One effect of the conservatism of crickets in changing their number of generations is prolonged north/south clines in adult size (Fig. 1.9 A). As the range of a species that maintains a univoltine life cycle approaches the poles, developing individuals have less time to garner resources and to reach the diapause stage; conversely, as the range approaches the equator, they have more time. Since large females are more fecund than small ones, females should use extra time to become larger, other things being equal. Clines in adult size are accompanied by clines in developmental and diapause characteristics (Masaki 1967).

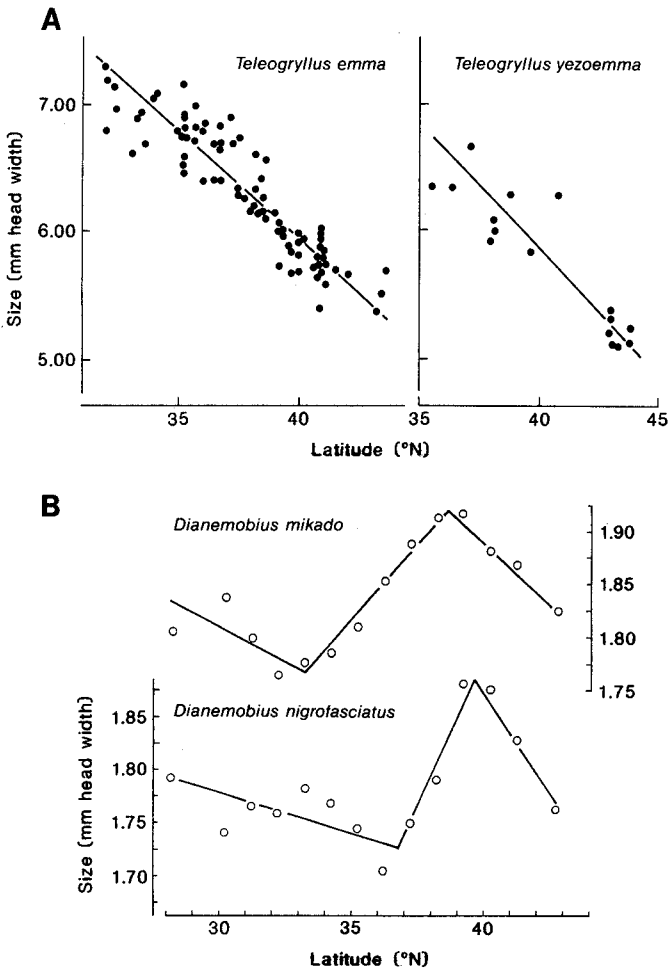


Fig. 1.9 Latitudinal clines in size of adult crickets. A, Two univoltine species. B, Two species that are bivoltine in the south and univoltine in the north; direction of clines at 35–40° is temporarily reversed in zone of voltinism transition. These are Japanese egg-overwintering species. Measurements were of head width) of female fall adults; measurements in A corrected for regression on altitude; those in B based on specimens collected at < 150 m altitude. (From Masaki and Walker 1987, courtesy of *Evolutionary Biology*.)

When a species with a wide latitudinal range shows a transition in voltinism, the direction of the cline in adult size should be temporarily reversed, resulting in a “sawtooth” pattern. Masaki (1978) documented such a pattern for *Dianemobius mikado* and *D. nigrofasciatus* (Fig. 1.9 B).

The latitudinal clines in adult size of univoltine crickets have a seasonal parallel. As the adult season progresses, the costs to an individual that

delays its final molt to become a larger adult become greater than the benefits. Consequently, adults that mature late in the reproductive season should be smaller than those that mature early. In *Scapteriscus acletus* egg laying occurs in April through June, but adults mature as early as September of the previous year. Fall-maturing males average 9.4 mm in pronotal length (\approx 740 mg). In the spring this dimension gradually declines to 8.5 mm (\approx 580 mg). Females show similar trends (Forrest 1987).

Dispersal and Migration

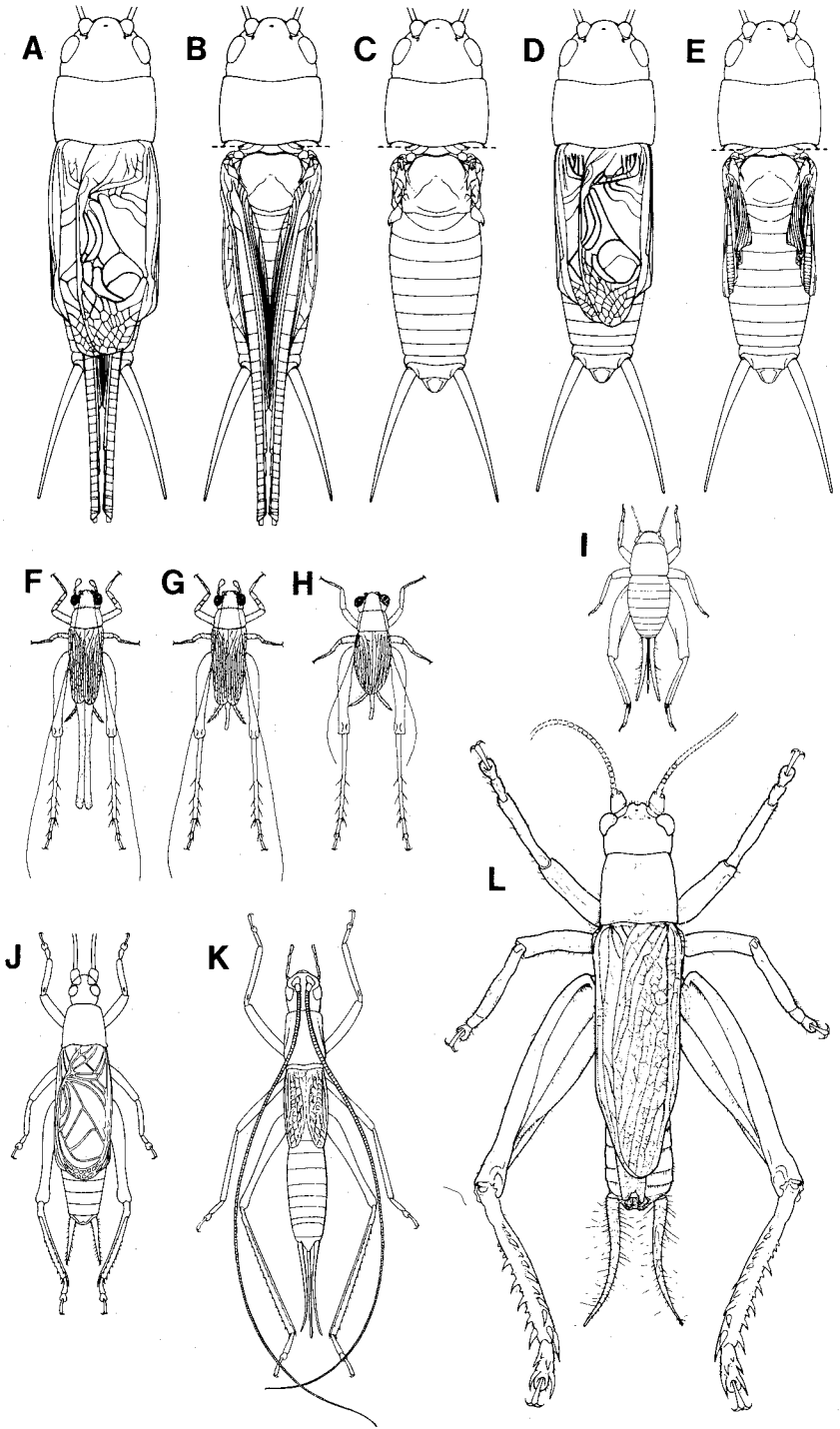
Moving about to find food and mates is essential in all cricket life cycles; and, for species that live in transient habitats, individuals must move to new habitats, at least in some generations. Adopting a distinction made by Southwood (1962), we distinguish interhabitat movements as *migratory* and locomotion within a habitat as *local*. For local movements, adult and juvenile crickets generally walk (see chapter 5). Adults of tree-dwelling species are more likely to use flight for local movements than are those of ground-dwelling species (Waloff 1983). Most migration is by flight, but the fact that flightless species also colonize newly available habitats shows that some interhabitat movement is by other means. For example, Simberloff and Wilson (1969) reported that flightless crickets (*Cycloptilum* spp.) colonized experimentally defaunated red mangrove islands. Rafting, swimming, "ballooning," or phoresy seem the major possibilities; and none can be excluded.

