

From: EVOLUTIONARY BIOLOGY, Vol. 21
Edited by Max K. Hecht, Bruce Wallace,
and Ghilleen T. Prance
(Plenum Publishing Corporation, 1987)

10

Cricket Life Cycles

SINZO MASAKI

and

THOMAS J. WALKER

LIFE-CYCLE TYPES

The life cycles of crickets can be divided into two basic categories, one with seasonality and the other without it (Alexander, 1968). Since adult crickets live a relatively long time and continue to lay eggs, this distinction may become vague in warm climates. Even in such cases, however, the two categories can be recognized when the underlying developmental characteristics are experimentally analyzed. A life cycle that shows a more or less fixed phase relationship with the seasonal cycle of environment usually involves physiological responses that buffer the life cycle from perturbing fluctuations in external conditions. Such responses form a coordinated system of seasonal homeostasis, in which diapause and photoperiodism are principal components. When development is controlled by this system, its rate is not always a simple function of temperature. The thermal coefficient Q_{10} is often shifted from an ordinary value of 2–3 to a lower or even a negative one by intervention of diapause or other photoperiodic responses. The life cycle thus includes thermally heterogeneous phases. This situation may be described by the classical though not widely used word *heterodynamic* (Roubaud, 1922). When there is no such switching of developmental phases, the cricket responds to

SINZO MASAKI • Laboratory of Entomology, Faculty of Agriculture, Hirosaki University, Hirosaki 036, Japan. THOMAS J. WALKER • Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611.

heat summation in more or less similar ways throughout the entire life cycle, so that its development is *homodynamic*. These words are used here because of their convenience and adequacy.

Homodynamic Life Cycles

If there are no clear seasonal changes, a homodynamic life cycle (with continuous growth and reproduction) is fitter than any heterodynamic one, because any delay in reproduction simply decreases the innate capacity for increase. Developmental synchronization among individuals could affect reproductive success, but no temporal or seasonal cue is available for such synchronization. Since most crickets are omnivorous, their life cycles are not likely to be shaped by seasonal food supply.

The occurrence of all developmental stages at all times of year is circumstantial evidence for homodynamic development. Such is the case in *Orocharis grylloides* (Walker, 1969a), *Cyrtoxipha gundlachi*, *C. confusa* (Walker, 1969b, and unpublished), *Gryllus assimilis* (Alexander and Walker, 1962), *Scapteriscus abbreviatus* (Walker, 1984), and *Cycloptilum slossoni* (Love and Walker, 1979) in south Florida, *Anurogryllus muticus* and *A. celerinctus* in the West Indies (Walker, 1973), and *Speonemobius litoreus* in Somalia (Vannini and Chelazzi, 1978). *Grylloides supplicans* (formerly *sigillatus*), which originated in the tropics, is found at various developmental stages even in higher latitudes, living in artificially heated places throughout the year. Nevertheless, its growth is considerably affected by photoperiod (Masaki, 1972; Arai, 1978a).

The climate may not be aseasonal even in tropical latitudes, where there is often a clear cycle of moist and dry periods that causes differential mortalities at different life stages. This may lead to evolution of a heterodynamic life cycle; therefore, the existence of a homodynamic life cycle can be confirmed only by rearing or by close observations in the field. Unfortunately, very few tropical crickets have been studied in this way.

Teleogryllus occipitalis [formerly *mitratus* (Townsend, 1980)] from Java and Sumatra (Masaki and Ohmachi, 1967), *T. oceanicus* from Tahiti (Masaki, 1972) and Queensland (Hogan, 1965b, 1966, 1971), *Dianemobius fascipes* from Bali (Indonesia), and *D. taprobanensis* from Cebu (the Philippines) and Colombo (Sri Lanka) (Masaki, 1978a) are virtually free of diapause and photoperiodism at any life stage, exemplifying the homodynamic type of life cycle.

Heterodynamic Life Cycles

Cricket, like most other organisms, may show different degrees of tolerance to environmental exigencies at different stages. This is primarily due to changes in size, structure, behavior, or physiological functions. Moreover, different stages may require different resources. If there are more or less regular seasonal changes, the temporal arrangement of life stages may become crucial for survival. The life cycle should then be kept in a more or less fixed phase relation with the environmental cycle. The best-fit seasonal arrangement varies from one species to another, for it should be coadapted with other species-specific physiological and ecological traits to form an integrated system of adaptation.

Due to this seasonal homeostasis, the heterodynamic life cycles of crickets can be classified into ten types as listed in Table I. The overwintering stage is the most important and convenient phase reference point in the life cycle, since at this stage most variations in phase between individual life cycles disappear. Each type of life cycle can thus be defined by the overwintering stage or stages and voltinism (number of generations produced a year).

Overwintering at all the three stages—egg, nymph, and adult—is known in crickets (Table I), but generally each species overwinters in a single stage. The exceptions are crickets with 2-year life cycles and some species at low, temperate latitudes. The frequency distribution of different stages for overwintering is far from random, suggesting that there are constraints for the evolution of an overwintering strategy (Table II). Egg overwintering is the most common type of cricket life cycle, representing about 80% of the known cases in Japan and the eastern United States. Second in frequency is nymph overwintering (~15%). Only a few species are known to pass winter regularly as an adult.

Only for those species that have clearly defined overwintering stages is the concept of voltinism meaningful. In a homodynamic cycle, the succession of generations is not perceived as a population phenomenon, since individual life cycles are not synchronized and there are no clear peaks of adult emergence. Each of the egg-overwintering and nymph-overwintering life cycles is divided into two types based on voltinism. Most species are persistently univoltine or bivoltine within the known ranges of their distribution, but some change from univoltine to bivoltine or multivoltine cycles equatorward, and the latter may merge into homodynamic cycles at lower latitudes. North Florida has more than ten species in which voltinism is difficult to define (Table I). Nonetheless, an apparent absence of young juveniles during winter months synchronizes life cycles to some degree.

TABLE I. Types of Cricket Life Cycles

Basic category	Overwintering stage	Voltinism	Examples
Homodynamic	Not defined	Not defined	<i>Teleogryllus occipitalis</i> (tropical), ^a <i>Gryllus assimilis</i> ^b
Heterodynamic	Egg	Univoltine	<i>Teleogryllus emma</i> , ^a <i>Gryllus pennsylvanicus</i> ^b
		Bivoltine	<i>Dianemobius nigrofasciatus</i> , ^c <i>Oecanthus quadripunctatus</i> ^d
	Nymph	Univoltine	<i>Gryllus campestris</i> , ^e <i>G. veletis</i> , ^b <i>Pteronemobius nitidus</i> ^f
		Bivoltine	<i>Teleogryllus occipitalis</i> (subtropical), ^a <i>Gryllus rubens</i> ^b
		Univoltine	<i>Gryllotalpa africana</i> ^g
	Adult	Univoltine	<i>Gryllus firmus</i> (North Carolina) ^h
	Egg or nymph	Univoltine	<i>Scapteriscus vicinus</i> ⁱ
	Nymph or adult	Univoltine	<i>Gryllus firmus</i> (northern Florida) ^h
	Egg, ^l nymph, ^m or adult	Multivoltine	<i>Nemobius sylvestris</i> ^j
Egg and nymph	Semivoltine	<i>Duolandrevus coulonianus</i> , ^k	
Nymph and adult	Semivoltine	<i>Gryllotalpa africana</i> ^g	

^a Masaki and Ohmachi (1967).^b Alexander (1968).^c Masaki (1973).^d Walker (1963).^e Fuzeau-Braesch (1966).^f Tanaka (1978a).^g Okamoto *et al.* (1956).^h Walker (1980a).ⁱ Hayslip (1943).^j Gabbutt (1959a).^k Tsuji (1951).^l Only diapause eggs can overwinter.^m Young nymphs are not found in winter.

The longest life cycle in crickets requires 2 years, i.e., it is semi-voltine, and the two winters are passed at different stages. For example, in the British Isles, *Nemobius sylvestris* passes the first winter as an egg and the second as a nymph (Brown, 1978; Gabbutt, 1959a). In northern Japan, *Gryllotalpa africana* overwinters as a nymph and again as an adult before reproduction (Okamoto *et al.*, 1956). Eggs that remain dormant for 2 years, as found in some katydids, are not known in crickets.

In both the egg-overwintering and nymph-overwintering types, the univoltine species outnumber the bivoltine or multivoltine ones. About 75% of heterodynamic crickets in Japan and the eastern United States

TABLE II. Distribution of Life Cycle Types among Species of Crickets in Japan and Eastern United States

Locality (approximate latitude)	Generations per year				Overwintering stage(s)				
	1/2	1	2	Not defined	Egg	Nymph	Adult	Nymph and adult	Adult and egg
Japan									
Hokkaido (42–45°N)	1	9	0	0	8	1	0	1	0
Tohoku (37–41°N)	(1) ^a	24	1 (1)	0	21	3	1	1	0
Kanto (35–37°N)	1	35	4 (1)	0	30	8	1	1	0
Kyushu (30–34°N)	1	29	7	0	26	9	1	1	0
United States									
Southeastern Ohio (40°)	1	25	1	0	23	3	0	1	0
Central Northern Carolina (35°)	1	22	7	0	26	3	0	1	0
Northern Florida (30°)	0	17	12	12	19	2	1	3	4

^a Voltinism shown by smaller part of the population.

are univoltine (Table II). The egg-overwintering, univoltine life cycle is the predominant type for crickets in temperate Japan and the United States.

Our use of overwintering stage as the basis for classifying heterodynamic life cycles reflects the fact that seasonal cycles in crickets have been studied almost entirely in temperate climates. Tropical insects often diapause during tropical dry seasons (Denlinger, 1986), and we anticipate that some tropical crickets have drought-passing stages that are analogous to overwintering stages in temperate crickets.

Eastern and Western Tendencies

Comparison of cricket life cycles in Japan with those in North America reveals impressive similarity in the distribution of different types. On

both sides of the Pacific, egg-overwintering is most common, nymph-overwintering comes next, and adult-overwintering is rare. This similarity suggests the importance of preadaptations shared by crickets in different parts of the world in evolving temperate seasonal life cycles. The parallel eastern and western tendencies are not ascribed to the same diapause genes, because the taxonomic comparison (see below) strongly suggests independent evolution in the two areas.

Another aspect of the life cycle similarity between the eastern and western crickets can be seen in voltinism. North of 30°N univoltinism seems to be prevalent among crickets. This is probably due to the relatively slow rate of growth and high thermal threshold for growth in crickets compared with insects that produce a number of generations each year.

Comparison of Taxonomic Groups

Similarity between eastern and western crickets becomes more impressive if we examine distributions of various life cycles among different taxonomic groups. In the subfamily Gryllinae, both egg-overwintering and nymph-overwintering species occur in the Japanese islands and North America. Most species are univoltine, but a few are bivoltine in Japan as well as in North America: *Telegryllus occipitalis* (formerly *taiwanemma*) (Masaki and Ohmachi, 1967), *Velarifictorus parvus* (Masaki, 1972) in Japan, *Gryllus rubens* in North America (Alexander, 1957, 1968). In the subfamily Nemobiinae, egg overwintering is the predominant type, but only one in each of the two areas hibernates as a nymph: *Pteronemobius nitidus* in Japan (Masaki and Oyama, 1963) and *Nemobius* [*Pictonemobius*] *ambitiosus* in North America (Alexander, 1968). Moreover, some species in this subfamily are bivoltine in the southern half of their distribution in both the eastern and western temperate areas, probably reflecting their rapid rate of maturation due to small adult size (Alexander and Thomas, 1959; Fulton, 1931; Masaki, 1978*a,b*, 1979*a,b*). In the subfamily Oecanthinae, all species hibernate as eggs in both areas (Ohmachi and Matsuura, 1951; Walker, 1962, 1963). The rarest type, adult overwintering, is represented by *Gryllotalpa africana* in Japan and *Neocurtilla hexadactyla* in North America (Fulton, 1951; Okamoto *et al.*, 1956), both belonging to the subfamily Gryllotalpinae.

These similar taxonomic distributions of life-cycle types are not due to the direct inheritance of genes controlling the life cycle. In the Gryllinae, for example, not even one genus is shared by the two areas being compared, except for recent immigrants. Both egg-overwintering and nymph-overwintering forms are represented by Japanese members of the

Afro-Asian genus *Teleogryllus* and by North American members of the Euro-American genus *Gryllus*. Moreover, each genus includes homodynamic tropical species, *T. occipitalis* in Asia and *G. assimilis* in America. There is the possibility that some homodynamic species in each genus is the ancestor of the heterodynamic temperate species. The similarity is likely due to independent parallel evolution in the two areas. Adaptation to temperate climates can occur repeatedly even in a single genus.

When the two closely related egg-overwinterers *Teleogryllus emma* and *T. yezoemma* are crossed, diapause is not properly expressed in hybrid eggs, suggesting a different, and therefore an independent origin, of their diapause genes (Ohmachi and Masaki, 1964). Based on electrophoretic data from five eastern species and two southwestern populations, on the other hand, Harrison (1978) suggested that each of the nymph-overwintering and egg-overwintering cycles has arisen only once in the evolution of the genus *Gryllus* in North America. This does not, however, refute the possibility stated above.

Regulation of Life Cycles

The various types of seasonal life cycles in temperate regions are generally controlled by diapause and developmental characteristics, but only about 1% of the known 3000 species of cricket have been studied experimentally. The occurrence of egg diapause can be easily recognized by the prolonged period of incubation at moderate temperatures. If eggs obligatorily enter diapause of considerable intensity, a univoltine life cycle is established. If diapause is facultative, the egg-overwintering life cycle can be either bivoltine or univoltine. In either case, the developmental rate in the nymphal stage is generally high compared with nymph-overwinterers, and at least some species—such as *Gryllus ovisopis*, *Teleogryllus emma*, *T. yezoemma*, and *Velarifictorus micado* (autumn form, formerly *aspersus*) among univoltine species and *Dianemobius nigrofasciatus* (formerly *fascipes*), *D. mikado* (formerly *taprobanensis*), and *D. csikii* among bivoltine species—control the timing of maturation, and therefore of oviposition, by response to photoperiodic cues.

On the other hand, nymph-overwintering species generally lack the ability to enter diapause at the egg stage, and their nymphal growth is somewhat slower than egg-overwintering species, at least under certain photoperiods (even at high temperatures).

The contrast between egg-overwintering and nymph-overwintering crickets was illustrated for the genus *Gryllus* by Bigelow (1962). At high temperatures, however, nymphs of nymph-overwintering species contin-

TABLE III. Summary of Diapause Types and Photoperiodic Responses Controlling the Four Major Types of Cricket Life Cycle

Overwintering stage	Life-cycle type		Photoperiodic response			Species studied
	Volitinism	Diapause	Factor controlled	Type		
Nymph	1	Obligatory	Prediapause development	Short-day		<i>Pteronemobius nitidus</i> , ^a <i>Velarifactorius micado</i> (spring), ^b <i>Gryllus campestris</i> ^c
Nymph	≥2	Facultative	Termination of diapause	Short/long-day		<i>Pteronemobius nitidus</i> , ^a <i>Velarifactorius micado</i> (spring), ^b <i>Gryllus campestris</i> ^c
Nymph	≥2	Facultative	Induction of diapause	Long-day		<i>Velarifactorius parvus</i> , ^d <i>Teleogryllus occipitalis</i> (subtropical), ^e <i>Dianemobius taprobanensis</i> , ^f <i>D. fuscipes</i> , ^f <i>Gryllus integer</i> , ^g <i>Gryllus</i> sp. ^h
Egg	1	Obligatory	Nymphal development	Short-day		<i>Dianemobius nigrofasciatus</i> , ⁱ <i>D. mikado</i> , ^f <i>D. furumagiensis</i> , <i>P. flavoantennalis</i> , <i>P. ohmachi</i> , ^j <i>T. emma</i> , ^k <i>T. yesoemma</i> , ^l <i>V. micado</i> (autumn), ^m <i>Loxoblemmus aomoriensis</i> , ⁿ <i>L. equestris</i> , ⁿ <i>Modicogryllus nipponensis</i> ^o
Egg	≥2	Facultative	Induction of diapause	Long-day		<i>Dianemobius nigrofasciatus</i> , ⁱ
Nymphal development			Nymphal development	Intermediate or short-day		<i>D. csiki</i> , ^{f,j} <i>D. mikado</i> ^f <i>Dianemobius nigrofasciatus</i> , ⁱ <i>D. csiki</i> , ^{f,j} <i>D. mikado</i> ^f

^a Masaki and Oyama (1963), Tanaka (1978a, 1979).^b M. Watanabe (unpublished).^c Fuzeau-Braesch (1966), Ismail and Fuzeau-Braesch (1976).^d Masaki (1972).^e Masaki and Ohmachi (1967).^f Masaki (1978a, 1979a).^g Alexander (1968).^h Fuzeau-Braesch (1975).ⁱ Masaki (1973).^j S. Masaki (unpublished).^k Masaki (1967).^l Masaki (1966).^m Saeiki (1966b).ⁿ Masaki (1977).^o Tanaka (unpublished).

ued to feed and grow, though at a reduced rate, and diapause was not so clear as in the egg stage. However, photoperiodic control combined with the seasonal change in temperature would ensure nymphal overwintering.

The diapause and development characteristics in each type of life cycle are summarized in Table III. Further details of the responses involved will be discussed below, following the life stages from egg to adult. We shall then discuss the evolution of such physiological functions and its impact on speciation.

EGG STAGE

Water Uptake

Cricket eggs, when deposited, contain all the necessary materials for embryogenesis but water. As in other insects that lay their eggs in moist substrates (such as soil or plant tissue), cricket eggs absorb water through their shells when the embryo has reached a particular stage of development (Fig. 1). In *Teleogryllus commodus*, this occurs just before the embryo reaches the stage at which diapause occurs (Browning, 1953, 1965). In eggs of *Acheta configuratus*, *Grylloides supplicans*, and two sibling species of *Acheta domesticus* (Canadian and Pakistani), the time of water absorption is generally the earlier, the more rapid is embryonic development, indicating that the embryonic stage during which water is absorbed is similar among them (McFarlane *et al.*, 1959). However, water can be taken in without the embryo; the serosa and yolk cleavage are responsible for water absorption in *Scapsipedus marginatus* (Grellet, 1971). In any case, the eggs must absorb water in order to develop beyond a certain stage, and the amount of water absorbed varies from about 60 to 120% of the weight of newly laid eggs, depending on the species or strain (McFarlane *et al.*, 1959; Browning, 1965).

This water requirement seems to be universal among crickets, and all the observed nondiapause eggs of *Dianemobius fascipes*, *D. taprobanensis*, *Pteronemobius nitidus*, *Velarifictorus parvus*, *Gryllus bimaculatus* (S. Masaki, unpublished data), *Scapteriscus acletus*, and *S. vicinus* (T. J. Walker, unpublished data) show a clear increase in egg size at certain times after deposition. When an egg undergoes diapause, water uptake occurs either before or after diapause, but this timing is fixed for each species. Thus, *Teleogryllus emma*, *T. yezoemma*, *Velarifictorus micado* (autumn form), and *Gryllus pennsylvanicus* absorb water before entering diapause, while *Loxoblemmus aomoriensis*, *Dianemobius nigro-*

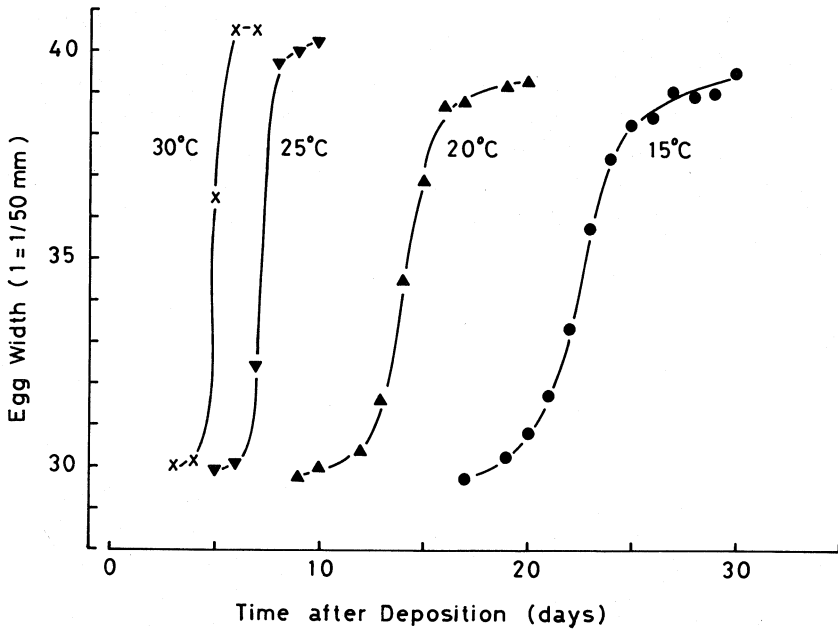


FIG. 1. Swelling due to water uptake of eggs of *Teleogryllus emma* at various temperatures. Width is given in units of 1/50 mm. [From Masaki (1960).]

fasciatus, *D. mikado*, and *Pteronemobius ohmachi* mainly do so only after the completion of diapause (Masaki, 1960). In the latter case, swelling is an unmistakable sign of the egg's termination of diapause. The fact that water absorption can take place either before or after diapause indicates that water supply is not generally involved in the induction of diapause. The shell is persistently permeable to water throughout the egg stage in *Teleogryllus commodus* (Browning, 1969a,b; Browning and Forrest, 1960). In *Acheta domesticus*, as far as is shown by water loss in an unsaturated atmosphere, the shell is more permeable during the period of water absorption than either before or after (McFarlane and Kennard, 1960). This conflicts with the observation that diapause-eliminated eggs of *T. commodus* and nondiapause eggs of *T. oceanicus* are much more sensitive to desiccation prior to the period of water uptake (Hogan, 1967). Most studies agree that water enters the egg through the general surface rather than through special structures.

Water uptake by eggs after oviposition contributes to the fitness of female crickets, since a larger number of "condensed" eggs will fit into the restricted space of the body cavity than fully hydrated ones. However, this imposes selection pressure on the length of ovipositor. Among Japa-

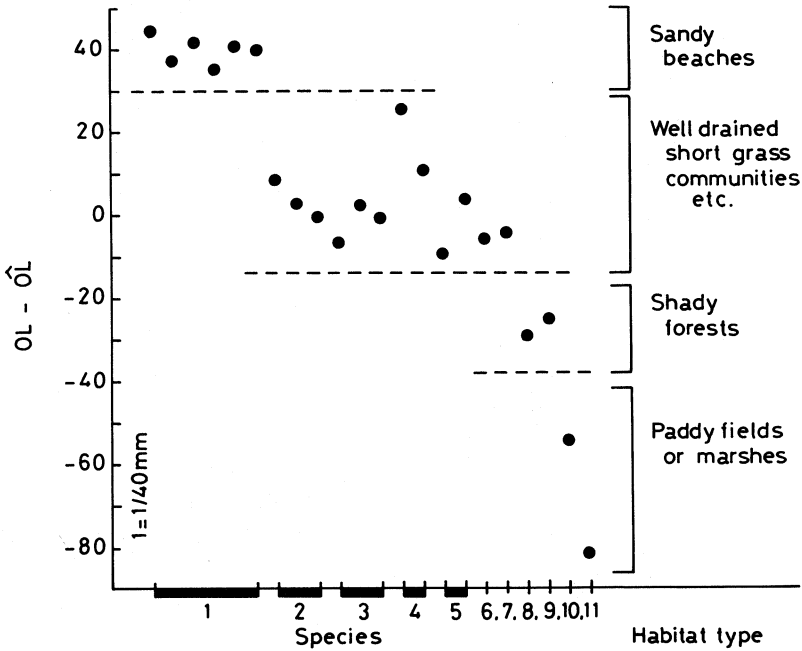


FIG. 2. Differences between observed means of ovipositor length OL and calculated values \hat{OL} based on the interspecific allometric equation $\ln \hat{OL} = 2.06 \ln HW - 3.94$, where HW is head width, in ground crickets belonging to *Dianemobius* and *Pteronemobius*. Along the abscissa, species are arranged according to the moisture conditions of their habitat (from dry to moist) as indicated on the right. Multiple points for a single species represent means of widely separated geographical samples. (1) *D. csikii*, (2) *D. mikado*, (3) *D. taprobanensis*, (4) *D. nigrofasciatus*, (5) *D. fascipes*, (6) *D. furumagiensis*, (7) unidentified species, (8) *P. flavoantennalis*, (9) *P. nigrescens*, (10) *P. nitidus*, (11) *P. ohmachii*. [From Masaki (1986).]

nese ground crickets, there is a tendency for species inhabiting drier places, such as *Dianemobius csikii*, *D. nigrofasciatus*, and *D. mikado*, to have longer ovipositors than those inhabiting moist places, such as *Pteronemobius nitidus*, *P. ohmachii*, and *P. nigrescens* (Fig. 2). A longer ovipositor, capable of inserting eggs deeper into the soil, is clearly more adaptive in drier sites than in moist sites, for it confers on the eggs a better chance to absorb water and also better protection against water loss.

Temperature Requirements for Embryogenesis

About 30 species of crickets have been examined for their duration of embryogenesis. These include species of Gryllinae, Nemobiinae, Oec-

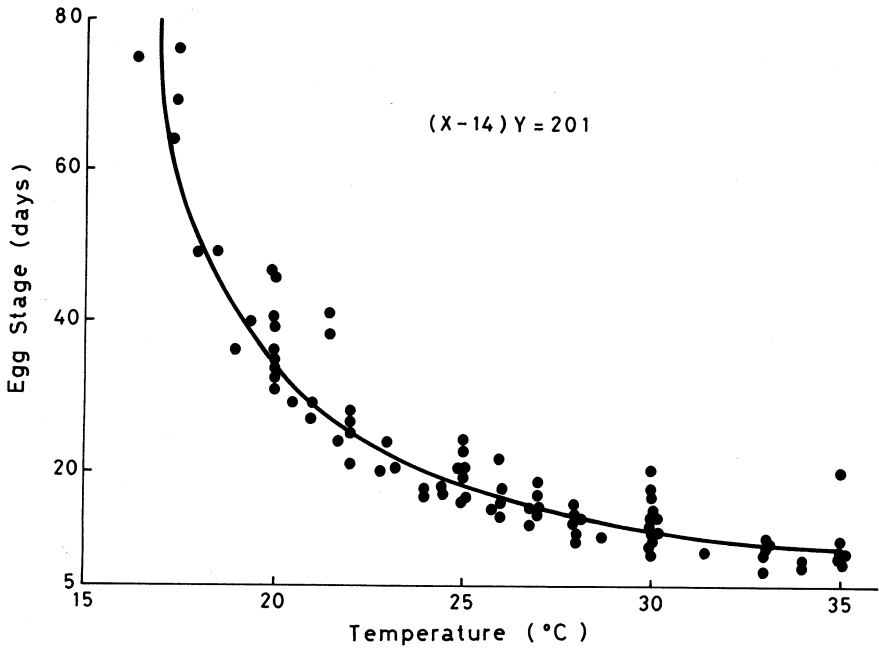


FIG. 3. Development time in nondiapausing or postdiapausing eggs of crickets as a function of temperature. Data from about 30 species; various sources.

anthinae, and Gryllotalpinae that have different geographical ranges, habitat preferences, egg sizes, and life cycles (e.g., Bell, 1979; Bigelow, 1962; Masaki, 1960; Okamoto *et al.*, 1956; Rakshpal, 1964). Despite their ecological diversity, their durations of embryogenesis as a function of temperature are very similar (Fig. 3). Data on the means or modes of nondiapausing and postdiapausing incubation period were combined, since diapause sets in within a few days after oviposition and embryogenesis occurs largely in the postdiapause stage.

A conventional hyperbolic function fitted to the data in Fig. 3 describes the relation between the incubation period Y in days and the temperature X in $^{\circ}\text{C}$ as

$$(X - 14.4)Y = 201.0$$

Browning (1952a) fitted a logistic equation to the development rate ($1/Y$) of *Teleogryllus commodus* eggs after cold treatment. Others (e.g., Logan *et al.*, 1976) have used even more complicated equations for similar data;

however, the accuracy of data in Fig. 3, from various species obtained by various workers, allows only rough fitting to any model. The hyperbolic equation estimates the development threshold as 14°C and thermal constant as 201 day-deg.

Utida (1957) compiled a frequency distribution of the development thresholds of insects and showed that a peak occurred between 10 and 12°C. Crickets, as eggs, are therefore thermophilous—i.e., they require higher temperatures for development than many other insects.

Intensity of Diapause at High Temperature

Even though most crickets enter diapause as eggs, the morphological state of the diapausing embryo has been examined only in a few species. Three species in the Gryllinae, *Teleogryllus commodus* in Australia (Brookes, 1952; Browning, 1952*b*; Hogan, 1960*a*), *T. emma* in Japan (Umeya, 1950), and *Gryllus pennsylvanicus* in North America (Rakshpal, 1962*b,e*), enter diapause at similar early stages in anatrepsis. Since these species are distributed in widely separated parts of the world, their similar diapause stages are the result of convergent evolution. *Homoeogryllus japonicus* enters diapause at a somewhat earlier stage (Umeya, 1950). *Allonemobius fasciatus* is able to enter diapause at two different embryonic stages. A summer diapause intervenes at an early stage in anatrepsis at 30°C, and a winter diapause at a later stage before catatrepsis at 20°C. If eggs diapausing at 30°C are transferred to 20°C, they resume development, but again enter diapause as they reach the stage for winter diapause (Tanaka, 1984). We have no example of crickets having diapause during catatrepsis or later. There may be some physiological preadaptation or constraint for the evolution of diapause at these particular stages. During the embryogenesis in *Gryllus veletis*, which has no egg diapause, there are three phases of sudden rises in respiratory metabolism: in anatrepsis to postanatrepsis, postkatatrepsis, and prehatching periods (Rakshpal, 1962*c*). The observed diapause stage in other species seems to be linked to the first phase, but the physiological implication is unknown.

During diapause the respiratory rate remains low even at high temperatures (MacFarlane and Drummond, 1970; Rakshpal, 1962*f*). In contrast to the rather uniform rate of embryogenesis, the duration of egg diapause at high temperatures is highly variable among different species (Fig. 4), among populations in the same species (Fig. 19), and even among individuals in the same population (Fig. 5). In some species of crickets, the temperature ranges for the completion of diapause and for embryo-

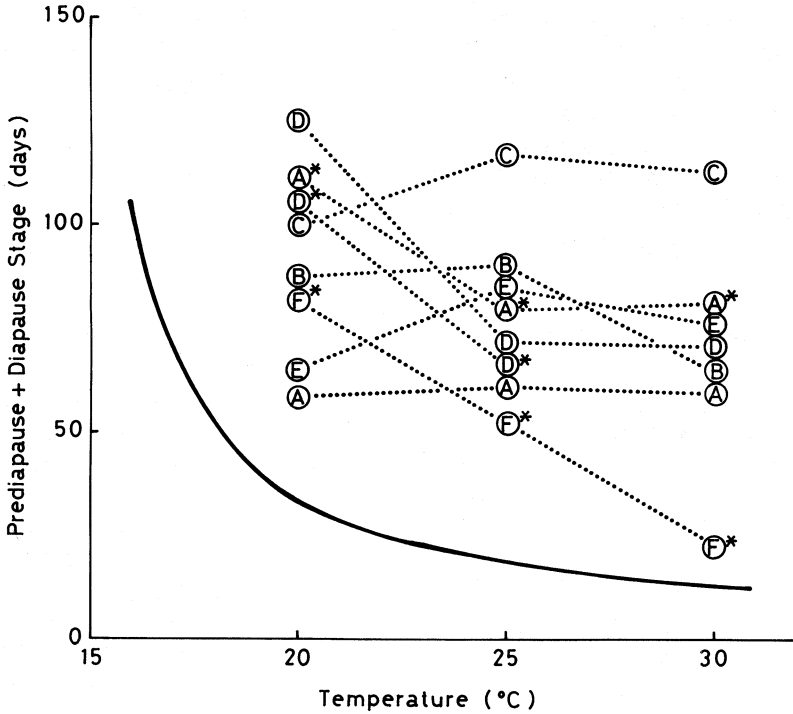


FIG. 4. Mean duration of diapause (including a few days of prediapause development) in several species of cricket at constant temperatures. (A) *Teleogryllus emma*, (A*) *T. emma* from Tsu (34°N), (B) *Velarifictorus micado* (autumn form), (C) *Loxoblemmus aomoriensis*, (D) *Dianemobius nigrofasciatus*, (D*) *D. nigrofasciatus* from Tsu, (E) *D. mikado*, (F*) *T. commodus* from Adelaide (35°S). All samples without asterisk are from Hirosaki (40°N). The curve is the development time versus temperature hyperbola redrawn from Fig. 3 to show what values were subtracted from total development time to yield the plotted points. [Data from Masaki (1960) and unpublished observations.]

genesis overlap broadly, and diapause eggs may hatch without any exposure to cold (Browning, 1952*b,c*; Hogan, 1960*a*; Masaki, 1960, 1962, 1963, 1965, 1978*a*; Masaki *et al.*, 1979; McIntyre, 1978; Rakshpal, 1962*e*, 1964; Tanaka, 1984; Walker, 1980*a*). The duration of diapause can therefore be measured at constant temperatures without any complicating influences of temperature change.