Wings and Winglessness

Most crickets, like other Orthoptera, have two pairs of wings, with the mesothoracic wings (forewings or *tegmina*) somewhat thickened and providing some protection for the membranes metathoracic wings, which are the principal organs of flight. The metathoracic wings are folded fanlike at rest (Fig. 1.10 B).

All crickets seem to have evolved from a Permian species that had hindwings specialized for flying and male forewings specialized for call-

Fig. 1.10 Wings in crickets. A–E, *Gryllus rubens*: A, long-winged male; B, long-winged male with tegmina (forewings) removed; C, long-winged male artificially dealated by tugging on hindwings; D, short-winged male; E, short-winged male with tegmina removed. F–H, *Trigonidium cicindeloides*: F, long-winged female (note tibial tympana); G, dealated long-winged female (note tibial tympana); H, short-winged female (no tibial tympana). I, *Cycloptilum bidens* female (no wings; see Fig. 1.3 K for male). J, K, *Prognathogryllus oahuensis*: J, male with acoustic tegmina; K, female with vestigial tegmina. L, *Tafalisca lurida* male (tegmina not acoustic). (F–H from Ingrisch 1977, courtesy of S. Ingrisch; J courtesy of D. Otte; K modified from *Insects of Hawaii*, vol. 2, by E. C. Zimmerman, © 1948, University of Hawaii Press.)



ing. Many recent species have both specializations, but flying and calling have been lost many times, both independently and in the same phyletic line. Three subfamilies were evidently founded by cricket species that had lost one or both specializations. Phalangopsines generally lack hindwings and are not known to fly; all mogoplistines lack hindwings (and cannot fly). Most males in both subfamilies have acoustically specialized forewings (and call). The myrmecophilines seem to have evolved from a mogoplistine ancestor that had lost its forewings (i.e., had no wings at all) and was mute as well as flightless, as in the modern mogoplistine genera *Arachnocephalus* and *Oligacanthopus*. Within each remaining subfamily, there are generally species that cannot fly, species that cannot call, and species that cannot fly or call. Calling, and its loss, will be addressed further below.

Flight

Crickets that fly have well-developed hindwings as well as forewings that partially protect the hindwings at rest (Fig. 1.10 A, B). Crickets that do not fly may have no hindwings (with or without forewings; Fig. 1.10 I, K), vestigial hindwings (always with forewings; Fig. 1.10 D, E), or fully developed hindwings (Fig. 1.10 A, B). The latter crickets can be classified as flightless through behavioral tests (e.g., Walker 1987a) or through dissection—since flight requires well-developed metathoracic muscles, which are lacking in some long-winged insects (Harrison 1980, Roff 1987).

The occurrence of both local and migratory flights is related to habitat. Most ground-dwelling crickets fly only when moving between habitats, and many species are flightless. Local movements are generally by walking. On the other hand, many vegetation-inhabiting crickets (e.g., most oecanthines, eneopterines, and trigonidiines) make some of their local movements by flying from one part of a plant to another or from one plant to another in the same habitat.

Migratory flights are most characteristic of crickets that live in transient habitats. To the extent that flight is restricted to migration in ground-dwelling crickets, the possession of flightworthy wings is correlated with habitat impermanence. For example, species that occupy early successional habitats are usually macropterous or dimorphic (see below and Fig. 1.11 A–C); species that live in woods (which are relatively permanent) are often flightless (Fig. 1.11 D, E). Vegetation-inhabiting crickets that make local flights often migrate as well, as illustrated by the sudden appearance of numerous adults in habitats where juveniles do not develop (e.g., Walker 1963).

Not all ground-dwelling crickets eschew local flights. Two species of mole crickets (*Scapteriscus acletus* and *S. vicinus*) are known to fly both within and between habitats. Within-habitat flights were proved by capture of marked mole crickets terminating their flights where they were released one or more nights before (e.g., 67% of 647 recaptures of *S. acletus*) (Ngo and Beck 1982). Local flights help these two species find

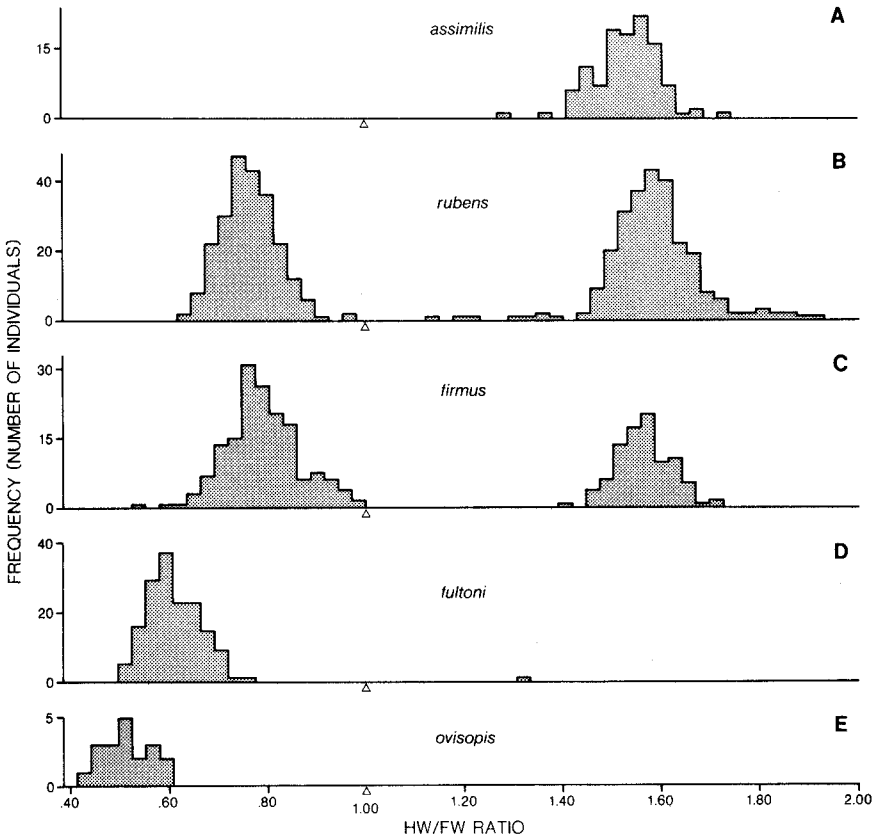


Fig. 1.11 Frequency distributions of hindwing length (HW) expressed as proportion of tegminal (forewing) length (FW) for five species of *Gryllus* from Florida. Species A invaded south Florida from the West Indies and is 100% long-winged. Species B and C live in early successional habitats and are dimorphic in hindwing length. Species D and E live in woods and are 100% short-winged (except that D produces a few flightless long-winged individuals when reared in the laboratory). Long-winged morphs of B and C frequently fly to lights, and A sometimes flies in pest proportions. The sequence from A to E probably represents the evolution of flightless crickets from flying forebears. (Modified from Walker and Sivinski 1986.)

mates and oviposition sites (Forrest 1983a). Evidence for migratory flights includes the rapid spread of these two species from ports of introduction in southeastern United States and the landing of large numbers in habitats where they could not have developed (Walker and Fritz 1983). Frequency of migratory relative to local flights can be estimated by comparing the numbers of flying mole crickets caught in traps in fields (where these two species develop) with those in woods (where they do not and therefore must be migrants) (Fig. 1.12) (Walker and Fritz 1983).