Masaki (1960) compared several species of egg-diapausing crickets from Hirosaki (40.5°N) at constant temperatures. The mean duration of the egg stage varies considerably from species to species inhabiting the same locality and therefore exposed to similar climatic conditions. If the duration of nondiapause or postdiapause egg stage is subtracted from the entire incubation period, the approximate duration or intensity of diapause

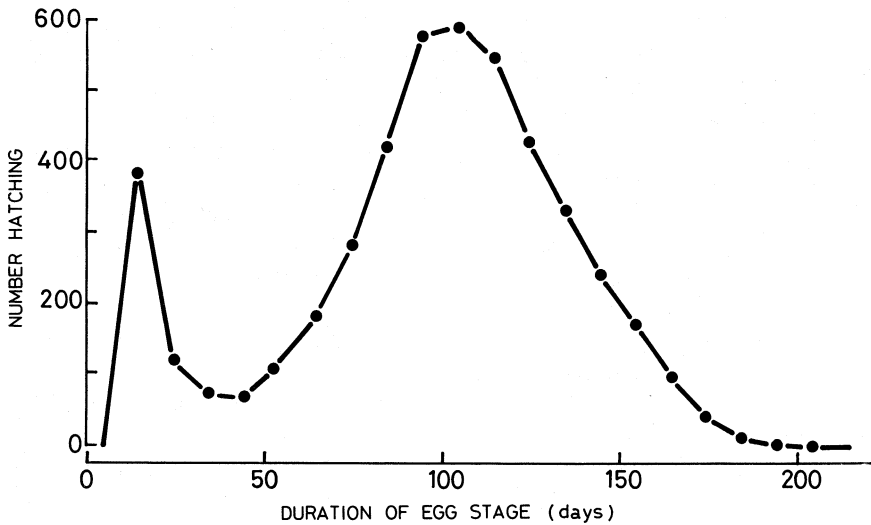


FIG. 5. Distribution of duration of egg stage at 25°C in a bivoltine strain of *Dianemobius mikado*, showing bimodality due to nondiapause and diapause pathways of development. These eggs were laid by females reared in various photoperiods (11L:13D to 16L:8D). [From Masaki (1979a).]

at each temperature is obtained (Fig. 4). The duration of diapause varies from one species to another at each temperature and also with temperature in each species. In most cases the mean duration of diapause falls between 2 and 4 months. It varies with temperature in different ways in different species. In *Teleogryllus emma* from Hirosaki (Fig. 4A), the mean duration of diapause varies less than 5 days when temperature is increased from 20 to 25 to 30°C, i.e., the duration of diapause is almost perfectly temperature-compensated. On the other hand, *Dianemobius nigrofasciatus* (Fig. 4D) shortens its diapause stage at 25 or 30°C to nearly half that at 20°C. Although overall incubation period in *D. mikado* at 30°C is slightly shorter than at 25°C, this is due to accelerated embryogenesis, and the time spent in diapause is shortest at 20°C, giving the rate of diapause completion a negative thermal coefficient between 20 and 25°C (Fig. 4E).

A remarkable positive coefficient for diapause completion is found in *Teleogryllus commodus* (Fig. 4F*). The mean duration of diapause varies from 80 to only 20 days with a temperature rise from 20 to 30°C and shortens further and almost vanishes at 35°C (Masaki *et al.*, 1979).

The maintenance of diapause at high temperatures is ecologically important, since eggs laid early in adult life should persist in diapause under warm conditions before winter. The observed intensity of diapause in the morphogenetic range of temperature seems to meet this require-

ment. In *Pteronemobius ohmachi*, diapause is more intense than in the examples given above, and this is presumably related to its rapid nymphal growth being completed in July, about 1 month earlier than other local univoltine egg-overwinterers. At 20°C the egg stage lasts on the average 224 days, twice as long as that of *T. emma* or *D. mikado*. At higher temperatures, many eggs fail to hatch in 300 days. This firm diapause keeps eggs in diapause until winter even when they are laid before the height of summer. In a semivoltine population of *Nemobius sylvestris*, the egg diapause seems to be even more intense, and all eggs fail to hatch when kept constantly at 20°C (Brown, 1978).

In *Teleogryllus emma*, diapause is intensified by an exposure to high temperature at the early egg stage (Masaki, 1962). This is probably an adaptation to maintain diapause before winter. When eggs of the Tsu (34°N) strain of this field cricket are kept at constant temperatures, the mean duration of incubation is 96 days at 30°C and 157 days at 20°C. If the eggs are exposed to 30°C for 8 days before incubation at 20°C, the duration of egg stage is prolonged by more than 1 month—from 157 to 193 days. Conversely, incubation at 30°C after exposure to 20°C for 20 days shortens the egg stage from 96 to 88 days.

This effect of temperature on the intensity of diapause changes during the course of diapause. When eggs of the Hirosaki strain of *T. emma* are exposed to 30°C for various periods before incubation at 20°C, the total incubation time increases with increased high-temperature exposure up to about 14 days, after which the effect gradually decreases (Fig. 6). The intensification of diapause by high temperature may decrease the risks of untimely hatching of those eggs laid early in the reproductive season. In *Allonemobius fasciatus* and *Gryllus pennsylvanicus*, the intensity of diapause decreases as eggs are laid later in autumn (Tanaka, 1984; Rakshpal, 1962*b*). This variation appears to be due to a maternal influence, but the actual environmental factor involved remains unknown.

Diapause Termination by Low Temperature

Like the eggs of many other hibernating insects, eggs are able to complete diapause at temperatures well below the developmental threshold. When diapausing eggs of *Teleogryllus emma* are incubated at 25°C after exposure to 5–10°C for 2–3 months, they resume development without appreciable delay and a clear peak of hatching occurs in 2–3 weeks (Masaki, 1962, 1963, 1965). Such eggs completed all or nearly all of diapause development during exposure to cold. The proportion of eggs hatching in 2–3 weeks increases in a sigmoid fashion as a function of the du-

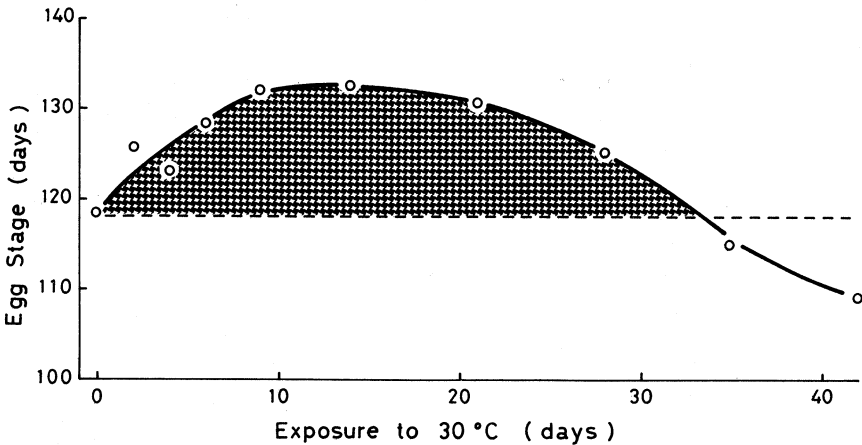


FIG. 6. Intensity of diapause in *Teleogryllus emma* eggs as a function of duration of exposure (from deposition) to a high temperature (30°C). Diapause intensity is represented by duration of the egg stage (ordinate). Shaded area indicates the lengthening of diapause due to the high-temperature treatment. Postexposure incubation was at 20°C. [Data from Masaki (1962).]

ration of cold. From such a curve the median effective duration of cold can be determined (Browning, 1952*b,c*).

The termination of diapause by artificial or natural exposure to cold has also been observed in *Loxoblemmus aomoriensis* (Masaki, 1960), *Teleogryllus yezoemma* (Masaki, 1961), *T. commodus* (Browning, 1952*b,c*; Hogan, 1960*a*; Masaki *et al.*, 1979), *Oecanthus nigricornis* (Bell, 1979), *Gryllus pennsylvanicus* (Rakshpal, 1962*d,e*), *Nemobius sylvestris* (Brown, 1978), *N. allardi* (Rakshpal, 1964), *Pteronemobius nigrovus* (McIntyre, 1978), and *P. ohmachii*, *Dianemobius nigrofasciatus*, and *D. mikado* (Masaki, 1960).

Among these, *T. commodus* has been studied most extensively. Browning (1952*c*) determining that 12.7°C is the optimum for promoting diapause development in treatments of eggs before the morphological stage of diapause, and that a lower temperature, say 8.5°C, is less effective. Hogan (1960*a*), using eggs already in diapause stage, found 10°C to be near the optimum in the nonfreezing range of temperature. He also observed that the time of cold exposure required for terminating diapause was shorter when the subsequent incubation temperature was higher. Similar tendencies are found in *Loxoblemmus aomoriensis* and *Dianemobius nigrofasciatus* (Masaki, 1960). Masaki *et al.* (1979) analyzed such interactions of temperatures in more detail with *T. commodus* and discovered that, in the late stage of diapause, a high temperature exerted a diapause-

terminating effect within a short period of time even without any previous exposure to cold. Thus, when eggs of this cricket that have been diapausing for about 60 days at 20°C are exposed to 30°C for only 3 days and returned to 20°C, many of them resume development and a clear peak of hatch occurs. A temperature rise seems to serve as a trigger for the resumption of development. Therefore, the effect of cold exposure on the diapause termination should be interpreted carefully, since the result may vary with the subsequent incubation temperature.

Hogan (1960*b*) ended diapause in *T. commodus* eggs by experimentally exposing them to temperature as low as -16.5°C. The rate of termination showed a negative temperature coefficient between -16.5 and +5°C. Only a 20-min exposure was required to terminate diapause at -16.5°C. On the other hand, exposure to -5 to -6°C for 2-3 weeks did not show any effect on the termination of diapause in the eggs of *Gryllus pennsylvanicus* (Rakshpal, 1963). The effect of subzero temperature in *T. commodus* is probably due to some disturbance of the mechanism maintaining diapause and has no ecological significance. In the field the eggs of this field cricket do not usually experience subzero temperature. However, these effects of subzero temperature, together with those of urea and ammonia, may provide means of approaching the physiological mechanism of diapause (Hogan, 1961, 1962*a,b*, 1964, 1965*a*; MacFarlane and Hogan, 1966).

Tolerance to Cold

Prediapause eggs of *Telegryllus commodus* are highly susceptible to cold (Hogan, 1960*b*). Even at 5°C all die within 25 days. At freezing temperatures, much shorter periods of exposure are lethal: about 120 hr at 0°C, 4 hr at -7.5°C, and 3 hr at -10°C. At the diapause stage, the eggs become more resistant and survive 2 months at 5°C. The association of cold tolerance with diapause is also shown by comparison with non-diapausing eggs of *T. oceanicus* from Queensland. In these eggs the mortality reaches 100% after 3 months at 12°C, while none of the diapausing eggs of *T. commodus* die (Hogan, 1966). Even in the latter, however, freezing temperatures are detrimental, and 50% mortality is reached in ~16 days at 0°C, 15 days at -5°C, and 9 days at -7.5°C. The eggs can withstand -10°C for only a few days (Hogan, 1960*b*).

High susceptibility to low temperatures, even to those well above 0°C, at the prediapause stage and an increased tolerance at the diapause stage are also demonstrated for *T. emma* (Fig. 7) (S. Masaki, unpublished data) and *Gryllus pennsylvanicus* (Rakshpal, 1962*d*, 1963). In the diapause

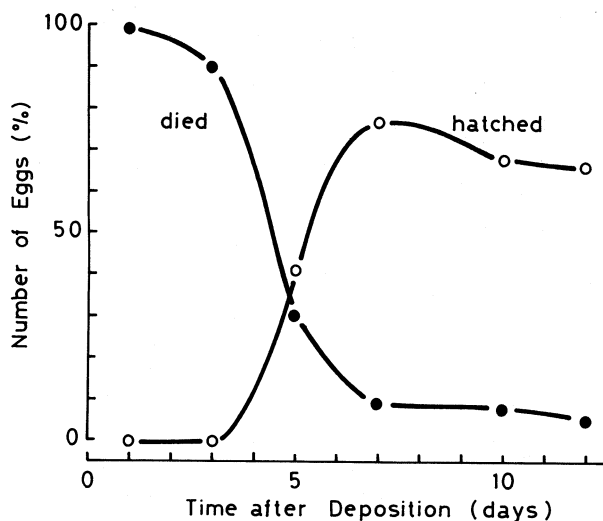


FIG. 7. Egg mortality and percentage hatching (ordinate) at 25°C following prolonged exposure to about 10°C at various times after egg deposition (abscissa) in *Teleogryllus emma*. Each point represents the mean of five cold exposures of 40–80 days. [S. Masaki (unpublished data).]

stage, *T. emma* is more cold-hardy than *T. commodus*, for it can survive exposure to 0–1°C for more than 4 months (Masaki, 1963, 1965). Post-diapause eggs of *G. pennsylvanicus* can withstand 6–7°C for 3 months, an exposure that is lethal to freshly laid eggs (Rakshpal, 1962d).

Glycerol, known as an antifreezing substance in some insects, is accumulated in the ovaries of *T. emma* and passes into the fresh eggs; however, its concentration drops sharply before the diapause stage is reached. Its bearing on the cold tolerance of the eggs is not known (Irie *et al.*, 1979).

Incidence of Diapause

Typical univoltine egg-overwinterers, such as *Teleogryllusemma*, *T. yezoemma*, *Loxoblemmus aomoriensis* (Masaki, 1960), *Gryllus pennsylvanicus* (Bigelow, 1958, 1960a, 1962; Rakshpal, 1962a), and *G. ovisopis* (Walker, 1974, 1980a) produce only diapause eggs. Their diapause is obligatory in the sense that no environmental modification of its incidence occurs in the range of normal ecological conditions.

On the other hand, bivoltine species can select one of two possible

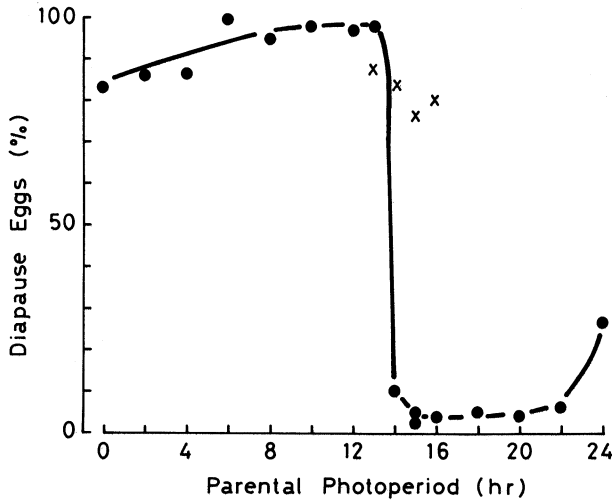


FIG. 8. Percentage diapause as a function of parental photoperiod in eggs of the Hachioji strain of *Dianemobius nigrofasciatus* (35°N). (●) 27°C, (×) 23°C. [T. Kidokoro (unpublished data).]

pathways: diapausing or nondiapausing. This facultative diapause is programmed through interaction between the genotypes and seasonally changing environmental conditions. Examples are afforded by several species of ground cricket, *Dianemobius nigrofasciatus*, *D. mikado*, *D. csikii*, and *Pteronemobius ohmachi* in Japan (Masaki, 1973, 1978a, 1979a) and *Pteronemobius bigelovi* and *P. nigrovus* in New Zealand (McIntyre, 1978). In *Nemobius sylvestris* in Europe, the egg diapause seems to be facultative, because it occurs in the northern semivoltine population with both nymph- and egg-overwinterings, but is averted in the southern univoltine populations with only nymph-overwintering (Brown, 1978). Many other bivoltine species of ground crickets and tree crickets should also have facultative egg diapause (e.g., *Allonemobius fasciatus*, *Oecanthus argentinus*, *O. celerinictus*, and *O. quadripunctatus* in the southeastern United States, and *O. indicus* in southern Japan).

Factors responsible for programming egg diapause in crickets are not well known. A few analyzed examples indicate that day length, the most reliable seasonal cue, is an important factor. As might be expected, the environmental determination of egg diapause is mainly a maternal function. In both *D. nigrofasciatus* and *D. mikado*, females reared in long days lay nondiapausing eggs and those reared in short days lay diapausing eggs (Fig. 8) (Kidokoro and Masaki, 1978; Masaki, 1973, 1978a). The expression of this maternal photoperiodic response is suppressed by a

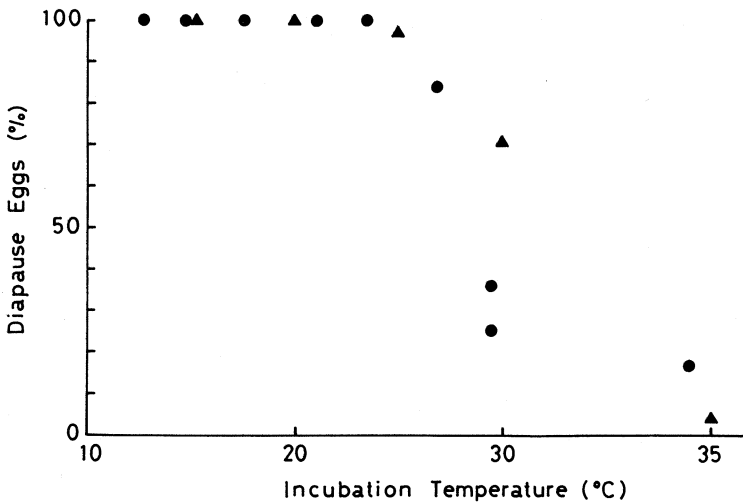


FIG. 9. Percentage diapause as a function of incubation temperature in eggs of *Teleogryllus commodus*. (●) Data by Hogan (1960a); (▲) data by Masaki *et al.* (1979).

low temperature, and many diapause eggs are produced even in long days. When day length is shifted from long to short or vice versa during the adult life, the type of eggs laid switches (Kidokoro and Masaki, 1978). Therefore, photoperiodic determination of egg diapause proceeds during oogenesis.

The maternal influence is to some extent modified by temperature acting directly on eggs. Adults of *D. nigrofasciatus* at Tsu (34°N) in October lay diapause eggs, which hatch after 75–152 days at 20°C. However, about 5% hatch between days 20 and 30 at 25°C and about 11% between days 14 and 21 at 30°C, that is, in times corresponding to the duration of non-diapause development at respective temperatures (S. Masaki, unpublished observations). A more remarkable effect of high temperature is seen in *T. commodus*; the critical temperature is about 23°C, below which all viable eggs enter diapause and above which the percentage diapause decreases with increasing temperature (Fig. 9) (Hogan, 1960a; Masaki *et al.*, 1979). Most eggs become free of diapause at 35°C. Eggs are most sensitive to this effect of temperature 5–6 days after oviposition at 23.3°C (Hogan, 1960a). Whether this temperature dependence of diapause is common or not among crickets is not known, but Walker's (1980a) data suggest that it occurs in *Gryllus firmus*. At least some strictly univoltine species, such as *T. emma* and *L. aomoriensis*, fail to avert diapause at 30°C. By contrast, *Allonemobius fasciatus* may avert summer diapause

at 20°C, but not at 30°C, although winter diapause at a later embryonic stage occurs at either the low or the high temperature (Tanaka, 1984).

Genetic Control of Egg Diapause

Although egg diapause in bivoltine ground crickets is apparently maternally induced, crosses between species with and without egg diapause demonstrate a direct effect of genes of the male parent. For example, in eggs from crosses between *Gryllus pennsylvanicus* females and *G. assimilis* males, the latter's nondiapause character is strongly expressed and most eggs hatch in 19 days (Bigelow, 1960*b*). Hogan (1965*b*) crossed the nondiapausing Ayr (19°S) population of *Teleogryllus oceanicus* to the diapausing Brisbane (27°S) and Melbourne (37°S) populations of *T. commodus*. In all the combinations including Ayr males or females, the eggs hatched in a period almost comparable to the nondiapause egg stage (see also Bigelow and Cochaux, 1962; Hogan, 1966). However, close morphological observations and measurements of the respiratory rate revealed a brief period of diapause whenever the male parents were the diapausing species (MacFarlane and Drummond, 1970).

When *Teleogryllus occipitalis*, a species that lacks egg diapause, is crossed with either of two egg-diapausing species *T. emma* and *T. yezoemma*, many hybrid eggs hatch within a short period, but the hatching peak is delayed for a few days and a small proportion of eggs persist alive after all eggs of the nondiapausing species have hatched (Ohmachi and Masaki, 1964). There was no clear difference between the reciprocal crosses.

The above four instances of crosses between diapause and nondiapause species have hybrid eggs in which diapause was remarkably shortened, if not completely averted. This similarity may or may not be ascribed to a common physiological mechanism, but there is no reason to assume a common genetic background. Unfortunately, further genetic analysis is not possible because most of these hybrids are sterile.

On the other hand, fertile hybrids can be obtained between the autumn (egg-diapausing) and summer (nymph-overwintering) forms of *Velarifictorus micada* (M. Watanabe, unpublished data) (Fig. 10). At 25°C the egg stage is on the average about 2 months longer in the former than in the latter. The reciprocal hybrid crosses produce eggs showing two peaks of hatch, corresponding to nondiapause and diapause incubation periods, respectively. The mean incubation time is more or less intermediate between the parental forms. A similar situation persists in F₂ eggs. The F₃ eggs derived from F₂ eggs that had hatched in 10–29, 46–75, and 85–134 days were incubated separately. All three groups showed

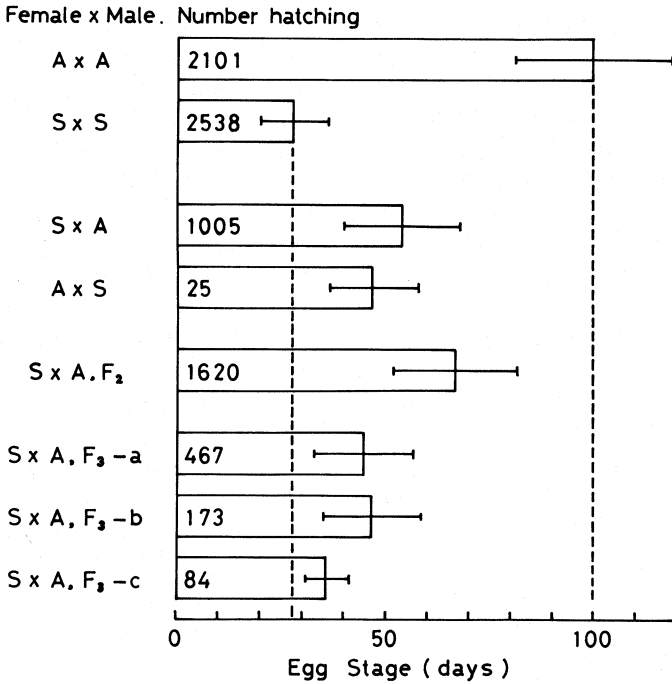


FIG. 10. Duration of egg stage at 25°C in the autumn and spring forms of *Velarifictorus micado* and hybrids between them. Rectangles show means and lines show standard deviations. A, Autumn form; S, summer form. F₂'s were derived from early (a), middle (b), and late (c) hatching F₂'s. [M. Watanabe (unpublished data).]

bimodal hatching curves and the mean hatching times were again intermediate between the summer and autumn forms. This suggests that hybrids have a polygenic system that produces a unimodal distribution of diapause intensity that translates, via a threshold effect, into a bimodal distribution of hatching times. In other words, diapause and nondiapause are not discrete, genetically segregating traits; and quantitative variations determine both the proportion and intensity of diapause.

NYMPHAL STAGE

Number of Molts

In crickets, the number of molts to reach adulthood varies considerably from species to species and also in the same species, due to either

genetic variation or environmental modification (Table IV). Information is available for only about 30 species, and no general tendency in the variation is apparent. Fulton's (1915) early observations on six North American species suggest constancy of five juvenile instars in the Oecanthinae, the smallest number of molts known for crickets. In other subfamilies, the number of nymphal instars is more variable. Fewer than five has not been reported, and the largest recorded number is 14 [*Acheta domesticus* (Bate, 1971)]. Practically the whole range of variation may be found even in a single species [*Gryllus* sp. from Algeria (Fuzeau-Braesch, 1975)].

Some variations in number of molts may be genetic. Under the same room conditions, the northern Hokkaido strains of *Teleogryllus yezoemma* mature after seven instars, while the southern Honshu strains usually take eight instars. This increased number of ecdyses accompanies increased development time and adult size (F. Ichinohe, unpublished data; Masaki, 1966). From the association of development time with number of molts, it can be predicted that the latter may be modified by exogenous factors affecting growth and differentiation. As will be shown later (pp. 376–382), crickets regulate their nymphal development in response to photoperiod, and this seems to be accomplished partly through the timing and number of molts. The egg-overwintering ground crickets *Dianemobius nigrofasciatus* and *D. mikado* mature after six nymphal stages in short days (12L:12D or 13L:11D), but require two or three additional molts during the prolonged nymphal stage in long days (14L:10D or 16L:8D) (S. Masaki, unpublished data).

At 12L:12D and 28°C, the nymph-overwintering *Pteronemobius nitidus* molts six or seven times to reach the penultimate instar, but the number of molts increases with longer photoperiods. In 15L:9D, the penultimate instar as identified by the reversion of the wing pads may be the eighth, ninth, tenth, or even 11th instar (Tanaka, 1979). A similar effect of photoperiod is observed at 20°C, although the number of instars is generally fewer than at the higher temperature.

Another nymph-overwinterer, *Gryllus campestris*, shows a similar trend (Ismail and Fuzeau-Braesch, 1972b), but its Algerian relative (grillon d'Algerie) has in most cases five nymphal instars (range five to nine) in 16L:8D while three or more supernumerary instars may occur in 8L:16D. In the latter case the number of molts ranges from five to 13 (Fuzeau-Braesch, 1975). Therefore, the molting response to similar changes in photoperiod may differ from species to species, reflecting species-specific ways of seasonal adaptation.

The effect of temperature is also variable. In *P. nitidus* there are subtle interacting influences between temperature and photoperiod. In a

TABLE IV. Number of Molts in Crickets

Subfamily and species	Number of molts									
	5	6	7	8	9	10	11	12	13	14
Oecanthinae										
<i>Oecanthus niveus</i> ^a	X									
<i>O. angustipennis</i> ^a	X									
<i>O. quadripunctatus</i> ^a	X									
<i>O. nigricornis</i> ^a	X									
<i>O. pini</i> ^a	X									
<i>O. latipennis</i> ^a	X									
Eneopterinae										
<i>Calyptotrypus hibinonis</i> ^b				X	X					
<i>Cardiodactylus novaeguineae</i> ^c				X						
Phalangopsinae										
<i>Homoeogryllus japonicus</i> ^d		X	X	X						
Nemobiinae										
<i>Allonemobius fasciatus</i> ^e		X								
<i>Nemobius sylvestris</i> ^f				X	X					
<i>Dianemobius nigrofasciatus</i> ^g	X	X	X	X	X					
<i>D. mikado</i> ^{g,h}	X	X	X	X	X					
<i>Pteronemobius nitidus</i> ⁱ			X	X	X	X	X	X		
Gryllinae										
<i>Gryllus bimaculatus</i> ^j				X	X	X	X			
<i>G. campestris</i> ^k					X	X	X	X		
<i>G. sp. (gryllon d'Algerie)</i> ^l	X	X	X	X	X	X	X	X	X	
<i>Teleogryllus yezoemma</i> ^m			X	X	X					
<i>T. commodus</i> ⁿ					X					
<i>Acheta domesticus</i> ^{o,p,q}			X	X	X	X	X	X	X	X
<i>A. configuratus</i> ^o						X				
<i>Grylloides supplicans</i> ^o				X						
<i>Plebeiogryllus guttiventris</i> ^r			X							
<i>Velarifictorus micado</i> (autumn form) ^s			X	X	X					
<i>Loxoblemmus doenitzii</i> ^t			X	X	X	X				
<i>L. equestris</i> ^u			X							
<i>Anurogryllus muticus</i> ^v		X								
<i>Duolandrevus coulonianus</i> ^w					X	X	X	X		
Gryllotalpinae										
<i>Scapteriscus acletus</i> ^x					X	X	X			
Frequency distribution	7	6	11	14	15	9	7	4	2	1

^a Fulton (1915).

^b Okazaki (1922, cited by Ohmachi and Kioku 1935).

^c Oshiro *et al.* (1981).

^d Ohmachi and Yamashita (1938).

^e Nielsson and Bass (1967).

^f Gabbutt (1959a,b).

^g S. Masaki (unpublished).

^h Tanaka (1971).

ⁱ Tanaka (1979).

^j Merkel (1977).

^k Ismail and Fuzeau-Braesch (1972b).

^l Fuzeau-Braesch (1975).

^m F. Ichinohe (unpublished).

ⁿ Smith and Harrow (1971).

^o Ghouri and McFarlane (1958a).

^p Woodring *et al.* (1977).

^q Bate (1971).

^r Dakshayani and Mathad (1975).

^s Saeki (1966b).

^t Ohmachi (1932), Ohmachi and Kioku (1935).

^u Tomimoto (1932, cited by Ohmachi and Kioku, 1935).

^v Liebermann (1955).

^w Tsuji (1951).

^x W. Hudson (unpublished).

short photoperiod of 12L:12D, most nymphs pass through one or two more instars at 20°C than at 28°C, but the situation is reversed in long photoperiods of 14L:10D and 15L:9D (Tanaka, 1979). In *Gryllus bimaculatus* reared at 16L:8D, the number of instars tends to decrease with increasing temperature under both constant and fluctuating conditions (Merkel, 1977). In this homodynamic species, higher protein content of the food decreases the number of instars, which varies from 8 to 11 in different rearing conditions.

In terms of interspecific comparison, number of molts is not necessarily correlated with adult size. Nemobiinae, the group with the smallest adults, has 6–12 molts, depending on the environmental conditions. This is quite comparable to groups having larger adults, such as *Gryllus* or *Teleogryllus* (Table IV).

Effect of Temperature on Nondiapause Growth

Like most other orthopterans, crickets grow at moderate to rather slow rates. The growth rate of course varies as a function of temperature.

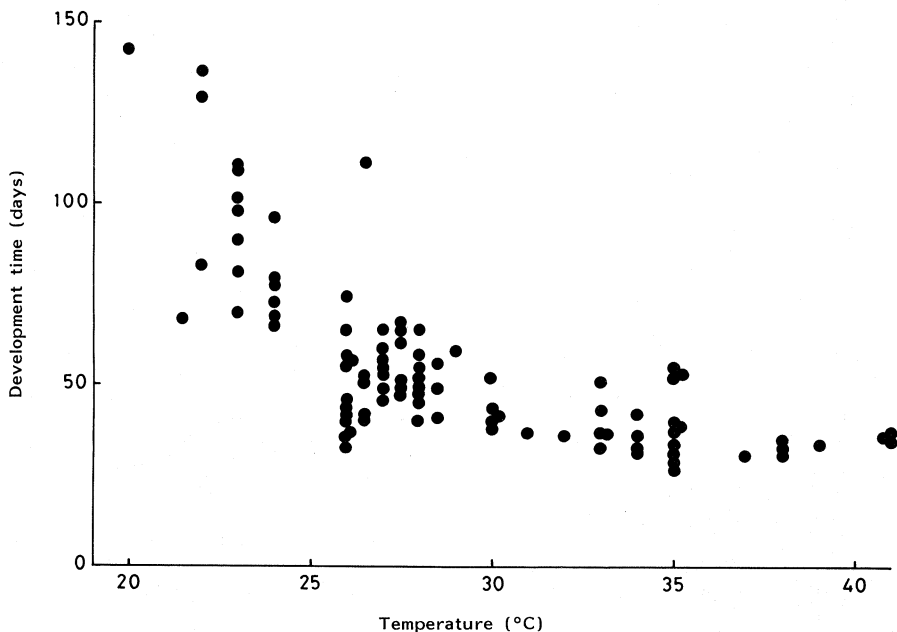


FIG. 11. Duration of nymphal development in crickets as a function of temperature. Various species and sources; for further explanation, see text.

TABLE V. Thermal Parameters for Nymphal Development in Four Species of Crickets

Species	T_0 , °C	K , day °C	Notes	Reference
<i>Gryllus bimaculatus</i>	19	469	Isolated	Fuzeau-Braesch and Ros (1965)
	18	518	Crowded	
<i>Acheta "domesticus"</i> ^a	16	683	Canadian	Ghouri and McFarlane (1958a)
	13	717	Pakistani	
<i>Gryllodes supplicans</i>	16	606	Crowded	Arai (1978a)

^a The Canadian and Pakistani strains of *A. domesticus* are actually sibling species (Ghouri and McFarlane, 1957).

To give some idea of the development rate of cricket nymphs, data on nymphal duration under known temperature conditions are plotted in Fig. 11. Factors other than temperature—such as food, crowding, or photo-period—also affect nymphal development. When development time was measured under two or more states of one factor at the same temperature, the shorter time was plotted (as an estimate of the maximum rate).

Compared with the similar graph for the egg stage (Fig. 3), the plotted points scatter widely, meaning that nymphal development is more variable than egg development among different species (r^2 of the regression of rate on temperature was 0.54 for nymphal development and 0.80 for egg development). Moreover, many species with different development times have been tested only within restricted ranges of temperature. Under such circumstances, computation of the common regression of developmental velocity on temperature is meaningless. The thermal parameters—the thermal constant K and the lower developmental threshold T_0 —can be estimated only for a few species tested over a reasonably wide range of temperatures (Table V). The five estimates of T_0 are all higher than the mode of the frequency distribution of T_0 for insects, showing that these crickets are thermophilous in the nymphal stage as in the egg stage. The upper threshold for normal development also seems to be high, close to 40°C. Since all these species are of tropical or subtropical origin, their thermophilous characters may not represent the general trend among crickets. Species occurring in cooler climates may have lower temperature requirements. Tanaka (1983) measured the duration of penultimate instar in the nondiapausing nymphs of *P. nitidus* at different temperatures under long-day conditions (16L:8D) and obtained $T_0 = 13^\circ\text{C}$ and $K = 132$ day °C for this single stage.

Group Effect on Development

One of the classic examples of group effect on growth is provided by a cricket species. In *Acheta domesticus*, growth is accelerated in crowded cultures as compared with isolated ones (Chauvin, 1958; McFarlane *et al.*, 1984). The effects of rearing density also have been examined in *Grylloides supplicans* (McFarlane, 1964*a,b*, 1966*a,b*; Masaki, 1972; Arai, 1978*a*). *Plebeiogryllus guttiventris* (Dakshayani and Mathad, 1973, 1975), and *Gryllus bimaculatus* (Fuzeau-Braesch and Ros, 1965). In these crickets, nymphal development time tends to be less in groups. Crowding may also result in smaller adults (McFarlane, 1964*b*).

Plebeiogryllus guttiventris clearly shows an optimum density (10 individuals per 850-ml jar), at which the development time is decreased by about 18% (10 days) and the adult weight is increased by about 40–50% compared with rearing in isolation (Dakshayani and Mathad, 1973).

Other effects of crowding are in body color and wing development. Crowded hoppers of *G. bimaculatus* become lighter in color than isolated ones (Fuzeau-Braesch 1960). Effects of crowding on wing polyphenism will be discussed in a later section (p. 387).

Photoperiodic Effect on Nymph Overwinterers

Although less than two dozen species of crickets have been examined, the photoperiodic control of nymphal development seems to be quite common, if not universal, among temperate crickets (Table III). Even strictly univoltine species with either egg or nymphal diapause utilize photoperiodic cues to harmonize their life cycles with the seasons.