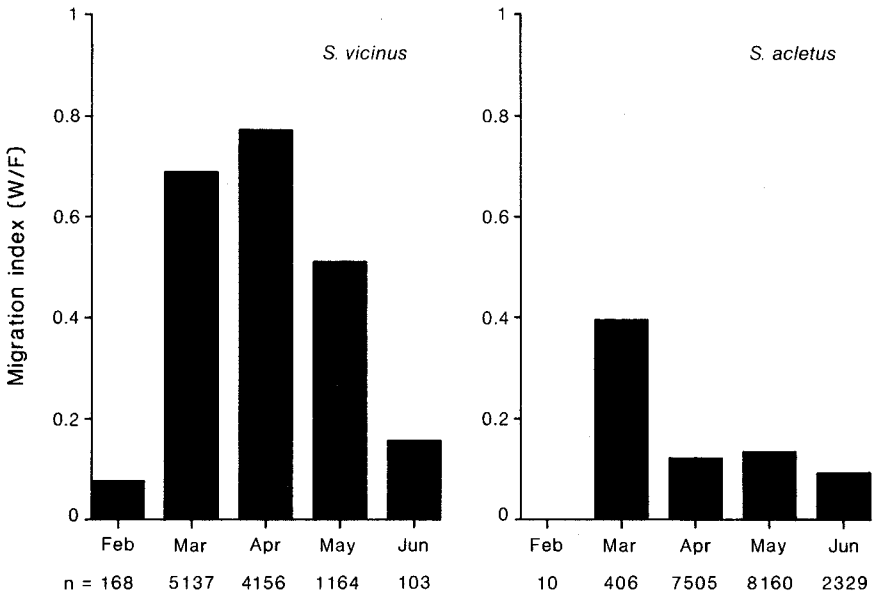


Fig. 1.12 Monthly migration indices for two species of *Scapteriscus* mole crickets, calculated from numbers that terminated their flights at sound-baited traps in woods and in fields. Because mole crickets that landed in woods (W) (where they do not breed) had to be migrants, and those that landed in fields (F) could include both migrants and locally flying crickets, W/F (migrants/[migrants + local fliers]) estimates the proportion of trapped mole crickets that were migrants. (Data from Walker and Fritz 1983.)

Wing and flight dimorphism. Wing dimorphism—the occurrence of long- and short-winged morphs within the same population—is widespread among crickets (Masaki and Walker 1987). Wing dimorphic species (Figs. 1.10 A–H; 1.11 B, C) occur in at least six of the seven major sub-families that fly. We know of no documented examples from oecanthines, but wing length has more than one mode in some herb-inhabiting oecanthines (T. J. Walker, unpublished). Wing morphs are usually discrete and easy to distinguish. Individuals that have the folded hindwings projecting from beneath the forewings are long-winged (macropterous), and individuals that have hindwings shorter than the forewings are short-winged (micropterous or brachypterous) (Figs. 1.10 A, D, F, H, 1.11).

Wing dimorphism generally reflects flight dimorphism, as evidenced by short-winged morphs never flying and by long-winged morphs flying to lights or sound in large numbers. However, as noted above, long-winged crickets do not necessarily fly. For example, we know of no reports of long-winged *Gryllus campestris* flying; and even though thousands of *G. rubens* may fly to one trap in one month, many long-winged *rubens* probably never fly (Walker 1986b, 1987a). Long-winged crickets should be viewed only as potential fliers.

Two aspects of wing dimorphism are of special importance in understanding cricket natural history: its adaptive significance and how the morph of an individual is determined.

In wing-dimorphic species the short-winged morph reproduces earlier and is more fecund than the long-winged morph (Tanaka 1976, 1986, Roff 1986b, Zera and Rankin 1989). On the other hand, flight-capable, long-winged individuals have the advantage of being able to escape a deteriorating or crowded site and to colonize new or sparsely occupied ones. Thus some individuals are specialized to exploit the home habitat, and others are specialized to leave it and colonize new ones. As expected, wing-dimorphic species occupy habitats that sometimes last long enough to favor the short-winged morph and yet are unstable and transient enough to favor (or require) the long-winged morph.

The genetic basis of wing dimorphism is twofold. In the first place, genetic differences among individuals are sometimes responsible for their developing into different morphs (Roff 1986a, Walker 1987a, Zera and Rankin 1989). The maintenance of these differences may depend on the environment favoring different morphs at different times and places, with the result that neither set of morph-determining alleles is eliminated. Of equal or greater importance is the fact that a genotype may be specifically adapted to switch development to one morph or the other in response to environmental cues. In some cases these cues are indicators of season (e.g., photoperiod, temperature) and condition of the habitat (e.g., food, crowding) that can cause an individual to develop into the morph that is appropriate to the particular season or habitat in which the adult must function (Masaki and Walker 1987). For example, Veazey et al. (1976) reported seasonal changes in morph frequency for two dimorphic *Gryllus* species, with long-winged morphs being most frequent during parts of the year most likely to have nocturnal temperatures favorable for flight and to provide habitats favorable for colonization.

An intriguing aspect of environmentally controlled wing development in wing-dimorphic crickets is that crickets reared under constant conditions (e.g., temperature, day length, food, and crowding) may remain dimorphic—even after eight generations of 100% selection for long and short wings (Walker 1987a). Computer modeling and theoretical considerations indicate that, in circumstances that are truly uncertain (i.e., no accessible environmental cues predict which morph is appropriate), natural selection favors genotypes that use inconsequential environmental differences to produce a mixture of morphs. This type of morph determination has been termed adaptive “coin flipping” or stochastic polyphenism (Cooper and Kaplan 1982, Walker 1986a).

Migratory flights and oogenesis. For many flight-capable insects, migration is the first major activity of the postteneral adult. After the migratory flight the wing muscles are histolyzed, and females use the materials in oogenesis. Males may or may not have an analogous ontogeny; they

cannot colonize by themselves, and females should mate before emigrating. The importance of females as colonizers is supported by the fact that, in wing-dimorphic crickets, females are more often long-winged than males and usually form the majority in samples of migrants.

The partitioning of adult activity into early migration and later flightlessness and reproduction is especially clear-cut in species that shed their hindwings.

Loss of hindwings. Hindwing shedding, *dealation*, occurs in some species of at least three subfamilies of crickets (Tanaka 1986, Masaki and Walker 1987, Roff, 1987). Individuals that have no hindwings projecting from beneath the tegmina are not necessarily short winged—what is concealed may be wing stumps rather than short wings (Fig. 1.10 C, G). If they have stumps, the wings they lost were long, because only long-winged individuals dealate. Dealation occurs both in monomorphic long-winged species, such as *Anurogryllus muticus* and *Loxoblemmus amoriensis*, and in wing dimorphic species, such as *Allonemobius fasciatus* and *Velarifictorus parvus*. Most long-winged crickets do not dealate; and those that do may not have flown or been able to fly (e.g., all *Anurogryllus arboreus* have long wings but shed them while still teneral) (Walker 1972).

Repeated migratory flights. Most crickets that migrate probably make a single, early migratory flight (followed by wing-muscle histolysis in species that make no trivial flights). However, in one of the few cases in which cricket flights have been studied intensively, migration can occur repeatedly. The pest mole crickets *Scapteriscus vicinus* and *S. acletus* migrate (as evidenced by their landing in habitats unsuitable for development) throughout their principal period of maturation (fall through mid-spring) and well beyond (early summer) (Walker and Fritz 1983). That individuals fly more than once is known from recaptures of marked individuals (up to 58 days between flights for *S. acletus*) (Ngo and Beck 1982) and from holding mole crickets in buckets of soil and recording when they fly out (Forrest 1986). Perhaps the most convincing evidence that repeated migration occurs (as opposed to repeated trivial flights) is that flights become more frequent when caged crickets are crowded or deprived of food (Walker, unpublished). This translates into their flying from a newly found habitat when it becomes unsuitable. Even when conditions are kept optimal, females will sometimes fly from oviposition buckets (Forrest 1986).

Some long-winged *Gryllus rubens* fly several times during periods of days or weeks, especially when deprived of food and oviposition sites (Walker 1987a).

Habitat Selection

Whether crickets are dispersing within their home habitat or terminating a long migratory flight, they must decide where to stop. Walking

crickets can conveniently monitor critical features of the habitat (e.g., soil moisture, vegetation, presence of conspecifics) as they travel; and for them, habitat selection should be straightforward (see chapter 5). However, in experiments with *Allonemobius fasciatus* and *A. allardi*, two closely related ground crickets that occupy wet and dry grassy areas, respectively, Howard and Harrison (1984a, 1984b) elicited no choice of habitat in *A. allardi* (the dry-ground species), except that females preferred to lay their eggs in wet soil. *A. fasciatus* (the wet-ground species) settled in wet areas when exposed to a gradient, but in oviposition tests females laid no more eggs in wet soil than in moist. Neither species was influenced in its choice of habitats by the presence of the other species.

Crickets that fly away from their home habitat and over land or water that they cannot colonize must make quick decisions as to whether to descend or keep flying and must do so with very limited information about potential stopping places. The problems that migrating crickets may encounter are well illustrated by swarms of *Gryllus bimaculatus* landing on ships as far as 900 km off the coast of West Africa (Ragge 1972). Perhaps their flying that far supports the speculation that migrating crickets avoid landing on bodies of water.