In *Gryllus campestris*, diapause usually occurs at the penultimate instar unless prediapause development is prolonged by low temperature. The time taken to reach the diapause instar is shorter and the weight gain is faster in short days than in long days (Fuzeau-Braesch, 1963, 1965, 1966). The feedback programming of diapause compensates for delayed or accelerated development preceding the penultimate stage. Shortening of photoperiod thus exerts such a synchronizing effect that all individuals arrive at the penultimate stage before autumn irrespective of variable dates of birth. This response is highly effective in stabilizing the univoltine life cycle.

An Algerian species of *Gryllus* has a more labile seasonal life cycle: some individuals undergo a univoltine cycle and others a bivoltine one, although the nymphs hibernate in both cases. In contrast to *G. campestris*, diapause occurs before the penultimate instar, and development is clearly

prolonged at 30°C in days of 8L:16D compared with LL or 16L:8D (Fuzzeu-Braesch, 1975). It is inferred that this polymorphic life cycle is an adaptation to the unstable continental Mediterranean climate in highland Algeria.

The photoperiodic response of *Pteronemobius nitidus* is another well-analyzed example of univoltine nymph-overwintering cycle. This ground cricket shows a response somewhat similar to that of *G. campestris* before the diapause stage. The nymph grows faster in short days than in long days. In other respects, its mechanism of seasonal regulation is unique. First, diapause in a later instar occurs at 20°C as well as at 28°C, and is not averted even when the initial development is delayed by low temperature (Tanaka, 1978a). Second, although diapause intervenes in any stationary photoperiod ranging from 12L:12D to 16L:8D, the diapause instar as counted from hatching varies as a function of photoperiods (Tanaka, 1979). Third, the nymphs are susceptible to diapause either before or after the reversion of the wing pads. Therefore, an overwintering population comprises a wide range of developmental stages, although the penultimate is the most common (Tanaka, 1983). Finally, the nymphal diapause is continually under the control of photoperiod. Although some nymphs terminate diapause in any stationary photoperiod between 13L:11D and 16L:8D at 28°C, others fail to mature and persist as nymphs for more than 140 days. When nymphs kept in short days are transferred to long days, however, they begin to mature in about 1 month. Previous exposure to 12L:12D for only 10 days is sufficient to elicit the diapause-terminating response to 16L:8D (Tanaka, 1978a). Even after hibernation, nymphs are still responsive to photoperiod. Exposure to artificial short days in spring will retard growth in some (Masaki and Oyama, 1963; Tanaka, 1983).

The photoperiodic responses of *P. nitidus* discriminate between increasing spring days and decreasing autumn days of similar lengths and more effectively stabilize the univoltine life cycle than a simple response to absolute photoperiod. Tanaka (1978a) was able to demonstrate that both the absolute duration and the relative change of photoperiod were responsible for the incidence and termination of diapause (Fig. 12). In a constant photoperiod of 14 hr, 40 min, the nymphs require on the average more than 110 days to mature, but less than 60 days when the photoperiod is increased to 16 hr, 20 days after hatching. This is not due to a special delaying effect of the 14 hr, 40 min photoperiod. When the insects first exposed to 12 hr light/day are transferred to 14 hr, 40 min on day 10, the nymphal development time reaches the minimum level of about 55 days. Clearly, an increase in photoperiod is important for averting diapause. However, a 2-hr increase in photoperiod to 14 hr, 40 min is much less

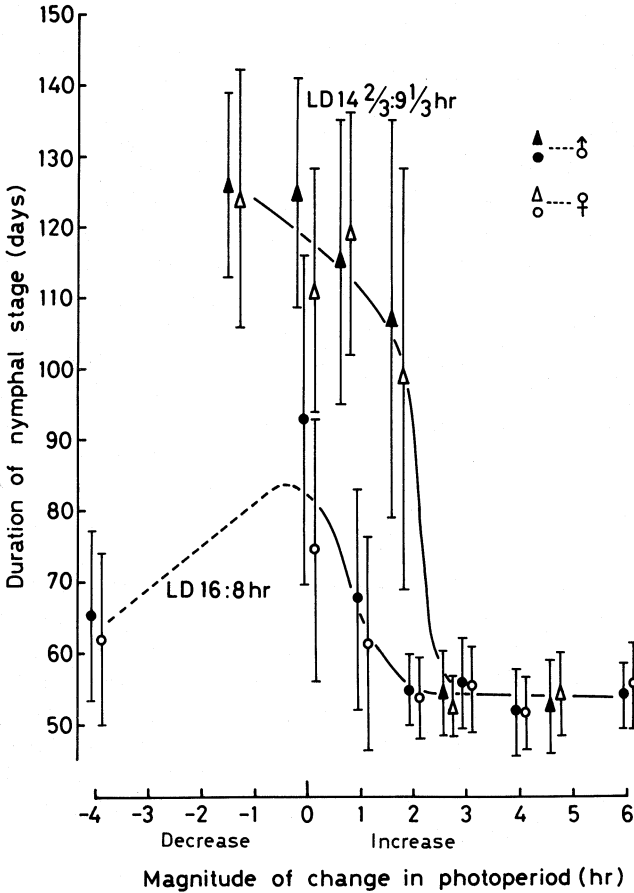


FIG. 12. Effect of transfer from different photoperiods to 14 hr, 40 min or 16 hr at day 20 from hatching on the development of *Pteronemobius nitidus* at 28°C. Symbols show means and vertical lines standard deviations. [From Tanaka (1978a).]

effective than the same magnitude of increase to 16 hr, suggesting that the length of photoperiod itself is also involved in determining the response (Tanaka, 1978a).

Another strictly univoltine nymph-overwinterer, the summer form of *Velarifictorus "micado"*, also responds to the change rather than to the absolute level of photoperiod. At 28°C this species will mature in stationary photoperiods of 10L:14D, 12L:12D, or 16L:8D, but the mean development time is as long as 3 months and the variance is very large. When a change from 10L:14D or 12L:12D to 16L:8D occurs after 2-4

weeks of nymphal life, the total development time is decreased by 2–3 weeks. A more drastic effect is observed in the distribution of adult emergence, which becomes highly synchronized (M. Watanabe, unpublished data). A reverse change, i.e., a decrease in day length, gives a much greater variance of development time than a stationary photoperiod, although the mean itself is only slightly increased.

Under the naturally changing cycle of daylength, *V. "micado"* shows a striking seasonal variation in development even when the temperature is kept at about 24°C. When nymphs hatch in late March and subsequently grow under increasing day lengths, they begin to mature in about 3 months (i.e., June); when they are reared from late June under decreasing day lengths, they take twice as long as the March brood and emerge over a 3-month period (October, November, or December).

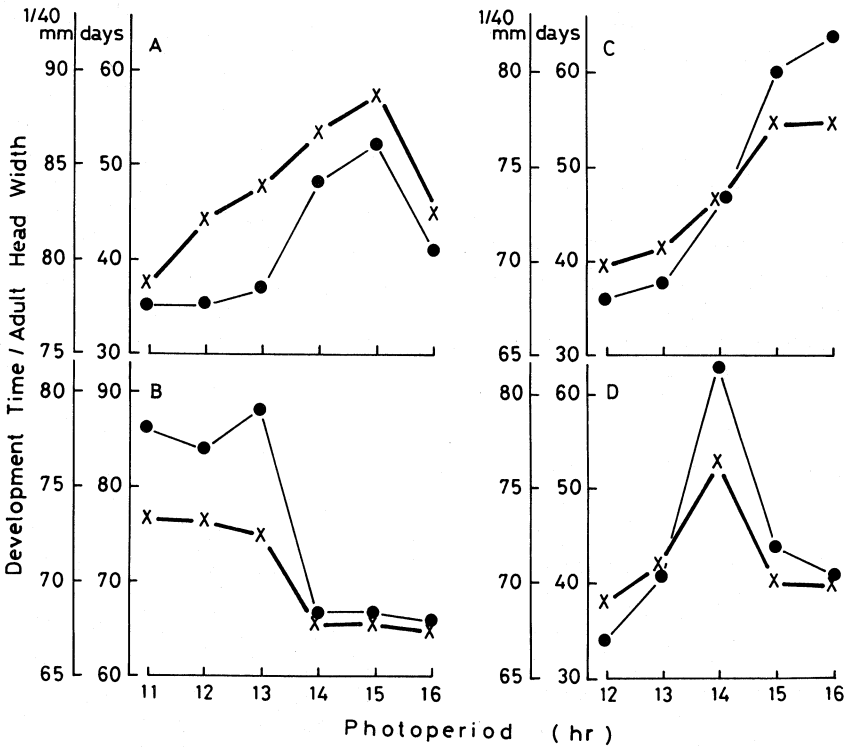


FIG. 13. Various types of photoperiodic control of nymphal development in ground crickets of the genus *Dianemobius*. (●) Mean times of nymphal development. (×) Means of adult head width; width is given in units of 1/40 mm. (A) *D. csikii*, (B) *D. taprobanensis*, (C) *D. mikado*, (D) *D. nigrofasciatus* (bivoltine). [Modified from Masaki (1973, 1979a, and unpublished data).]

Although no bivoltine, nymph-overwintering species has been analyzed as extensively as the univoltine cases described above, data suggest that a simpler photoperiodic response controls the nymphal diapause. Subtropical strains of *Teleogryllus occipitalis* mature faster in long days than in short days (Masaki, 1972; Masaki and Ohmachi, 1967). In the short days there is no clear syndrome of diapause except for a prolonged nymphal stage so long as the temperature is kept high. The short-day and long-day ranges of development time overlap to some extent. A similar overlap occurs in *Gryllus integer* (Alexander, 1968).

In *Velarifictorus parvus*, development times with and without diapause are quite distinct, and at 28°C the two peaks of adult emergence are more than 50 days apart (Masaki, 1972). A long day prevents and a short day induces nymphal diapause. At 28°C a few nondiapause nymphs may occur even in short days, and their development is like that of long-day nymphs. Other multivoltine species showing responses of the long-day type, i.e., development retarded by short days but not by long days, are *Dianemobius taprobanensis* (Fig. 13B) and *D. fascipes* (Masaki, 1978a, 1979a).

Photoperiod also influences the nymphal development in a strain of *Grylloides supplicans* originally collected from central Honshu (34–35°N), where it lived near fireplaces in old farmhouses and sang all the year round. At 27°C the mean development time is about 1 month longer in 11L:13D than in 16L:8D (Masaki, 1972). At 35°C the retarding effect of short days disappears (Arai, 1978a). *Grylloides supplicans* is of tropical origin, but this population's sensitivity to photoperiod proves that this population is not homodynamic. Comparison with tropical populations will be interesting.

Photoperiodic Effect on Egg Overwinterers

All of the hitherto examined univoltine egg overwinterers—*Teleogryllus emma* (Masaki, 1967; Masaki and Ohmachi, 1967; Masaki, 1978a), *T. yezoemma* (Masaki, 1966), *Velarifictorus micado* (autumn form) (Saeki, 1966b; M. Watanabe, unpublished data), *Loxoblemmus aomoriensis* (Masaki, 1977), *L. equestris* (Masaki, 1977), *Modicogryllus nipponensis* (S. Tanaka, unpublished data), *Dianemobius mikado* (Masaki, 1979a), the northern population of *D. nigrofasciatus* (Masaki, 1973), *D. furumagiensis* (S. Masaki, unpublished data), and *Gryllus ovisopis* (T. J. Walker, unpublished data) show responses of short-day type, i.e., the nymphal development is accelerated by short days compared with that in long days (Fig. 13C). In the southern bivoltine population of *D. nigro-*

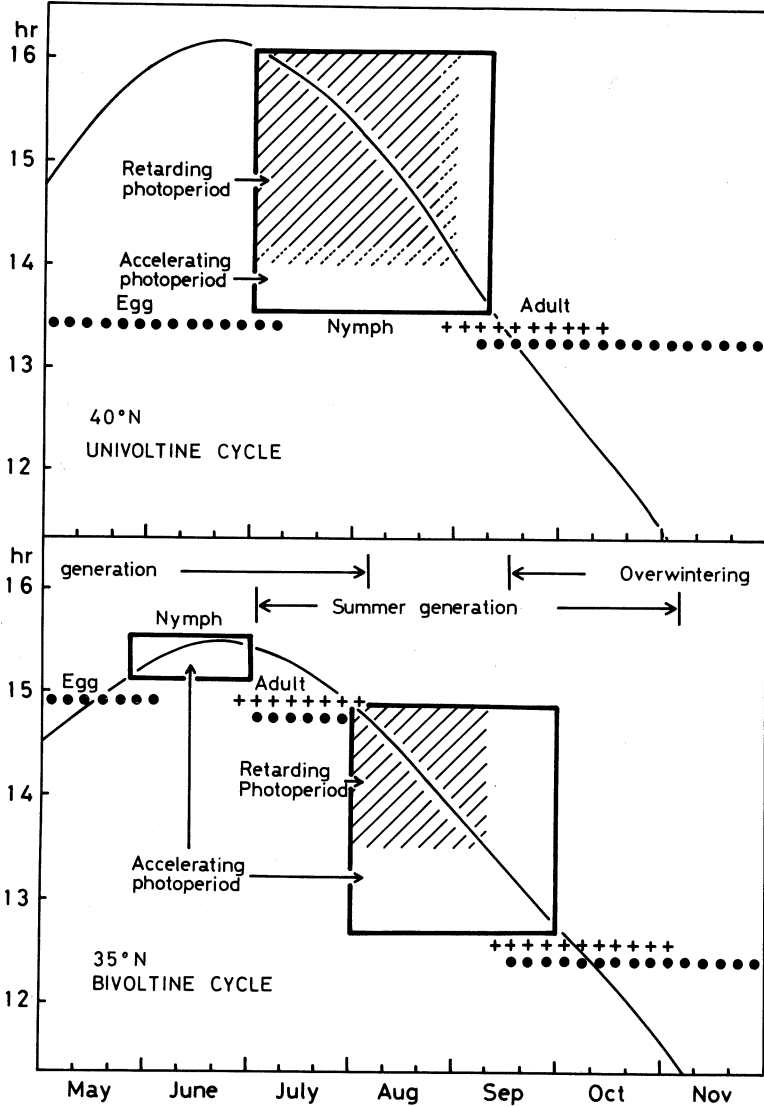


FIG. 14. Schematic presentation of the photoperiodic regulation of seasonal life cycle in *Dianemobius nigrofasciatus*. The life cycles at 40°N (upper panel) and at 35°N are represented. The latter is based on Z. Yamashita (personal communication).

fasciatus, the response is intermediate between the long-day and short-day types, for the nymphal development is delayed only by an intermediate photoperiod, but by neither short nor long ones (Fig. 13D) (Masaki 1973). In the multivoltine strain of *D. csikii* from Tokunoshima (27°N), the response is also an intermediate one, but the retarding photoperiod is longer (Fig. 13A). In all these cases, adult size is more or less proportional to development time. Therefore, photoperiodic control is mainly through the timing of sexual maturity rather than by accelerating or retarding growth.

The ecological significance of these responses is obvious. Reproductive activity is timed to occur in autumn so that diapause eggs are laid before winter (Fig. 14). The continued growth in long days results in larger adults and females that can accumulate more material and hold more developing eggs.

ADULT STAGE

Functional Division of Adult Life

Cricket adults live relatively long (Table VI). Although precise data on adult longevity are scanty, Table VI contains information on species belonging to several different subfamilies, indicating that long adult life is a general trend. Adults of both sexes commonly survive 2 or 3 months, and in extreme cases more than 6 months. In a few species overwintering as adults, such as the mole cricket, *Gryllotalpa africana*, the life span after reaching maturity may extend to a full year (Okamoto *et al.*, 1956). The adult of *Nemobius sylvestris* does not regularly overwinter, but occasionally survives till spring (Richards, 1952). Undoubtedly, long adult life is a prerequisite for the evolution of the subsocial habit, as in *Neocurtilla hexadactyla* and *Anurogryllus* spp. (Hayslip, 1943; West and Alexander, 1963).

At least some species of crickets undergo functional change during their long adult life. If they have well-developed hind wings, they may be able to fly a few days after emergence, when their exoskeleton becomes sclerotized. Some species indeed fly actively and are attracted to lights and to conspecific calls. Swarms of *Gryllus bimaculatus* have landed on ships in the Atlantic Ocean as far as 900 km off the coast of West Africa (Ragge, 1972). Even subterranean species such as mole crickets fly 4 km or more to locate suitable habitats for colonization (Walker and Fritz, 1983).

A light trap designed for flying moths and operated in the University Farm at Hirosaki in 1975 caught more than 200 adults of both sexes of *Teleogryllus emma*. Although the main singing period of this cricket extends from mid-August to mid-October, they flew to the trap only during the short period from the last week of August to the first week of September (Fig. 15) (K. Kawashima, unpublished data). This suggests that their dispersal activity is restricted to the first few weeks of adult life. Although *T. emma* retains the long hind wings for life, the adults may lose the ability or at least become reluctant to fly when their reproductive organs mature.