Two features of habitat selection by migrating crickets are well substantiated: (1) migrating crickets frequently terminate their flights at conspecific sounds (Fig. 1.12) (Campbell and Shipp 1979, Walker 1986b); and (2) at the beginning of their migratory flights they are refractory to cues that later cause them to land (e.g., they will fly directly away from a sound-baited trap that will soon attract and capture hundreds of conspecifics) (T. J. Walker, unpublished).

Results of phonotactic tests with tettigoniids (Morris and Fullard 1983) suggest that migrant crickets can find suitable habitat by homing on sounds other than the conspecific calling song. Specifically, flying crickets may detect conspecifics by the song's carrier frequency even though the species-specific amplitude modulation is obscured, and they may land at the songs (or carrier frequencies) of other species that occur in suitable habitat. Landing at any insect sound would, for example, preclude landing on open water.

Experimental results, incidental to other studies, support the hypothesis of acoustical habitat selection. Ulagaraj (1974) reported 27 *Scapteriscus aletus* landing at a continuous tone of 2.7 kHz, while none landed at a silent control (and 270 landed at a call-simulating, modulated 2.7-kHz tone). Sound traps that broadcast the synthetic call of one cricket catch significant numbers of crickets of other species and subfamilies (Mangold 1978, Walker 1987a). For example, a trap broadcasting *Gryllus rubens* call (4.8 kHz, 50 pulses/s) in a forest captured 113 migrating *S. vicinus* (3.3 kHz, 130 pulses/s) in 51 days (T. J. Walker, unpublished). In north Florida, species of the following subfamilies land at the calls of species of other subfamilies: Gryllotalpinae, Gryllinae, Nemobiinae, Oecanthinae, Trigonidiinae. Whether woodland species favor woodland

sounds (other than their own calls) and pasture species favor pasture sounds merits investigation.

Acoustic detection of habitat is one of two special functions known for tympanal organs in flying crickets. The other is bat detection (see chapter 11). Since the frequencies of the echo-locating calls of bats are much higher than those of sounds likely to be used in locating suitable habitats, determining the tuning curves (hearing spectra) for the tympanal organs of migrating crickets could refute one function or the other. In the case of *Trigonidium cicindeloides* it could refute both, since that species has no calling song and develops tympana only when long winged (Fig. 1.10 F–H) (Ingrisch 1977).

Food Selection and Feeding

Most, if not all, crickets are omnivorous. This by no means implies that their diets are similar. Indeed, within a single genus, natural diets may vary from nearly 100% herbivorous to largely predaceous (Fig. 1.13).

The chief basis for declaring that most crickets are omnivores is that, when captured and deprived of natural foods, they will eat a wide variety of organic materials. For example, species from the eastern United States will generally survive and develop on a diet of ground dry pet food. Walker (1957a) reared tree crickets (*Oecanthus nigricornis*) from egg to adult by provisioning juveniles solely with ground dog food, lettuce, or aphids, as well as with various combinations of foods. The reared adults were of normal size, except that the ones fed only ground dog food were stunted. The sole exception we know to the rule that caged crickets will eat a variety of foods is a Japanese nemobiine (*Parapteronemobius sazanami*), which lives on the beaches of Honshu and Kyushu. Furukawa (1970, pp. 65–66) reported that it “denies every food (including dried shrimp) except fresh crab meat.”

The natural foods of crickets can be learned by watching crickets in nature, by dissecting the alimentary canal of field-collected crickets (Fig. 1.13), by examining feculae, and by examining food caches of burrowing crickets. Laboratory food choice experiments and studies of mandibular morphology are of limited value in predicting natural diets (Gangwere 1961).

Many crickets are predominantly herbivores, and their feeding on plants and fruits valued by man is of major economic consequence. Vegetation-inhabiting crickets often eat the blossoms, fruit, and leaves of the plants they occupy. Ground-inhabiting crickets cut and eat small or young plants. Mole crickets feed on grasses and other plants both above and below ground.

Relatively few crickets are known to take living prey. When this is recorded, the prey are usually inactive or nearly defenseless (e.g., eggs, pupae, molting insects, scale insects, aphids). The most formidable preda-

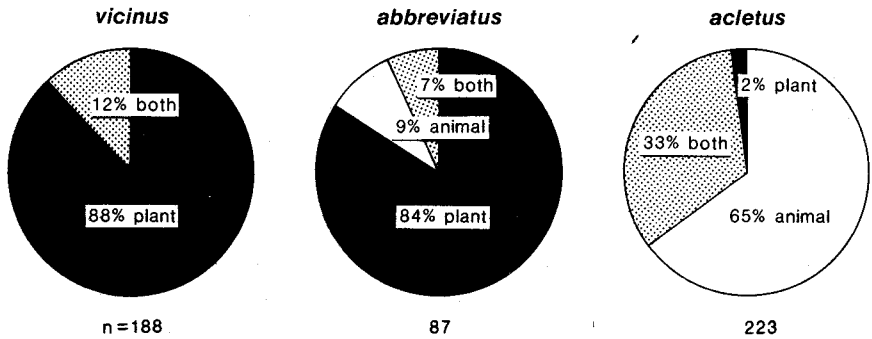


Fig. 1.13 Feeding habits of three species of *Scapteriscus* mole crickets, based on examination of gut contents of field-collected juveniles and adults. (Data from Matheny 1981 and E. L. Matheny, Jr., and J. A. Reinert, unpublished.)

tors among the crickets are certain mole crickets, which, because of their size and subterranean agility, have little trouble in dispatching most of the insects and annelids they encounter as they tunnel through the soil. *Oecanthines* feed avidly on aphids that are offered them, but examination of crop contents reveals that most individuals of most species feed chiefly on plant tissues and fungal spores (Fulton 1915, Gangwere 1961). Even small crickets can be active predators; for example, *Anaxipha gracilis*, a trigonidiine, was noted feeding on blood-engorged sand flies (Christensen and Herrer 1975). Cannibalism is occasionally a problem in laboratory culture of crickets. Those eaten are generally much smaller than the attacker, or they are molting. In nature, cannibalism is probably less frequent because of fewer contacts and more escape routes.

The natural diets of common ground-dwelling crickets are poorly known. In analyzing crop contents and fecal materials of *Gryllus pennsylvanicus* and *Allonemobius allardi*, Gangwere (1961) found mostly "organic debris" and dicotyledonous leaf materials, lesser amounts of insect remains, and least amounts of spores, pollen, and fragments of grass leaves. Gangwere (1961) summarized other records of natural foods of *Gryllus* spp., including cow manure, dead vertebrates, mantid eggs, and live termites. Monteith (1971) concluded that *G. pennsylvanicus* and *Allonemobius* sp. were major predators of apple maggot pupae and observed the older juveniles and adults detecting and quickly excavating pupae he had buried 1–3 cm in the soil.

Some plant-dwelling crickets are known from one or a few plant species, but host-specific crickets do not necessarily eat the plant they dwell on. For example, *Oecanthus pini* in southeastern United States occurs only on pines, and its color and resting behavior is specially adapted to concealment in pine foliage. Captive *O. pini* feed little, if at all, on host pine needles, but they feed readily on lettuce, aphids, and ground dog food. The fact that we know of no case in which a host-specific cricket feeds

primarily on the tissues of its host is not surprising in view of how poorly known are the natural diets of plant-dwelling crickets.

Because myrmecophilines live as unwelcomed guests in ant nests, their feeding behavior is of special interest (Wheeler 1900, Henderson and Akre 1986). Although they can survive on other foods, myrmecophilines use two techniques to feed directly from their hosts. One is by using the mouthparts to strigilate oily secretions from the surface of the legs and body of an ant (Fig. 1.14 A). They are allowed to do this apparently because the feeding resembles the grooming behavior of their hosts. Indeed, the cricket usually gains access when the ant is self-grooming or being groomed by another ant. (Myrmecophilines also mouth the surfaces of dead ants and greasy nest walls.) The second technique mimics the mutual feeding behavior of their hosts. The cricket elicits trophallaxis by antennating the ant and, if accepted, by manipulating the ant's mouthparts with its maxillary and labial palps. The ant may then allow the cricket to feed on regurgitated gut contents for a few seconds before aggressively terminating the process (Fig. 1.14 B).

Mating in Call-less Species

All crickets reproduce sexually. Facultative or obligatory parthenogenesis, as known in other orthopteroids (Lamb and Willey 1975), is not known for crickets. Most crickets use calling songs in sexual pair formation, as outlined in chapter 2. Here we discuss call-less sexual pair formation.

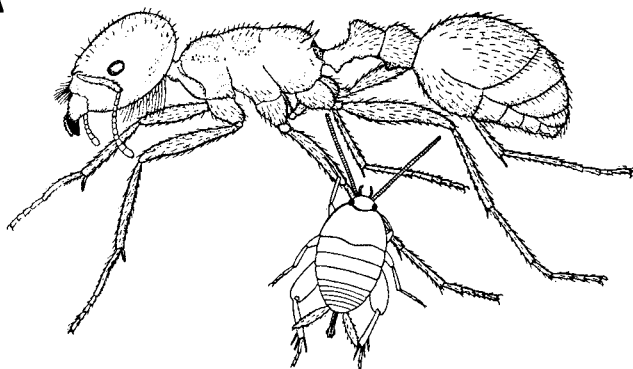
Occurrence of Call-less Species

In most cricket species sexual pairs are usually formed by the female homing on a male-produced, species-characteristic calling song. However, in many genera or subfamilies that generally form pairs acoustically, males of one or more species produce no calling song. Call-less species in eastern United States include *Gryllus ovisopis* (grylline; other *Gryllus* spp. call), *Scapteriscus abbreviatus* (gryllotalpine; other *Scapteriscus* spp. call), *Hapithus brevipennis* (eneopterine; its sister species, *H. melodius*, calls), and *Tafalisca lurida*, *Oligacanthopus prograptus*, and *Falcicula hebardi* (eneopterine, mogoplistine, and trigonidiine; these genera have no calling species, but calling species occur in many other genera of these subfamilies). Species that do not call range from having well-developed courtship and aggressive songs (e.g., *G. ovisopis*) to being totally mute (Otte 1977). Those that are mute may have male forewings with stridulatory files (e.g., *H. brevipennis*), male forewings that are female-like (*T. lurida*, Fig. 1.10 L), or no forewings (*O. prograptus*).

Pair Formation without Calling

Pairing has been studied in only a few call-less crickets. In *Amphiacusta maya* (a phalangopsine) the final nymphal instars and, later, the adults

A



B

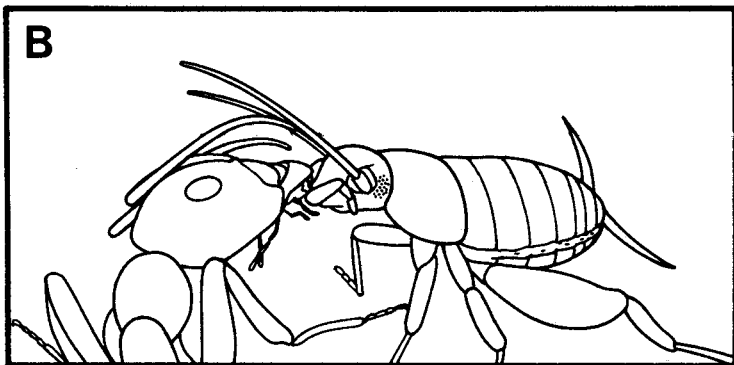


Fig. 1.14 Two species of *Myrmecophilus* ingesting materials from ants. A, *M. nebrascensis* feeding on secretions of a *Pogonomyrmex* ant. (From Wheeler 1900.) B, *M. manni* receiving regurgitated gut contents from a *Formica* ant. (Drawn from photograph in Henderson and Akre 1986.)

congregate in natural cavities during the day; mating occurs in these diurnal aggregations (Boake 1984a). In *Phaeophilacris spectrum* (another phalangopsine) adult females aggregate, and a male may join the group and defend it from other males (Dambach and Lichtenstein 1978). In *Gryllus ovisopis* populations in north Florida most individuals become adult within a few days during mid-September, and females are quickly mated without the aid of airborne pheromones or long-lasting trail pheromones (T. J. Walker, unpublished). In *Trigonidium cicindeloides* (a trigoniidiine) pairs are said to be formed through random contact (Ingrisch 1977).

Some vegetation-inhabiting mute crickets, including *T. cicindeloides*, make substrate vibrations during courtship (Matsuura 1984). Body jerking and tapping the substrate with the abdomen or foretibia are among the techniques used. The same or similar signals could function in pair

formation. (For more on vibrational signals, see Bell 1980, Belwood 1988, and chapters 2 and 6, this volume.)

What Causes Loss of Calling?

Circumstances that correlate with loss of calling song are high densities, sedentary colonies, and synchronous maturation. These facilitate alternative means of pair formation but are not sufficient to explain loss of calling. Calling should be lost when its costs are increased or when its reproductive benefits are reduced relative to alternative means of pair formation. Circumstances that increase the energy costs of calling include small size (small insects are not as efficient at producing sounds that will carry long range as are large insects: Michelsen and Nocke 1974; chapter 8, this volume) and living under or on the ground (sound travels poorly through or along the ground: Markl 1968, Wiley and Richards 1978, Paul and Walker 1979). Risks of calling are increased by acoustically orienting predators and parasites (see below and Belwood 1988). Satellite males (i.e., conspecific acoustic freeloaders) can decrease the benefits of calling relative to other pair forming strategies (Cade 1979).

The fact that calling has been lost independently in many phyletic lines suggests that intermediate steps in song loss should be encountered fairly frequently, and they are. Southern populations of *Hapithus agitator* call, and northern ones do not (Alexander and Otte 1967a). Some males of *Gryllus integer* call for hours each night, and some do not call at all; selection for much calling or no calling quickly produces lines that are significantly different in calling frequency (Cade 1981b). Males of *Anurogryllus arboreus* call for less than an hour each evening and spend most of the night searching for females, which are in burrows. Most females are found and mated by searching males; mated females generally do not go to calling males (Walker 1983a; and T. J. Walker, unpublished).

Natural Enemies

Crickets have many natural enemies. Their life expectancy under field conditions is low compared to their longevity under protected laboratory conditions. For example, male *Anurogryllus arboreus* held in the laboratory survived 69 days on average (T. J. Walker, unpublished); under field conditions estimated mean survival was less than 1 week (Walker 1980a). In most circumstances neither food shortages nor cold nor drought are common causes of death in the field. A variety of natural agents are common causes.

Pathogens

Cricket pathogens have been studied chiefly as causes of mass mortality in laboratory colonies or commercial cricket "farms" and as potential biological control agents of pest species. Only in the latter case does the

mortality occur under natural conditions, ensuring its relevance to natural history.

Teleogryllus commodus is a major pest of pastures in New Zealand and Australia. In samples from more than 200 sites in Victoria, Australia, Reinganum et al. (1981) found significant frequencies of two fatal pathogens: 43% of the samples were infected with cricket paralysis virus, and 5% had the fungus *Metarhizium anisopliae*.

Similarly three introduced species of *Scapteriscus* mole crickets are important pests of turf and pastures in southeastern United States. In assays of individuals collected in their South American homeland, infection rates for the pathogens *Metarhizium anisopliae*, *Aspergillus* sp., *Beauveria bassiana*, and *Serratia* sp. ranged from 1 to 20% (H. G. Fowler, personal communication, 1985). Other mole cricket pathogens, identified from Brazil or Florida, are an iridovirus, a microsporidian (*Pleistophora* sp.), and two more fungi (*Entomophthora* sp. and *Sorosporrella* sp.) (Pendlan and Boucias 1987, Boucias et al. 1987; D. G. Boucias, personal communication, 1988).

Gregarine sporozoans occur in the midguts of some field-collected gryllines and nemobiines (Corbel 1964). In *Gryllus veletis* and *G. pennsylvanicus* frequency of infection is 30–70%, and pathological effects include slower development and reduced spermatophore production (Zuk 1986).

In laboratory colonies or in mass-reared crickets, fatal diseases have been attributed to a rickettsia and three additional viruses (Martoja 1963, Huger 1985). In such circumstances cannibalistic feeding on the dead or dying may unnaturally aid the transmission of pathogens.

Parasites

Metazoan parasites of crickets include nematodes, mites, and parasitoid wasps and flies. Little is known of the extent of parasitism under natural circumstances, but because crickets sometimes reach pest proportions when introduced to new geographical areas without their parasites, several parasites of pest species have been introduced in hopes of permanently suppressing pest populations. Other parasites are currently under study.