This inference is supported by observations in *Acheta domesticus*. The flight muscles shrink and degenerate a few days after adult molting, and this is accompanied by ovarian growth (Woodring *et al.*, 1979). Clearly, there is a switch in activity phase from dispersal to sedentary egg production during the adult life. Some species go a step further in this temporal division of adult function, and shed the hind wings after the dispersal phase is over. This has been reported for *Acheta domesticus* (Walker, 1977), *Platygryllus brunneri*, *Tartarogryllus brudigalensis*, and *Trigonidium cicindeloides* (Ingrisch, 1978), *Anurogryllus muticus* and *A. celerinictus* (Walker, 1972), and *Allonemobius fasciatus* (Roff, 1984). Shedding of hind wings seems to be more common than hitherto reported, since the phenomenon has long been known in *Homoeogryllus japonicus*, *Loxoblemmus doenitzi*, *L. aomoriensis*, *L. equestris*, the long-winged forms of *Dianemobius nigrofasciatus*, *D. fascipes*, *D. mikado*, *D. taprobanensis*, *Velarifictorus micado* (both summer and autumn forms), *V. parvus*, and some other species of the same genus (Matsuura, 1978; S. Masaki, unpublished observations). The species of the last two genera named above are dimorphic in wing form, and wing shedding is observed only in the macropterous form. One species that always develops long hind wings, *Anurogryllus arboreus*, sheds them within a few days and never flies (Weaver and Sommers, 1969; T. J. Walker, unpublished observations).

The reciprocity between dispersal and reproductive functions in the adult stage was experimentally demonstrated by Tanaka (1976). In *D. mikado* the micropterous form begins to lay eggs much earlier than the macropterous form, and the latter deposits most of its eggs after dealation. If, however, the hind wings are artificially removed immediately after emergence, egg production is accelerated. The rate of ovarian development in virgin females is faster in the micropterous form than in the macropterous one. The maturation of ovaries is therefore negatively correlated with the existence or development of hind wings. A further

TABLE VI. Adult Longevity in Some Species of Crickets

Species	Longevity ^a	Conditions	Reference
<i>Cardiodactylus novaeguineae</i>	64 (32-92) days	Room temperature	Oshiro <i>et al.</i> (1981)
<i>Xenogryllus marmoratus</i>	62 (23-106) days	Room temperature	Oshiro and Tamashiro (1985)
<i>Trigonidium cicindeloides</i>	130 days	Room temperature	Ingrisch (1977)
<i>Homoeogryllus japonicus</i>	62 (38-102) days	Room temperature	Oshiro and Gaja (1979)
<i>Plebeiogryllus guttiventris</i>	55-66 days	30°C	Dakshayani and Mathad (1975)
<i>P. guttiventris</i>	Mean 51-72 days	30°C, various photoperiods	Bentur and Mathad (1975)
<i>Acheta domesticus</i> : Male	34 (-105) days	28°C, isolated	Nowosielski and Patton (1965)
Female	31 (-105) days		
<i>A. domesticus</i>	64 days	28°C	Ghouri and McFarlane (1958a)
	57 days	35°C	Ghouri and McFarlane (1958a)
<i>A. configuratus</i>	51 days	28°C	Ghouri and McFarlane (1986a)
<i>Grylodes supplicans</i>	61 days	28°C	Ghouri and McFarlane (1958a)
<i>Gryllus bimaculatus</i>	55 (37-65) days	Variable/22°C ^b	Rivnay and Ziv (1963)
	38 (18-55) days	30/30°C	Rivnay and Ziv (1963)
	35 (17-45) days	30/34°C	Rivnay and Ziv (1963)
	32 (6-44) days	34/30°C	Rivnay and Ziv (1963)
	23 (9-36) days	34/34°C	Rivnay and Ziv (1963)

Cricket Life Cycles

<i>G. assimilis</i>	48 (16–62 +) days	27°C	Mello <i>et al.</i> (1980)
<i>G. ovisopis</i>	≤52 days	Field	T. J. Walker (unpublished)
<i>Teleogryllus occipitalis</i>	28 (12–67) days	Room temperature	Oshiro <i>et al.</i> (1981)
<i>T. commodus</i>	2–4 months	Field	Smith and Harrow (1971)
<i>Anurogryllus arboreus</i> : Female	8–10 weeks	Field	Weaver and Sommers (1969)
Male	5 days	Field	Walker (1980 <i>b</i>)
Male	69 days	Caged	T. J. Walker (unpublished)
<i>Nemobius sylvestris</i>	≤1 year	Field	Richards (1952)
	66, 86 days	Room temperature	Gabbutt (1959 <i>a</i>)
<i>Dianemobius fascipes</i> : Micropterous	29 (5–75) days	25°C	E. Seno (unpublished)
Macropterous	45 (15–95) days	25°C	E. Seno (unpublished)
<i>D. taprobanensis</i>	71 (20–130) days	25°C	E. Seno (unpublished)
<i>Gryllotalpa africana</i>	10–12 months	Field	Okamoto <i>et al.</i> (1956)
<i>Scapteriscus aletus</i>	18 (6–40) weeks	Outdoors	T. G. Forrest (unpublished)
<i>S. vicinus</i>	17 (1–36) weeks	Outdoors	T. G. Forrest (unpublished)

^a Mean (range). Single values are means or approximate durations.

^b Nymphal/adult temperatures.

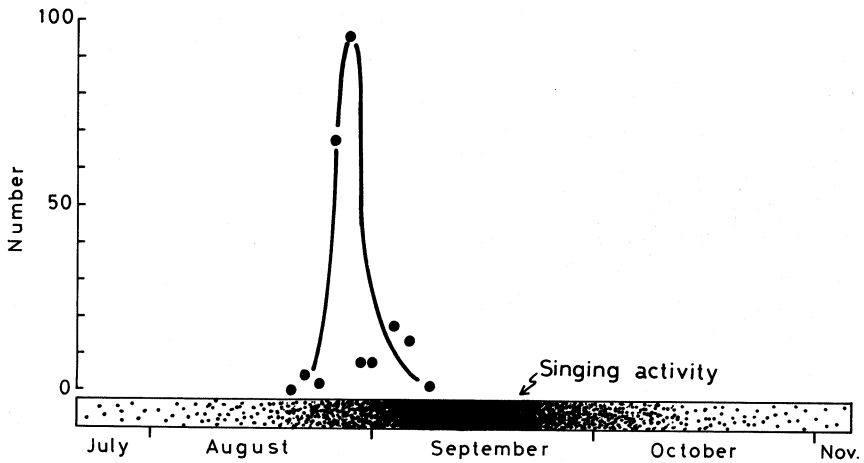


FIG. 15. Number of adults of *Teleogryllus emma* caught by a light trap near Hiroasaki. Singing activity as expressed by the density of stippling at the bottom continues for several months, but flight to the trap light occurs only around the end of August. [K. Kawashima (unpublished data).]

adaptation of the macropterous form to dispersal is that it is more tolerant of starvation than the micropterous form.

Two species of mole cricket are the only crickets known that sometimes make dispersal flights between successive egg clutches. One of the two, *Scapteriscus acletus*, is much more likely to do so than the other, *S. vicinus* (Forrest, 1986). The longest time recorded between successive flights of the same individual of *S. acletus* is 58 days (Ngo and Beck, 1982). Whether individuals of *S. acletus* and *S. vicinus* that fly in fall are among those that fly in spring is unknown (Walker *et al.*, 1983), but it has been shown that females of *S. acletus* that mate in fall can lay fertile eggs 7 months later (Walker and Nation, 1982).

Wing Dimorphism

Wing dimorphism is fairly common among crickets, occurring in species of at least six subfamilies (Chopard, 1969; Otte and Alexander, 1983). In wing dimorphic species the micropterous morph has the hind wings shorter than the tegmina and cannot fly, whereas the macropterous morph generally has hind wings that extend well beyond the tegmina and flies. In some instances the macropterous morph has wings that extend only slightly beyond the tegmina and its flightworthiness is questionable [e.g.,

Gryllus fultoni and *G. campestris* (Walker and Sivinski, 1986)]. The proportion of micropterous and macropterous individuals in wing dimorphic species is under both environmental and genetic control. Genetic control is suggested by the occurrence within a genus of some species that are 100% micropterous and others that are 100% macropterous (e.g., *Scapteriscus*, *Gryllus*, *Anurogryllus*). It is confirmed by laboratory studies in which crosses of individuals of the same morph produce progeny with a higher proportion of that morph (Harrison, 1979; Roff, 1984; Walker, 1987). However, in none of these instances was a pure breeding line of either morph achieved, suggesting that genetic differences within wing dimorphic species are generally subordinate to environmental differences in determining that an individual becomes one morph or the other. [Selection experiments with no significant effect are unlikely to be reported, however McFarlane (1966c) does report little effect after the mating of three generations of only macropterous *Grylloides supplicans*.]

From a functional analogy to the phase variation in locusts or wing forms in aphids, one might expect high population density to favor the development of long-winged adults. This has been experimentally confirmed in *Grylloides supplicans*, which in most field populations is 100% micropterous (Arai, 1978a,b; McFarlane, 1966c; Nakamura, 1968). *Velarifictorus micado* (autumn form) is another micropterous cricket, but when two or more individuals are reared together in a jar, macropterous specimens are obtained (Saeki, 1966a). Crowding is also known as a factor responsible for wing development in *Dianemobius fascipes* (S. Masaki, unpublished data) and may account for the development of long wings in a few jar-reared individuals of the normally micropterous *Gryllus fultoni* (Walker and Sivinski, 1986).

Occurrence of long-winged *Trigonidium cicindeloides* in the laboratory may also be due to crowded culture conditions (Ingrisch, 1977). This phenotypic modification is accompanied by a striking side effect. In the field, *T. cicindeloides* in the usual micropterous phase lacks the tibial tympana (as well as the male stridulatory organ). In association with the development of long wings, a tympanum appears on each fore leg (Ingrisch, 1977). This fact suggests that the tibial tympanum had a function during flight that did not end with the loss of calling in males. Possible functions include bat avoidance (Moiseff *et al.*, 1978; Nolen and Hoy, 1984) and acoustical detection of suitable habitat (Morris and Fullard, 1983).

Wing polyphenism is not, however, exclusively a response to population density. For example, the proportion of macropterous adults under crowded conditions is affected by temperature. In *G. supplicans* percentage macroptery is not high at temperatures below 30°C even when

the culture is crowded. A temperature of 35–38°C is necessary to obtain a substantial proportion of macropterous adults (Arai, 1978a; Nakamura, 1968; Ghouri and McFarlane, 1958b; McFarlane, 1962, 1966b).

Discovery of photoperiodic effects opened a new line of interpretation of wing polyphenism in crickets. Such an effect was first observed in *Pteronemobius nitidus*, which is rarely macropterous in the field (Masaki and Oyama, 1963). When nymphs are kept continually crowded and under artificial long-day (16L:8D) and warm (25°C) conditions, about half of them become macropterous. If they are exposed to decreasing natural day length for 40 days after the summer solstice before being subjected to 16L:8D, the proportion of long-winged adults exceeds 70%. Longer exposures to the natural (shortening) day length or shifts to artificial short days (12L:12D) at 25°C prevent the wing development. This explains the virtual absence of macroptery in the field, for the nymph overwinters and usually experiences a long period of short days.

Tanaka (1978b) analyzed this photoperiodic response in detail. It is quite similar to the photoperiodic responses widely known to control insect diapause. The nymphs are particularly sensitive to photoperiod at the third and fourth instars, and show a clearly defined critical photoperiod of about 15 hr. The macroptery-promoting effect of long days is enhanced when nymphs are exposed to a short day of 12L:12D for the first 10–20 days of their life. By transferring from various photoperiods to either a 14 hr, 40 min or 16 hr photoperiod, Tanaka gave different magnitudes of photoperiodic change and showed that, within a certain range of photoperiods, a relative increase in photoperiod promotes wing development.

Photoperiodic effects on wing form are also known in *G. supplicans* (Mathad and McFarlane, 1968; Arai, 1978a), *V. micado* (autumn form) (Saeki, 1966b), *D. nigrofasciatus* (Masaki, 1973), *D. mikado* and *D. taprobanensis* (Masaki, 1979a; Tanaka *et al.*, 1976), *Gryllus integer* (Alexander, 1968), and *G. rubens* (Walker, 1987). In all these species, long days favor and short days prevent the development of long-winged adults. In *D. mikado*, changes from long to short days or vice versa are more effective than constant long days (Tanaka *et al.*, 1976).

The photoperiodic control of wing form is probably more common than is known at present. The switch in wing form is not merely an adaptation to unpredictable fluctuation in population density. It is an integral part of seasonal adaptation in crickets. Two factors at least can be inferred to be responsible for the evolution of this photoperiodism: (1) the seasonal change in weather conditions affecting flight and dispersal activities and (2) the more or less regular seasonal trend in population density. If

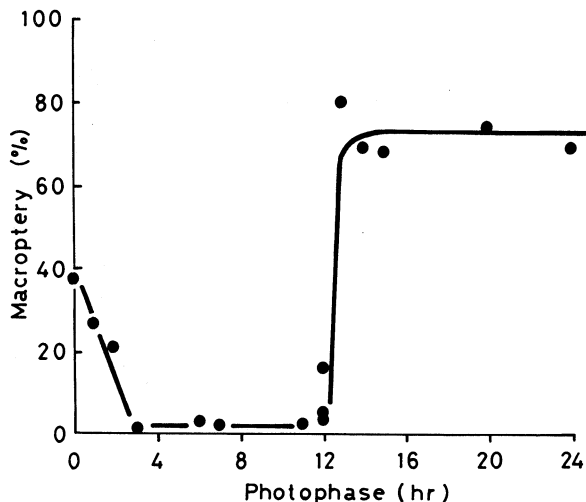


FIG. 16. Percentage macroptery as a function of photoperiod in crowded cultures of *Dianemobius fascipes* at 26°C. [Modified from Masaki (1984).]

crowded conditions recur regularly in response to seasonal changes in the environment, adaptation to such conditions can be achieved best through an anticipatory response to the reliable seasonal cue.

The wing-form response curve obtained for *D. fascipes* over the whole range of photoperiod is surprisingly similar to typical photoperiodic induction curves for diapause [Fig. 16 (Masaki, 1984); compare with Fig. 8]. Moreover, resonance experiments of both Nanda-Hammer and Bünsow protocols strongly suggest the involvement of circadian components, as in the photoperiodic clocks of some other species of arthropods (Masaki, 1984). The control of wing form thus seems to be based on a functional extension of the photoperiodic regulatory system.

Although density and photoperiod may be usefully correlated with conditions influencing the relative fitnesses of long- and short-winged morphs, some crickets are faced with unpredictable circumstances that cause the production of a mixture of morphs to be the most successful course of action. Producing a mixture could contribute to the evolutionary success of an individual [maternal manipulation (e.g., Harrison, 1980)] or an allele [stochastic genes (e.g., Walker, 1986)]. The fact that neither genetic selection (Walker, 1987) nor environmental manipulation (e.g., Fig. 16) of dimorphic species produces alternative treatment groups that are 100% micropterous and 100% macropterous supports the hypothesis

TABLE VII. Examples of Fecundity in Crickets

Species	Number of eggs	Conditions ^a	Reference
<i>Xenogryllus marmoratus</i>	200 (133-304)	Room temperature	Oshiro and Tamashiro (1985)
<i>Gryllus bimaculatus</i>	Maximum 3000	30 or 34°C	Rivnay and Ziv (1963)
<i>G. firmus</i>	506/week	25°C	Ibrahim and Walker (1980)
<i>Teleogryllus commodus</i>	500-1500	30 ± 3°C	Smith and Harrow (1971)
	1086 ± 339/64 days		Mason (1973)
<i>Gryllodes supplicans</i> : Macropterous	374	35°C	Nakamura (1968)
Micropterous	492	30°C	Nakamura (1968)
	862	28°C	Ghouri and McFarlane (1958a)
<i>Acheta configuratus</i>	667	28°C	Ghouri and McFarlane (1958a)
<i>A. domesticus</i>	728	28°C	Ghouri and McFarlane (1958a)
	1060	35°C	Ghouri and McFarlane (1958a)
	90/day	Days 10-30 ^b	Woodring <i>et al.</i> (1979)
	50/day	Day 40	Woodring <i>et al.</i> (1979)
	30/day	Day 50	Woodring <i>et al.</i> (1979)
	20/day	Day 60	Woodring <i>et al.</i> (1979)
	1395	+Cu, 17.2 µg/g E ^c	McFarlane (1976)
	302 (maximum 1095)	26.5°C, DD ^d	Bate (1971)
	66 (maximum 218)	26.5°C, DD ^e	Bate (1971)

<i>Plebeigryllus guttiventris</i>	2493	Natural LD	Bentur and Mathad (1975)
	2369	30°C, LL	Bentur and Mathad (1975)
	2245	30°C, 10L:14D	Bentur and Mathad (1975)
	1902	30°C, DD	Bentur and Mathad (1975)
<i>Anurogryllus arboreus</i>	≤129	In burrow	Weaver and Sommers (1969)
<i>Nemobius sylvestris</i>	134-225	Room temperature	Richards (1952)
	~100	Room temperature	Gabbutt (1959a)
<i>Dianemobius fascipes</i>	93 (≤541)	25°C	E. Seno (unpublished)
<i>D. taprobanensis</i>	141 (≤649)	25°C	E. Seno (unpublished)
<i>D. mikado</i> : Macropterous	123/50 days	28°C	Tanaka (1976)
Micropterous	216/50 days	28°C	Tanaka (1976)
<i>Gryllotalpa africana</i>	95 (39-177)	Room temperature	Okamoto <i>et al.</i> (1956)
	[508 (434-624)] ^f		
<i>Scapteriscus acletus</i>	212 (80-486)	Outdoors	T. G. Forrest (unpublished)
<i>S. vicinus</i>	158 (22-246)	Outdoors	T. G. Forrest (unpublished)

^a LL, Continuous light; DD, continuous darkness.

^b Days from adult emergence.

^c Cu and vitamin E were added to diet.

^d Collected as nymphs in January.

^e Collected as nymphs in September.