Nematodes. Nematodes are commonly found within crickets, but in most cases their effects, if any, on the longevity and reproduction of the host are unknown (Webster and Thong 1984). Two groups that have received special attention because they are lethal and have potential as biological control agents are Mermithidae and Steinernematidae (Poinar 1983, Walker 1984). The mermithids are pale, threadlike worms much longer than the host when fully developed. They are most often seen when one emerges from a recently collected cricket. Mermithids invade their definitive hosts in several ways (Poinar 1983), and the life cycles of those occurring in crickets have apparently not been studied. Unlike mermithids, steinernematids do not develop singly in a host, and they kill

the host quickly though indirectly. They invade the host as infective larvae, release a symbiotic bacterium that kills the host, and undergo one or more generations while feeding on the host cadaver. The end result is thousands, or hundreds of thousands, of bacterium-carrying, infective larvae. *Neoplectana* sp., a steinernematid that is a major mortality agent of *Scapteriscus* mole crickets in Brazil and Uruguay, has recently been established in Florida as a biological control agent (Hudson and Nguyen 1989, Hudson et al. 1988).

Mites. Large red mites are occasionally found on crickets. McGregor (1929) reported that in California's Imperial Valley many crickets (*Gryllus* sp.) were so weakened from attacks of *Euthrombium* sp. that they could barely move about. The mites were mostly attached on the dorsum beneath the wings.

Egg-parasitic wasps. Two genera of scelionid wasps, *Leptoteleia* and *Oethecoctonus*, contain, so far as is known, only species that develop as solitary endoparasites of cricket eggs laid in plant tissues—specifically the eggs of oecanthines and eneopterines (Masner 1978). One or more species in four other families of wasps have been reported to parasitize oecanthine eggs: Mymaridae, Eulophidae, Eupelmidae, Eurytomidae (Thompson 1951, Herting 1971).

Ectoparasitic wasps. Larvae of *Rhopalosoma* spp. (Rhopalosomatidae) and *Larra* spp. (Larridae) are ectoparasites on adult or large juvenile crickets and kill the host as they complete their development. Little is known of *Rhopalosoma* spp., except that the larvae develop on eneopterine and nemobiine crickets (Gurney 1953, T. J. Walker, unpublished). *Larra* spp. develop only on mole crickets and, largely because of their potential as biocontrol agents, are better known (Smith 1935; Castner 1984, 1988). Whereas in most sphecids the female provisions her brood with permanently paralyzed prey, the *Larra* female only briefly paralyzes the mole cricket that she has chased from its tunnel—just long enough to remove any other *Larra* egg and lay one of her own. The mole cricket then resumes an active underground existence until 2–3 weeks later, when the *Larra* larva (Fig. 1.15) reaches its final instar and kills and devours its host. Species of *Larra* have been introduced to Hawaii, Puerto Rico, and Florida in efforts to control introduced mole crickets.

Phonotactic flies. Female tachinids of the genus *Euphasiopteryx* are attracted to certain cricket calls and larviposit in the vicinity. The larvae attach to crickets they contact, burrow in, and develop endoparasitically (Cade 1984, Fowler and Kochalka 1985, Walker 1986b, Fowler 1987). The host cricket is killed in 6–8 days when the mature larva or larvae emerge to pupate. *E. ochracea* is an important mortality agent for *Gryllus integer* and *G. rubens* in southern United States. *E. depleta* parasitizes *Scapteriscus*

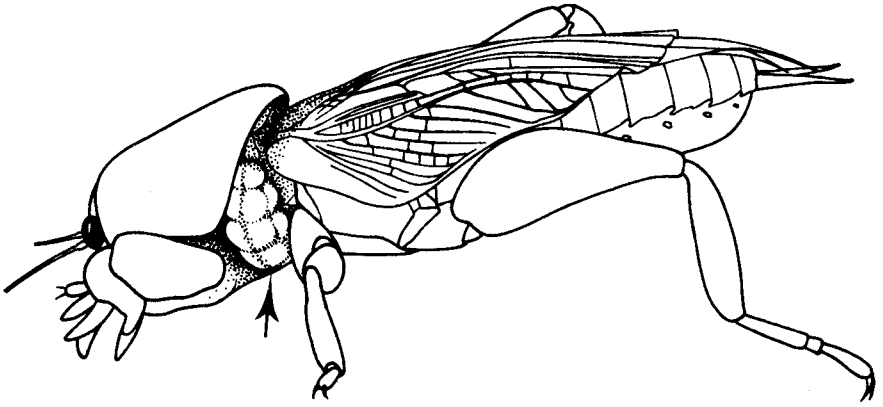


Fig. 1.15 Wasp larva ectoparasitic on a mole cricket. *Larra bicolor* developing on *Scapteriscus vicinus*. When the larva (indicated by arrow) reaches about twice this size, it will kill its host and devour the remains before pupating.

mole crickets in South America and has recently been released in Florida for biological control of introduced pest mole crickets (T. J. Walker, unpublished). The ease with which larvipositing females can be attracted to broadcasts of crickets' songs should facilitate further study of these poorly known flies.

Other endoparasitoids. In studies of field-collected grylline crickets, fully developed fly larvae occasionally emerge from dying adults. These pupate and produce tachinid, sarcophagid, or conopid flies (e.g., *Exoristoides* sp., *Blaesoxipha* sp., *Stylogaster* sp.) (Thompson 1951; T. J. Walker, unpublished).

Predators

Crickets are generally tasty food for vertebrate and invertebrate predators. Their palatability and the ease with which some species can be reared have resulted in crickets being used as food for many zoo and laboratory animals. The extent to which various predators feed on crickets in the wild is poorly known, but the fact that crickets are frequently found in the guts of birds, mammals, reptiles, and amphibia confirms the idea that crickets are at risk from a multitude of vertebrates. They are also palatable to generalist invertebrate predators such as lycosid spiders and mantids.

Two subjects of particular interest and relevance to predation on crickets are phonotactic predators and specialist predators.

Phonotactic predators. The calls that make cricket males conspicuous to their females and to naturalists can also reveal them to hungry, insect-eating predators. Use of cricket calling songs to locate prey has

been experimentally demonstrated in cats, little blue herons, and geckos (Walker 1964a, Bell 1979a, Sakaluk and Belwood 1984) and should be expected whenever the predator hears well at the cricket's carrier frequency. No invertebrate predators are known to hunt crickets by their sounds, but predaceous katydids (e.g., Listroselinae, Decticinae) seem likely candidates. Walker (1979) used pitfall traps baited with calling crickets to test for previously unrecognized acoustically orienting predators; results were negative. Similarly, Cade and Rice (1980) failed in attempts to attract the cricket-eating toad *Bufo marinus* to its prey's call.

Specialist predators. Generalist predators often feed on crickets and probably account for most deaths of crickets in the wild. In addition, a few predators are known or suspected to specialize on crickets. Several groups of sphecid wasps provision their nests mostly or entirely with crickets, including species of *Liris* (Larrinae), which prey on gryllines (see chapter 7); *Isodontia* (Sphecinae), which prey on oecanthines; and *Chlorion* (Specinae), which prey on gryllines (some species are *Larra*-like parasitoids of *Brachytrupes* spp.) (Bohart and Menke 1976, Steiner 1976). The larvae of certain bombardier beetles are specialized predators of the eggs of mole crickets. In Japan *Stenaptinus jessoensis* larvae attack the eggs of *Gryllotalpa africana* and undergo hypermetamorphosis within the egg chamber (Habu and Sadanaga 1965, 1969). In the New World *Pheropsophus aequinoctialis* larvae feed on eggs of *Scapteriscus* spp. (Hudson et al. 1988).

Defensive Strategies

Crickets have evolved a variety of ways to thwart their enemies. We categorize their defenses as hiding, fleeing, attacking, and threatening.

Hiding

When crickets are not seeking food, mates, or oviposition sites, they generally conceal themselves. Many species hide in naturally occurring crevices, but others construct their own hiding places.

Vegetation-inhabiting species often hide in tree holes or leaf curls or squeeze beneath loose bark. A few can tunnel in soft wood. Caged individuals of *Tafalisca lurida*, a New World eneopterine usually found on red mangrove, tunneled into the cork stoppers of their water vials and completed their concealment by folding their long antennae within their retreat (T. J. Walker, unpublished). *Mjobergella warra*, an Australian grylline, evidently makes blind tunnels in the wood of downed trees (Otte and Alexander 1983).

Ground-dwelling species often hide beneath debris, stones, and fallen logs. In areas where the soil shrinks during dry spells, the resulting cracks provide a haven and access to moist soil.

Burrowing. Many ground-dwelling species improve their places of concealment by excavation. For example, most gryllines (especially the more robust ones) will, under appropriate circumstances, either enhance natural shelters—by enlarging soil crevices or spaces beneath rocks or logs—or dig a simple burrow. Unbranched, blind borrows without noteworthy chambers are often occupied for short periods and generally serve only for shelter. For example, wandering males of *Anurogryllus arboreus* dig simple burrows, hide in them during the day, and abandon them to call and search for females the next evening (Walker 1983a). On the other hand, simple burrows are sometimes a site for mating and oviposition (e.g., *Gryllus campestris*: Turček 1967; *Teleogryllus commodus*: Evans 1983).

Mole crickets and some gryllines, including species of *Brachytrupes*, *Anurogryllus*, *Apterogryllus*, and *Cephalogryllus*, construct elaborate burrows and occupy them for long periods (Chopard 1938, Büttiker and Bünzli 1958, Bell 1979b, Otte and Alexander 1983, Walker 1983a).

All mole crickets spend most of their lives underground in tunnel systems they construct with powerful forelegs specially modified for digging. Temporary tunnels, probably used in foraging, are made just beneath the surface and are apparent as trails of upthrust soil. Deeper, more lasting tunnels and chambers are made by compacting the soil with the pronotum and pushing soil to the surface or into old tunnels. Mole cricket burrows are extensive and frequently modified. Few have been described in detail, but the acoustic burrows of males (see Chapter 8) and the egg chambers of females (Chopard 1938) are evidence of their subterranean construction skills.

The powerful fossorial forelegs of mole crickets enable them to tunnel out of sight in a few seconds when placed on loose soil. Gryllines use a different, slower burrowing technique. The mandibles loosen the soil, which is then carried in the mouth parts, kicked rearward by the legs, or bulldozed with the head (Büttiker and Bünzli 1958, Alexander 1961).

Juveniles of *Brachytrupes membranaceus* occupy permanent burrows that they enlarge as they develop. The burrow of the adult is 50–80 cm deep, has a chamber where food is stored, and boasts an emergency exit as well as a main entrance (Büttiker and Bünzli 1958). Mating occurs within the male's burrow, and females may remain in the male's burrow in sand-plugged side tunnels (Costa and Petralia 1984). *Anurogryllus arboreus* also has permanent burrows, which include a deep tunnel for defecation and one or two chambers for living and food storage. Mating usually occurs in the male's or female's burrow; in either case the male leaves, and the female uses the burrow for oviposition and brood rearing (Walker 1983a; T. J. Walker, unpublished). If the male does not attract a female to his home burrow, he abandons it anyway after a few days and begins a wandering existence.)

Camouflage. Crickets that fail to find (or build) dark retreats benefit from colors and patterns that make them difficult for visually hunting

predators to detect. Host-specific oecanthines match their host's colors and may have patterns that aid concealment. For example, *Oecanthus pini* has a brown head and pronotum and pine-green tegmina. At rest the cricket keeps its head and pronotum next to a branchlet amid the brown needle-bundle sheaves and holds the rest of its body parallel to and among the green needles (Walker 1963; T. J. Walker, unpublished).

Except for oecanthines, most vegetation-dwelling crickets are brown or gray rather than green, supporting the notion that most hide in crevices or against dark backgrounds during the day. The occurrence of green trigonidiines and eneopterines (e.g., *Cyrtoxipha* spp. and *Orocharis vaginalis*) suggests that the rarity of green is a matter of selection rather than phylogenetic restraints.

Ground-inhabiting crickets sometimes match the color of their substrate. A noteworthy case is *Dianemobius csikii*, an inhabitant of sandy beaches. Other *Dianemobius* species are mostly brown to black, but *D. csikii* has dark specks on a light yellow, light brown, or even whitish background. To some extent it matches local variation in the color of the beach sand. For instance, crickets on Shimokita beach, where the sand is usually dark, are dark, whereas those from Tokunoshima Island beach, where the sand is much lighter, are pale. Members of each population are difficult to spot on their own sand and more easily seen on the sand of the other population (S. Masaki, unpublished).

The hatchlings of two woodland *Gryllus* spp. have a bright yellow thorax that sharply contrasts with the black head and abdomen (T. J. Walker, unpublished). The resulting spots of black and yellow may make it difficult for a predator to recognize them as edible. (Cott [1957] termed this phenomenon "disruptive coloration.")

Freezing. When some mole crickets (e.g., *Scapteriscus vicinus*) are excavated, they remain motionless for several seconds. Until they start to run or dig, they are difficult to find. Males of *A. arboreus* often climb perches at sunset and begin to call. When a caller is approached before darkness, he leaps from his station and freezes wherever he lands—eliminating motion and sound as cues to his whereabouts (T. J. Walker, unpublished).

Ventriloquism and silence. Calling males are acoustically conspicuous to most vertebrate predators and to some parasitoids. Anyone who tries to catch calling crickets by homing on their calls soon learns that some calls are notably difficult to localize and that crickets usually cease calling when they are approached.

Neither ventriloquism nor silence has been carefully studied in crickets, but larger crickets calling from more exposed places are the ones that quit calling soonest as they are approached; and some large, exposed callers produce brief, irregularly repeated chirps that are more difficult to localize acoustically than regularly repeated chirps or continuous trills. A study of what artificial cricket songs are most attractive to phonotactic

parasitoids such as *Euphasiopteryx ochracea* should give clues as to the auditory capabilities of the flies and to acoustic avoidance strategies of host crickets.

Fleeing

Most crickets are quick and agile. When a predator tries to capture a cricket, the cricket may dash into a retreat, such as a burrow or soil crack, or concealment, such as beneath leaf litter or to the other side of a stem or leaf. It may leap once or twice and freeze or conceal itself, or it may leap and fly like a grasshopper, or it may continue to distance itself from danger by running along a branch or stem or through grass clumps.

Males of the riparian nemobiine *Thetella oonoomba*, when disturbed at night, leap into the water and swim straight away from the bank (Otte and Alexander 1983). A lakeside nemobiine, *Pteronemobius lineolatus*, leaps onto the water surface in daytime when disturbed; as it swims back to shore it can orient by celestial cues (Beugnon 1986).

Myrmecophilines survive as unwelcome guests within ant colonies by dodging and darting among their hosts. Rarely is one captured and killed (Wheeler 1900, Henderson and Akre 1986).

Even if a cricket is seized by a predator, it may succeed in fleeing by breaking loose from one or both hindlegs or its hindwings.

Attacking

Most crickets have no means of fighting back when threatened. However, the larger more robust species can kick viciously with spine-lined, spur-tipped tibiae and deliver a painful bite. When attacked by *Liris niger*, *Acheta domesticus* assumes characteristic postures that may make it harder for the wasp to sting the cricket and/or make it easier for the cricket to kick effectively (see chapter 7, Fig. 7.6 B, C).

A few species have chemical weapons. Most notable are some mole crickets that have anal glands from which a sticky material is ejected. *Neocurtilla hexadactyla*, attacked by *Larra* spp., often entangle their attackers with the secretion and escape; *Gryllotalpa oya* can eject a mucilaginous liquid from the glands to a distance of at least 23 cm (Baumgartner 1910, Tindale 1928, Castner 1984). The anal glands of *Scapteriscus* mole crickets secrete a smelly, nonsticky fluid that may deter attack (W. G. Hudson, personal communication, 1982). When an individual of *A. arboreus* is chased into a blind tunnel, it will often exude a drop of anal fluid and hold it between itself and the potential attacker.

Threatening

Males of *Brachytrupes membranaceus*, a giant among crickets, will stridulate when cornered and, if pressed further, will attack and bite viciously (D. Otte, personal communication, 1986). Similar warning sounds are made by some large tettigoniids (Sandow and Bailey 1978), but smaller crickets and katydids do not stridulate defensively or counterattack.

Threats can be false. The trigonidiine *Phyllopalpus pulchellus* may be an

example of a false chemical threat. Its metallic blue body and reddish head and thorax make it resemble a bombardier beetle, which delivers a powerful blast of benzoquinones when attacked.

Cultural and Economic Roles

In Western folklore, a cricket in the house is an omen of good or bad luck, but in Eastern cultures crickets have had a much more prominent role. In China and Japan crickets are actively sought and brought into the home as music-making pets and, in China, as pugilists.