^f Number of ovarian eggs.

that a mixture of morphs is sometimes the gene effect that is most adaptive (Cooper and Kaplan, 1982; Walker, 1986).

Fecundity

Female crickets generally continue to lay eggs throughout their long life. In most crickets there is no evidence of a gonotrophic cycle. So long as food is available, mated females may lay eggs almost every day [e.g., *Acheta domesticus* (Woodring *et al.*, 1979)]; therefore, estimating fecundity (total number of eggs laid during the lifetime) is not an easy task. Table VII gives examples of cricket fecundity. Maximum values may be better estimators of genetic capacity for egg production than average values.

Females of the larger grylline species, such as *Gryllus bimaculatus*, *G. firmus*, *Teleogryllus commodus*, *Acheta domesticus*, and *Plebeiogryllus guttiventris*, can produce 1000 eggs or more and rank among the more prolific groups of insects. On the other hand, females of the subsocial cricket *Anurogryllus arboreus* lay a single clutch of no more than 130 eggs in an underground nursery chamber (Weaver and Sommers, 1969). Females of a similar tropical species, *A. muticus*, can produce a second clutch about 2 months after the first (Walker and Whitesell, 1982). Mole crickets of the genus *Scapteriscus* also lay clutches of eggs in underground burrows, but they seal and abandon the egg chamber rather than caring for the hatchlings. Their clutches contain up to 60 eggs each and are produced at intervals of 7–12 days for as many as ten clutches (Forrest, 1986).

In the smaller, nemobiine crickets, the number of eggs is an order of magnitude less than in the larger, grylline species. This is probably due to the large size of eggs relative to body size. Among 20 species of crickets of different body sizes, the relation

$$EL = 1.10 HW^{0.55}$$

is tentatively obtained, where *EL* is the egg length and *HW* the head width (S. Masaki, unpublished data). This equation predicts that the ratio of *EL* to *HW* decreases with increasing body size. Since smaller crickets can populate more densely than larger ones, their lower fecundity may be to some extent compensated for by their higher population density.

The crickets with the lowest fecundity, and the largest eggs relative to body size, may be the myrmecophilines (Wheeler, 1900), but we have no exact data.

GEOGRAPHICAL ADAPTATIONS

Homodynamic versus Heterodynamic Life Cycles

Environmental conditions vary in space as well in time. The major and regular variations in time are seasonal and those in space are geographical. Cricket life cycles are exposed to natural selection by these two categories of environmental variations. In the preceding sections we have seen how they are temporally organized. We next consider the geographical modification of their temporal organization and its impact on their evolution.

Crickets as a whole range roughly between 55°N and 55°S (Alexander, 1968). Except for species such as *Acheta domesticus* and *Grylloides supplicans* living in artificially heated sites, however, no single species occupies the full extent of this latitudinal range. Each species is more or less restricted within a rather narrow climatic area. Historical factors are undoubtedly involved in determining geographical distribution, but adaptations to climate accomplished by different life cycles are equally important. This is supported by the frequent geographical replacement of homodynamic by heterodynamic species or the shift of life cycles from nondiapausing to diapausing ones. However, due to the paucity of experimental analyses and detailed field observations at the critical latitudes where such replacements or shifts occur, we are able to draw only a rather vague picture of these biogeographical events.

In the Japanese islands north of 30°N, all "outdoor" crickets have seasonally defined periods of singing. As one proceeds south along the island chain between 28 and 24°N, an increasing number of species are heard singing in winter. Thus, of the 36 species recognized by Matsuura (1976, 1977, 1978, 1979, 1982) in the Ryukyu Arc, at least 15 are active as adults in winter as well as in the other seasons. A few of these are conspecific with northern heterodynamic species; others are very closely related to northern species. Still others occur farther south in tropical regions, but not in the north.

Of course the occurrence of adults throughout the year cannot be taken as conclusive evidence for homodynamic cycles. For example, the subtropical ground crickets *Dianemobius fascipes* and *D. taprobanensis* show rather clear responses to photoperiod, but they are more or less active throughout the year in Ishigaki Island (24°N) and their adults as well as late-instar nymphs are common even in late winter (S. Masaski, unpublished observations). Their life-cycle patterns are thus less clearly fixed in spite of their heterodynamic development and differ from those

prevalent in temperate areas, where overwintering in more than one stage is exceptional.

At 30°N in the eastern United States (Gainesville, Florida), 19 of 36 cricket species call during winter (December–February) (T. J. Walker, unpublished observations). Yet 600 km farther north (36°N; Raleigh, North Carolina), none of 29 species do so (Fulton, 1951). Seventeen of the Raleigh species are also heard in Gainesville; of these, seven call during winter, but none has changed to a completely homodynamic cycle. Young nymphs apparently cannot survive the prolonged winter cold spells in Gainesville, but other stages—including adults of winter-calling species—do.

If the cold dormant season can be tolerated only in a state of diapause, a homodynamic cycle cannot persist where the temperature becomes persistently lower than the development threshold, roughly 15°C for most species of crickets (pp. 360, 375, 376). Such temperature conditions occur southward to about 28°N in the Japanese islands. If the temperature is often above 15°C but close to it, activity can be continued, but fitness may be decreased because of the lowered development rate and reproductive activities. If the rate of increase becomes smaller than unity, escape by diapause or other similar means should be selected for.

One of the possible adaptations to such transitional conditions is a polymorphic life cycle in which diapause and nondiapause genotypes are kept in a dynamic balance under the influence of fluctuating climatic conditions. *Gryllus firmus* in Florida and *Dianemobius fascipes* and *D. taprobanensis* in the Ryukyu Islands probably represent this situation. If a species requires so long a period of time for growth that it can complete no more than one generation each year, an obligatory diapause will help maintain an optimal seasonal arrangement of life stages.

For example, *Xenogryllus marmoratus* takes about 4 months to mature and is univoltine with an egg diapause in the subtropical area (Matsuura, 1979; Oshiro and Tamashiro, 1985). In this case, the possibility cannot be entirely ruled out that its diapause has been derived from the northern temperate populations. *Cardiodactylus novaeguineae* has an obligatory egg diapause and is strictly univoltine, taking 5–6 months for growth in Okinawa (about 26°N) (Oshiro *et al.*, 1981). This arboreal species, or at least its close relative, is widely distributed in tropical Asia and New Guinea (Chopard, 1968), but not to the north of the Amami Group (about 28°N). Its firm diapause is therefore not of northern origin and has probably evolved near the northern margin of its distribution as an adaptation to the subtropical climate.

What is occurring in the region of overlap between homodynamic

and heterodynamic populations should be studied in order to give deeper insight into the evolution of cricket life cycles.

Egg versus Nymph Overwintering

Another important aspect of geographical adaptation is the divergence of the two major types of heterodynamic life cycles, i.e., egg- and nymph-overwintering ones. Both types of overwintering occur near the northern limit of cricket distribution. In Europe, the northernmost species, *Nemobius sylvestris*, overwinters in both these stages of development (Brown, 1978; Gabbutt, 1959a). In the Japanese islands, both the nymph-overwintering *Pteronemobius nitidus* and the egg-overwintering *P. ohmachi* extend north to about 44°N in Hokkaido. In North America, the two northernmost *Gryllus* species hibernate in different stages, *G. pennsylvanicus* as eggs and *G. veletis* as nymphs. Although the former extends north a little farther than the latter, both reach almost to the northern limit of cricket distribution in North America (Alexander and Bigelow, 1960; Alexander, 1968).

From these facts alone, the two kinds of life cycle seem to be equally adapted to temperate climates. However, if the proportions of the species with the different overwintering stages are plotted for different districts of Japan, a definite trend emerges (Fig. 17). Nymph overwinterers are only about 10% of the total in the northernmost island, Hokkaido. They gradually increase in frequency southward and reach about 30% in Kyushu. Farther south, the comparison cannot be made in the same way because of the occurrence of species with year-round activities. If only those species with a definite overwintering stage are taken into account, the proportion of nymph overwinterers reaches as high as 40%. The regression of the proportion of nymph overwinterers on the geographical position of area (number 1–9 roughly from north to southwest as arranged in Fig. 17) is significant ($r^2 = 0.86$, $p < 0.01$; after arcsin transformation of the percentage data). On the other hand, nymph-overwintering shows no significant trend between 30 and 40°N in the eastern United States (Table II).

In Japan, when there are pairs or groups of very closely related northern and southern species, the northern members tend to hibernate as eggs and the southern members as nymphs. The egg-overwintering (autumn) form of *Velarifictorus micado* extends to the northern tip of the main island (Honshu) at about 41°N, while the nymph-overwintering (summer) form (probably representing a different species) is found only in southern Honshu facing the Pacific Ocean and farther south (Masaki, 1961; Mat-

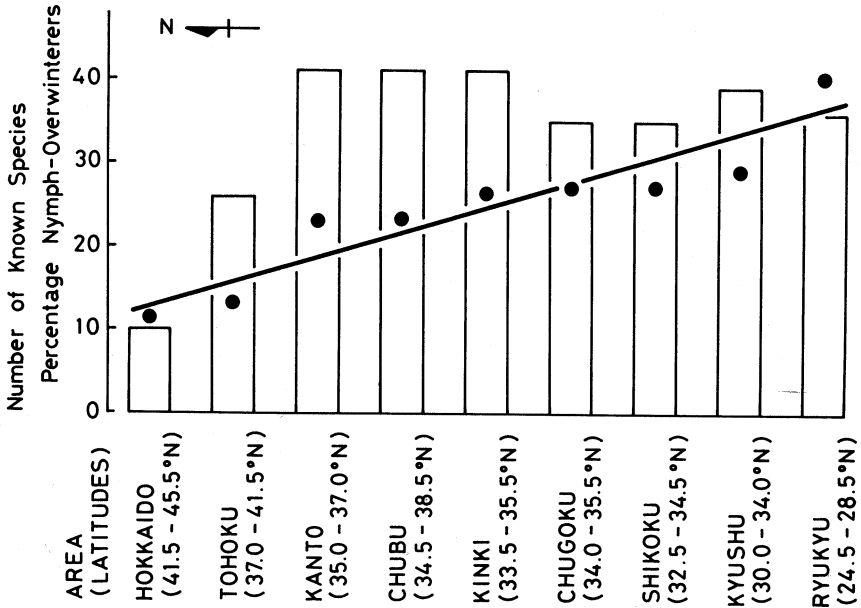


FIG. 17. Number of cricket species (histograms) and proportion of nymph-overwinterers in various districts (roughly arranged from north to south) of the Japanese islands. [Primarily from Matsuura (1976, 1977a, b, 1978a, b, 1979a, b, 1982a, b, c, and personal communication) and Masaki (1983).]

ura, 1978b). Among the three species of *Teleogryllus* in Japan, the two egg-diapausing ones (*T. emma* and *T. yezoemma*) reach Hokkaido, but the nymph-diapausing *T. occipitalis* is restricted to south of the Kii peninsula in Honshu, Shikoku, and Kyushu (Ohmachi and Masaki, 1964; Masaki and Ohmachi, 1967). Again the ground crickets *Dianemobius nigrofasciatus* and *D. mikado*, which hibernate as eggs, replace their predominantly nymph-overwintering relatives *D. fascipes* and *D. taprobansensis*, respectively, in the north of the Ryukyu Arc. An interesting case in eastern North America is the geographical variation of the complicated life cycle of *Gryllus firmus*. In the south, nymph- and egg-overwintering cycles are intermingled in the same locality, but only egg-overwintering populations are found in the north (Alexander, 1968; Harrison and Arnold, 1982; Walker, 1980a).

These facts suggest that the different types of life cycles are selected for in different climates. If all other conditions are equal, there would be higher chance for selection of an egg diapause in cold climates and of a nymph diapause in warm climates. Physiological and behavioral char-

acteristics of the species may modify this direction of selection and blur the general tendency.

Possible reasons for such differential selection have been discussed by Masaki (1978a). Photoperiodic information is continuously available for nymphs to input the feedback system controlling their development. This is particularly effective in establishing a seasonal homeostasis where the winter is not consistently cold and brief warm periods otherwise invoke untimely development. Egg diapause usually begins at relatively early stages of embryogenesis before the development of the neuroendocrine system. The onset of diapause should mainly be programmed by the parental genotype or parental response to seasonal cues (pp. 368–372). Diapausing eggs have to rely on the predetermined intensity of diapause and on the less reliable temperature effect in timing the resumption of activity (pp. 361–366). They are more susceptible to temperature fluctuations around the developmental threshold than to those consistently low.

On the other hand, the surface area through which various kinds of deleterious external actions might be exerted is far smaller in the ellipsoid eggs than in the nymphs with many protruding and delicate structures. This presumably makes the eggs more able to endure a long and consistently cold northern winter. The nymphs can move in search of a better shelter even during hibernation when their dens deteriorate in one way or another (e.g., drought, erosion, flood), and they can even take food and water if opportunity allows, increasing their ability to endure a further period of dormancy. However, all these benefits of nymph overwintering disappear when the winter is cold.

Variation in Voltinism

In temperate regions, the number of annual generations in a given area is more or less fixed in each species. In some species, voltinism varies as a function of temperature, producing several generations a year in the south, but only one near the northern limits of distribution. Crickets are, however, generally conservative in voltinism (Table VIII). In Japan, 26 of 39 species that have a north–south distribution of more than 5° are univoltine throughout their geographical range, in spite of large local differences in available heat. In the eastern United States, 24 of 40 such species have only univoltine life cycles. We know of 22 species (11 in Japan, 11 in the United States) that seem to make the transition from one generation in the north to two generations in the south. These include small, ground-dwelling crickets (e.g., *Dianemobius nigrofasciatus*, *D. mi-*

TABLE VIII. Latitudinal Variation in Voltinism in Species of Japanese and Eastern United States Crickets Occupying More Than 5° Latitude

Locality	Variation in voltinism for given latitudinal range			
	5-9°	10-14°	15-19°	20-22°
Japan ^a				
Univoltine only	18	8	0	0
Bivoltine only	0	2	0	0
Change in voltinism	0	8	3	0
United States ^b				
Univoltine only	4	15	5	0
Bivoltine only	1	3	0	0
Change in voltinism	1	0	7	4

^a Matsuura (1976, 1977, 1978, 1979, 1982); S. Masaki (unpublished data).

^b Walker *et al.* (1983), with the following additions: *Scapteriscus vicinus* (univoltine, 7°), *Scapteriscus aletus* (change, 9°), *Velarifictorus micado* (univoltine, 9°), *Neocurtilla hexadactyla* (semivoltine to univoltine, 19°).

kado, *Eunemobius carolinus*, and *Miogryllus saussurei*) and tree crickets (e.g., *Oecanthus niveus*, *O. argentinus*, and *O. quadripunctatus*). Interestingly, six species persist in the bivoltine cycle to the northern extreme of their distribution. These include *Teleogryllus occipitalis*, *Gryllus rubens*, *Oecanthus indicus*, *O. celerinictus*, and *Orocharis luteolira*. The last two species in this list have northern sibling species that are univoltine, raising the possibility that some of the species that seem to make the transition from univoltine to bivoltine cycles are actually undetected sibling pairs.

A shift from univoltine to semivoltine can occur northward, but must be accompanied by overwintering at two different stages. A well-known example is *Nemobius sylvestris* in England. The life cycle of *Gyllotalpa africana* in Japan and of *Neocurtilla hexadactyla* in the United States is univoltine in the south (adult overwintering) and semivoltine in the north (adult and juvenile overwintering). The semivoltine cycle of *Duolandrevus coulonianus* in Japan may represent the northern marginal situation of this apparently tropical species (Tsuji, 1951). Cases of semivoltinism are exceptional, and in most cases northern limits of distribution seem to be determined by the growing season required for a univoltine life cycle.

Linear Geographical Clines

Climatic conditions, especially temperature, show clear latitudinal gradients from the equator to the poles. In the Japanese islands, annual

mean temperature is 23°C at about 24°N and 6°C at about 45°N. The gradient is almost linear, the mean temperature changing at a rate of about 1°C for each shift of 1°N. Along this gradient, more than ten species of cricket occupy a latitudinal range of over 10 deg.

In univoltine species, the sum of heat available for each generation varies latitudinally. Nevertheless, seasonal homeostasis is maintained. For example, *Teleogryllus emma* matures earlier in the north than in the south, corresponding to the earlier northern autumn. This contradicts what is predicted from heat accumulation. That the photoperiodic response is of the short-day type, effective in establishing the seasonal homeostasis in each locality, does not explain this contradiction. In the north, summer is shorter, but the days are longer; consequently, the photoperiod itself does not provide a means to adjust the development time to the local growing season. Only by genetic means can a geographical homeostasis of the life cycle be accomplished.

This situation is illustrated by both physiological and morphological clines in the univoltine field crickets *T. emma* and *T. yezoemma* (Figs. 18 and 19). These two species show very similar size clines that can be described by almost the same regression equations. The northward decrease in adult size is due to selection for shorter development time in proportion to the shortening growing season, because there is a close correlation between development time and adult size (Masaki, 1967, 1978a).

The intensity of egg diapause in *T. emma* also decreases northward, as measured by incubation time at constant temperatures (Masaki, 1965). At first sight, this seems to contradict the northward increase in duration of hibernation. However, more intense diapause is required to prevent untimely development in the warmer south. In the cooler north, winter is consistently cold, so there is no risk of untimely development, and the eggs can survive if diapause suppresses their development only during the short autumn.