Crickets became an important part of Chinese culture more than 1,000 years ago. During the T'ang Dynasty (A.D. 618–906) members of the imperial court kept crickets in cages so that their songs might be more conveniently enjoyed, and the custom gradually spread throughout the country. Cages ranged from delicately carved art objects to simple bamboo containers. Later, during the Sung Dynasty (A.D. 960–1279) the sport of cricket fighting was established, and it and the keeping of caged crickets for their songs remained a noteworthy part of Chinese culture into the twentieth century. The importance of cricket fighting is attested by the many books that describe the methods of collecting, rearing, and fighting crickets. Even though more than 60 varieties of fighters are recognized in Chinese cricket manuals, all belong to four species (*Velarifictorus aspersus*, *Teleogryllus testaceus*, *T. mitratus*, and *Gryllus bimaculatus*). Fighting crickets were reared, collected, or bought, kept in special pottery cricket houses, and fed special diets (e.g., rice mixed with fresh cucumbers, boiled chestnuts, lotus seeds, and mosquitoes). For a fight, two male crickets of approximately equal weight were placed in a large clay bowl and excited by touching their antennae and cerci with mouse whisker hairs affixed to one end of a small stick. The outcome of a match usually became clear after a few minutes of fierce fighting, when one of the combatants was disabled or killed. Gambling was an important part of cricket fighting, and bets on a single match sometimes were equivalent to thousands of dollars. It was thought that cricket champions were the incarnation of great warriors of the past, and they were treated with great respect—sometimes including solemn burial in a small silver coffin (Anonymous 1928, Hsu 1929, Yasumatsu 1965). Cricket fighting is apparently in eclipse in the Peoples' Republic of China, but it is still popular in Hong Kong, where the best fighters are imported from the mainland (Kevan and Hsiung 1976). What makes a winner in a cricket fight has been investigated by Alexander (1961), Burk (1983), Simmons (1986a), and Dixon and Cade (1986).

In Japan, as in China, the appreciation of cricket music can be traced back more than 1,000 years. For example, the two species most esteemed for their songs, the matsumushi (*Xenogryllus marmoratus*) and the suzumushi (*Homoeogryllus japonicus*), are in poems of the Engi period (A.D. 901–922). Crickets were caged for their songs as early as A.D. 1095 (Hearn

1898). When the 17-syllable haiku form of poem became popular (late Muromachi period, A.D. 1336–1573), the concept of seasonal words emerged. By one of these words, seasonality is given to each haiku. Words relating to crickets and katydids are regarded as autumn words and constitute nearly half of about 70 autumn words concerned with insects. *Mushi* is the Japanese word for insect in general, but in poems it means insects singing in autumn—in most if not all cases, crickets.

The keeping of caged crickets for their songs led to the trade of insect seller (*mushiya*) by the seventeenth century and to thriving businesses in nineteenth-century Japan (Hearn 1898). The market has waned, but there is still at least one professional grower of singing crickets; and the *suzumushi* and several other species of singing insects are still sold in department stores in Tokyo, along with horn and stag beetles for children (M. Konishi, personal communication, 1986). In the Suzumushi Temple in Kyoto thousands of *suzumushi* are reared in front of the altar. However, this seems to have no religious meaning and is just a tourist attraction.

Commercial trade in crickets is currently thriving in the United States. These crickets, alas, are not raised as songsters but as fish bait and as food for laboratory and zoo animals. The species reared is invariably *Acheta domestica*, an Old World species that was Milton's "cricket on the hearth." Although cricket growers are secretive about the magnitude of their business, sales are probably about \$3 million annually. Purina Company, the producer of Cricket Chow, reported selling 445 metric tons to growers in one state (Louisiana) in 1985.

Dried, chopped crickets are sold as medicine in China. *Xi-shuai*, used as a diuretic, incorporates four species of gryllines (Inagaki et al. 1984).

In many countries crickets are used as food for humans. Those most often eaten are *Brachytrupes* sp. and mole crickets. In Taiwan, Thailand, and Burma, *Brachytrupes* sp., either raw or fried, are sold in food markets (Sonan 1931; Taylor 1975; I. Matsuura, personal communication, 1986).

A few cricket species are major agricultural pests. In southeastern United States, introduced *Scapteriscus* mole crickets, principally *S. vicinus*, cause an estimated \$35 million damage annually, mainly to turf and pasture (Southern 1982). In New Zealand, *Teleogryllus commodus* reaches numbers that consume as much pasture as 21 ewes per hectare (Blank and Olson 1981). In 1983, to control *T. commodus* in Northland, New Zealand, farmers applied 950 metric tons of bait (Blank 1984).

Other species sometimes are damaging, but the effects are usually more sporadic. For example, the eneopterine *Hapithus agitator* scars oranges in Florida (Bullock 1973), *Gryllus* spp. eats alfalfa pods in South Dakota (Walstrom 1971), *Teleogryllus emma* harms forage crops in Honshu (Kobayashi and Oku 1973), tree crickets damage raspberries by eating the flowers and young peach trees by ovipositing (Smith 1930, Elliott and Dhanvantari 1973), and *Anurogryllus arboreus* destroys pine seeds and pine seedlings in Louisiana (Campbell 1971). *Brachytrupes* spp. are pests of crops in Africa and Asia (Büttiker and Bünzli 1958, Szent-Ivany 1958).

Crickets are sometimes pests merely because of their numbers. Flights

of a *Gryllus* sp. in southern California have been so large as to clog the cooling system of large compressors in a natural gas pumping station (Caruba 1980). So many *Scapteriscus* sp. mole crickets flew one evening at Disney World in Florida that a portion of the tourist attraction had to be closed (J. Hagedorn, personal communication, 1980).

Finally, it should be mentioned that crickets are valued for their songs in at least one respect in this age of television. Producers sometimes signal that the action in a show is taking place outside on a summer's evening by dubbing in the songs of crickets. They often use the song of *Oecanthus fultoni*, a sound Nathaniel Hawthorne described as "audible stillness" (1846) and declared, "If moonlight could be heard, it would sound just like that" (1851).

Conclusions

Because of their musical songs, crickets are among the most appealing and accessible of insects. Nonetheless, only a small number of species in very few parts of the world have been carefully studied, and most of these species belong to one subfamily (Gryllinae) and live at temperate latitudes, where most scientists studying them also live. Species that are small, tropical, or vegetation-dwelling have generally been neglected. The most serious limitation to really understanding crickets stems from the fact that nearly nothing is known about most aspects of the natural history, behavior, or neurobiology of the majority of cricket taxa.

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A cricket is
a lovely thing
that likes to sing.

Rose Ann Walker, age 9 (Kevan 1974)

Hark to those tinkling tones,—the chant of the suzumushi!
—If a jewel of dew could sing, it would tinkle with such a
voice!

Hoshu Tokunaga, 1871 (Hearn 1898)

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Contents and authors of chapters

1 Natural History	<i>Thomas J. Walker and Sinzo Masaki</i>
2. Reproductive Behavior	<i>Werner Loher and Martin Dambach</i>
3. Temporal Organization of Reproductive Behavior	<i>Werner Loher</i>
4. Structure and Function of the Endocrine System	<i>Werner Loher and Malcolm D. Zaretsky</i>
5. Vision and Visually Guided Behavior	<i>Hans-Willi Honegger and Raymond Campan</i>
6. Vibrational Responses	<i>Martin Dambach</i>
7. Mechanoreceptors in Behavior	<i>Werner Gnatzy and Reinhold Hustert</i>
8. Songs and the Physics of Sound Production	<i>Henry C. Bennet-Clark</i>
9. Neural Basis of Song Production	<i>Wolfram Kutsch and Franz Huber</i>
10. Phonotactic Behavior of Walking Crickets	<i>Theo Weber and John Thorson</i>
11. Evasive Acoustic Behavior and Its Neurobiological Basis	<i>Gerald S. Pollack and Ronald R. Hoy</i>
12. Biophysical Aspects of Sound Reception.....	<i>Ole Naesbye Larsen, Hans-Ulrich Kleindienst, and Axel Michelsen</i>
13. Auditory Organ Structure, Development, and Function.....	<i>Eldon E. Ball, Brian P. Oldfield, and Karin Michel Rudolph</i>
14. Central Auditory Pathway: Neuronal Correlates of Phonotactic Behavior	<i>Klaus Schildberger, Franz Huber, and David W. Wohlers</i>
15. Perspectives for Future Research	<i>Franz Huber</i>
Glossary	
Glossary of Song Terms	<i>Thomas E. Moore</i>
Literature Cited	