The physiological and morphological clines observed are results of selection by the general climatic gradient; therefore, they may also occur in other univoltine crickets. Although the information is limited, northern and southern populations of *Velarifictorus micado* (autumn form) show differences in adult body size, nymphal development time, and duration of egg diapause, all conforming to the tendency stated above (Table IX). In North America, adult size in both the egg-overwintering *Gryllus pennsylvanicus* and the nymph-overwintering *G. veletis* tends to be smaller northward (Alexander and Bigelow, 1960). The difference in overwintering stage does not therefore substantially modify the latitudinal tendency.

Similar selective responses might be expected to the altitudinal cli-

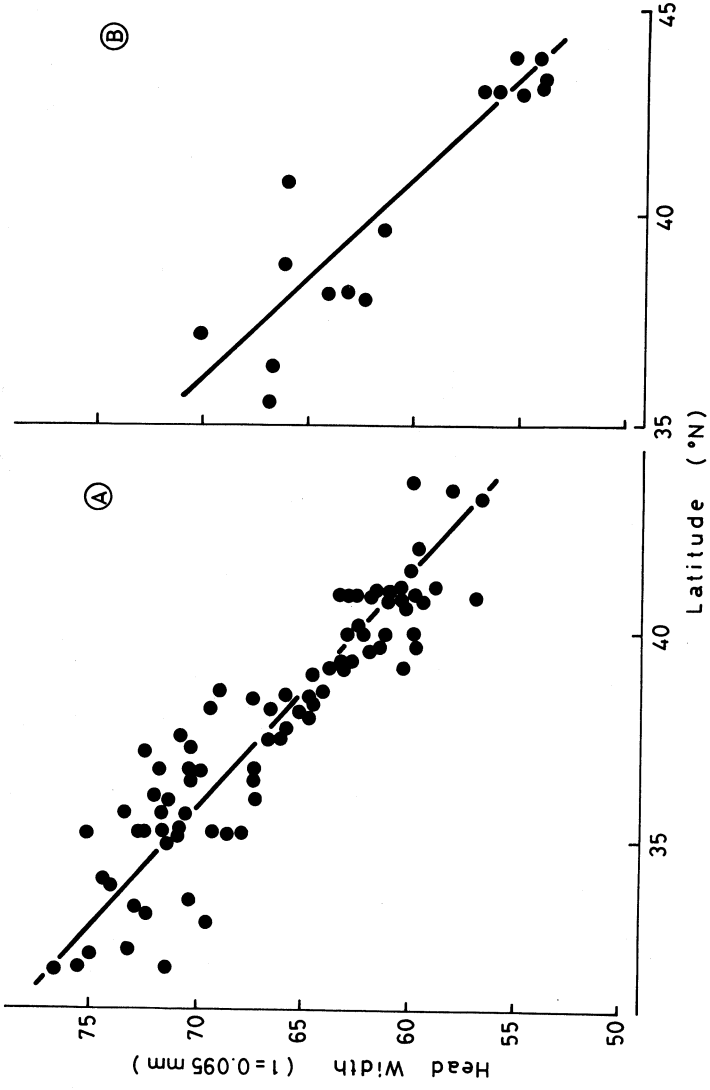


FIG. 18. Latitudinal size clines in two field cricket species, (A) *Teleogryllus emma* and (B) *T. jezoemima*. Each symbol represents the mean for a local sample. Head width is given in units of 0.095 mm. [From Masaki (1978a).]

TABLE IX. Comparison of Northern and Southern Populations of *Velarifictorus micado* (Autumn Form)^a

	Hirosaki (40°N)	Kure (34°N)
Duration of egg stage at 28°C, days	110 ± 19 (N = 2101)	145 ± 20 (N = 635)
Duration of nymphal stage:		
12L:12D at 28°C, days	46 ± 6 (N = 32)	53 ± 7 (N = 26)
16L:8D at 28°C, days	54 ± 5 (N = 48)	64 ± 4 (N = 37)
Adult head width (× $\frac{1}{8}$ mm)		
Male	71 ± 3 (N = 25)	78 ± 3 (N = 25)
Female	69 ± 2 (N = 26)	71 ± 2 (N = 22)

^a M. Watanabe (unpublished data); Means ± S.D. N, sample size.

matic gradient. The adult size of *T. emma* is in fact described by multiple regression equations taking both latitude and altitude as independent variables (Masaki, 1967). Ismail and Fuzeau-Braesch (1972a) compared development and diapause of three local populations of *Gryllus campestris* collected from different altitudes. Although the number of instars before reaching the penultimate diapause stage varies from seven to ten in all strains, the modal instar number is eight in the alpine (1200 m above sea level) strain, while it is nine in the two lowland strains. This is accompanied by a 10- to 20-day difference in the duration of prediapause development.

Saw-Toothed Patterns of Variation

When voltinism varies, climatic selection results in more complicated patterns of variation, because the amount of heat available for nymphal development in each generation varies with the number of generations per year. In a given locality, selection for shorter development time is much stronger with a bivoltine cycle than with a univoltine cycle. Therefore, the selection pressure would be reversed with a shift in voltinism. This is in fact reflected in the saw-toothed patterns of adult size variation in the two species of multivoltine ground cricket, *Dianemobius mikado* and *D. nigrofasciatus*, in the Japanese islands (Fig. 20) (Masaki, 1978a, 1979a). These patterns are quite different from those found in univoltine species, but very similar to each other. From the northern limit of distribution, adult size increases southward, reaches its maximum at about 38–48°N, and sharply decreases to about 33–36°N. Farther south in the bivoltine area, there is again a slight southward increase of adult size.

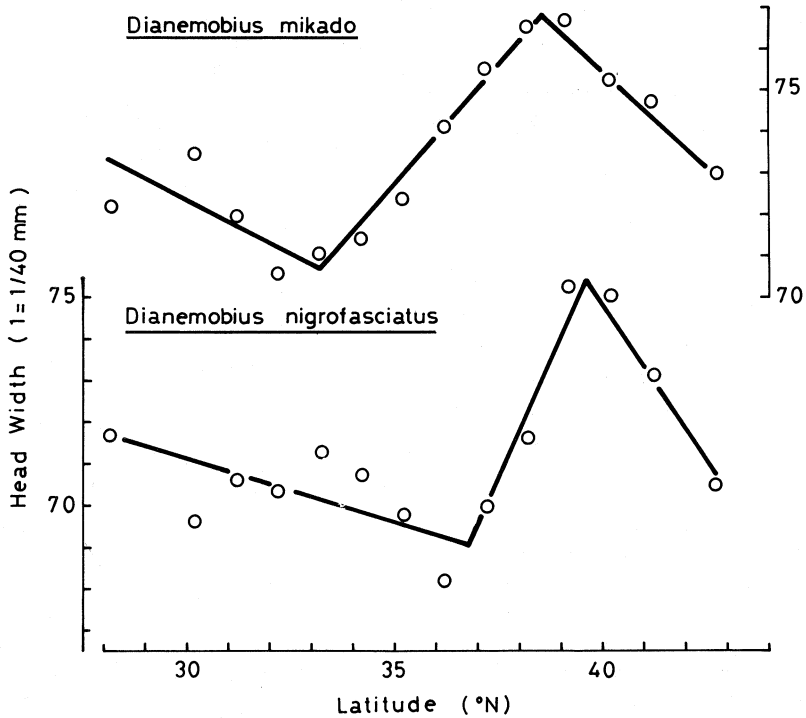


FIG. 20. Saw-toothed latitudinal clines of adult size in two ground cricket species. Symbols represent latitudinal means. Width is given in units of $\frac{1}{40}$ mm. [Modified from Masaki (1978a).]

These variations are accompanied by variations in the mode of parental programming of egg diapause. The egg diapause is prevalent even under long-day conditions in the large northern populations, but it is induced only by short days in the smaller southern populations (Kidokoro and Masaki, 1978). This transition of photoperiodic response in *D. mikado* occurs at around 35°N, roughly corresponding to the change in direction of size variation (Fig. 21) (Masaki, 1979a).

Although *D. mikado* maintains its short-day type of nymphal development throughout its range, the duration of the nymphal stage in long days varies considerably, being longest near the southern limit of the univoltine area (Masaki, 1979a). In *D. nigrofasciatus* a similar trend occurs in the univoltine area, but the retarding photoperiod is shifted from a long to a shorter intermediate range in the bivoltine area (Figs. 13D, 14) (Masaki, 1973).

It is highly probable that the saw-toothed clines in adult size are by-

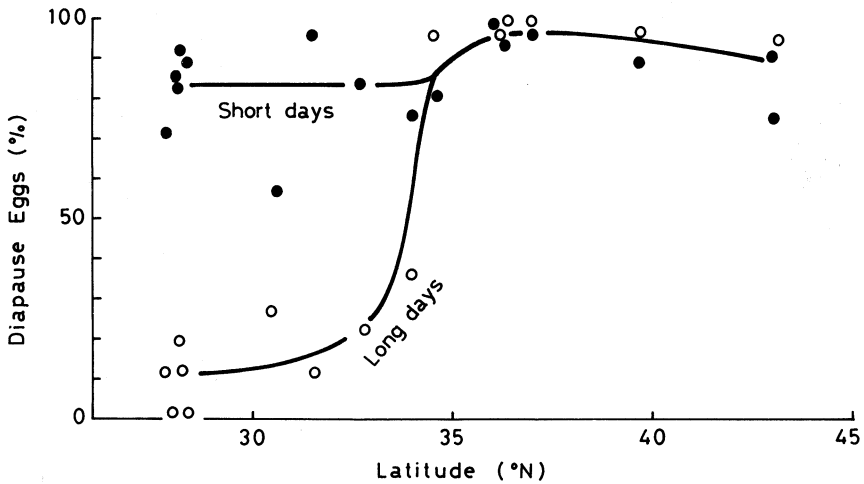


FIG. 21. Incidence of egg diapause in short (11–13 hr) or long (15–16 hr) photoperiods in various local populations of *Dianemobius mikado* reared at 26°C. [Modified from Masaki (1979a).]

products of climatic selection on development time as in the univoltine species. The same climatic gradient thus results in quite different patterns of geographical variation according to the constancy or variability of voltinism.

Although adult size is generally proportional to nymphal development time under given conditions of temperature (Masaki, 1973, 1978*b*), multiple regression analysis in *D. mikado* shows a significant northward increase in adult size even after the correction for the regression on development time (Masaki, 1978*b*). There is therefore the possibility that the rate of growth or size gain per unit time is increased to a certain extent as an adaptation to the cooler northern environment. This sort of adaptive response is also indicated by comparison between the northern and southern sibling species. The two species of ground cricket mentioned above are clearly larger than their respective southern relatives, *D. taprobanensis* and *D. fascipes*, and yet they complete nymphal development faster than the latter, at least in nonretarding photoperiods. The time available for reproduction is much longer in tropical and subtropical regions, so that the smaller southern adults can produce more eggs than the larger northern adults. Selection for larger body size in hot climates would not therefore be as strong as in cool climates.

Polymorphism in Life Cycles

In multivoltine species, different types of life cycles may coexist in the same area. Such a situation is usually expected in the transitional zone between univoltine and bivoltine cycles. Since the different life cycles are subject to different selection pressures even under the same climate, how such polymorphism in life cycle is maintained in a single population is an important problem in adaptation.

In *Dianemobius nigrofasciatus* collected from a transitional zone between the univoltine and bivoltine areas, the fast- and late-growing fractions of the nymphs show different photoperiodic responses, the intermediate and short-day types, corresponding to the bivoltine and univoltine cycles, respectively (Kidokoro and Masaki, 1978). As a consequence, the emergence curves in long photoperiods are bimodal. Since, however, the autumn short days accelerate the nymphal development in both types of response, the first generation of the short-day type and the progeny of the intermediate type should emerge as adults in overlapping periods in autumn and interbreed. Hybrids are intermediate in growth rate between the parents. Since they retain the development-accelerating response to short days, the seasonal cycle of day length exerts a feedback effect to compensate for the variable rates of maturation in summer. In addition to this, the relatively long adult life enhances interbreeding between individuals with different life cycles. The annual fluctuation in climatic conditions is another factor supporting the coexistence of the different types of photoperiodic response, for the relative fitnesses of the different responses will vary from year to year.

Gryllus firmus in north Florida represents an extreme in life-cycle polymorphism (Ibrahim and Walker, 1980; Walker, 1980a, and unpublished). The most frequent life cycle is apparently bivoltine, egg-overwintering, with adults peaking in late June and July and in late September and October. However, all stages occur at all times, except that young juveniles are absent during January–March. The continual mix of stages is a result of both eggs and nymphs having varying proportions of individuals showing diapause of varying intensity. Eggs laid by one female during 1 week may take from 2 to 34 weeks to hatch under field temperatures (and 2–17 weeks to hatch at 25°C). Most eggs laid in spring hatch quickly (i.e., within 4 weeks at 25°C). Later, increasing portions of diapause eggs are laid and in late fall those eggs that are nondiapause when laid (as assayed at 25°C) become diapause eggs when left outdoors under naturally cool temperatures (Walker, 1980a). Nymphal development in outdoor cages (with ample food and moisture) requires 2–10 months; in-

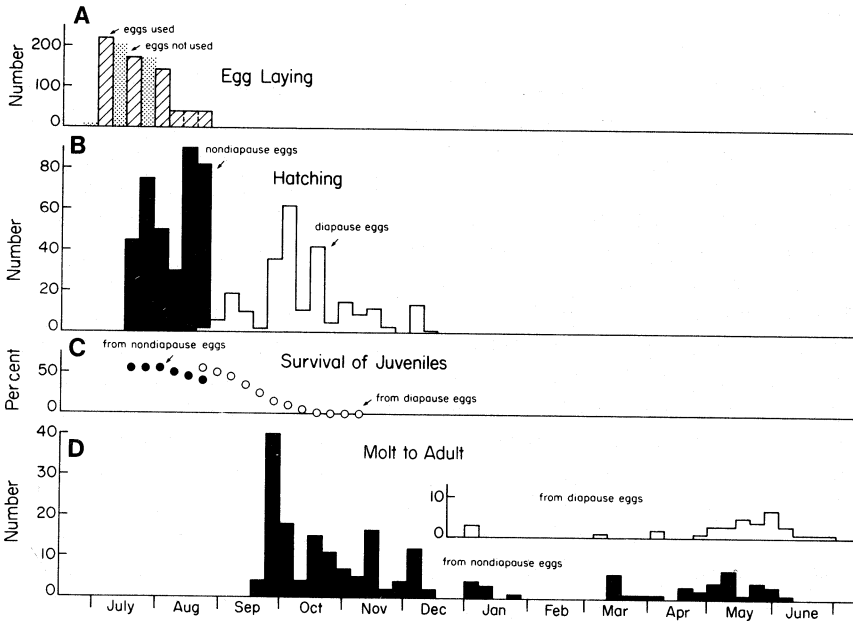


FIG. 22. Outdoor development of progeny of one field-caught *Gryllus firmus* female at Gainesville, Florida. (A) Only eggs laid during weeks 2, 4, 6, and 7–9 (hatched bars; 2 July–27 August 1972) were monitored outdoors. (B) Hatching occurred between 16 July and 20 December; late-laid nondiapause eggs overlapped slightly in hatching dates with early-laid diapause eggs. (C) Juveniles hatching after mid-September had reduced chances of surviving the winter and none that hatched after 22 October survived (deaths were not the direct results of cold snaps). (D) Adults were produced from 20 September until 28 June. Outdoor rearing cages were censused and food and moisture were replenished weekly. Similar data were obtained with other females (Walker, 1980a, and unpublished data).

doors at 25°C, 16L:8D, 2–7 months (T. J. Walker, unpublished results). Figure 22 illustrates how eggs laid by one female during 8 weeks can produce adults for the next 10 months.

Gryllus firmus lives in sandy, open habitats that, except during the summer rainy season, are subject to severe, unpredictable droughts. Its developmental strategy spreads the risks, as does its wing polymorphism (Roff, 1984). Northward from Florida, increasing duration and severity of winter gradually curtail developmental options until only egg-overwintering remains (Harrison and Arnold, 1982; Walker, 1980a). Given the diversity of development occurring in north Florida, *G. firmus* could have diverged northward into separate egg-overwintering and nymph-overwintering populations. However, to the extent that varied life cycles enable *G. firmus* to survive unpredictable hazards occurring at uncertain seasons,

selection should favor genetic continuity. Conforming to this prediction is the fact that in coastal North Carolina, the northernmost locality known for nymph-overwintering in *G. firmus*, the nymphs and egg-overwintering populations are apparently kept in genetic communication by some life cycles being bivoltine (Walker, 1980a).

Although detailed field data are yet not available, *Dianemobius fascipes* in the southwestern islands of Japan may have a life cycle as complex as north Florida *G. firmus*. It shows a photoperiodic induction of egg diapause, though the incidence is very low, and at the same time a short-day retardation of nymphal development that apparently increases the possibility of nymph overwintering (Masaki, 1978a).

LIFE CYCLE AND SPECIATION

Seasonal Isolation

Although polymorphic life cycles are kept in balance and exist permanently under certain circumstances, divergence in hibernating stage may lead to seasonal isolation, particularly when the life cycle is strictly univoltine. A model of allochronic speciation was thus put forward by Alexander and Bigelow (1960) to explain the speciation of the fall-breeding *Gryllus pennsylvanicus* and the spring-breeding *G. veletis*. Later electrophoretic and cytological studies revealed these two species to be more distantly related to each other than to some other members of the same genus (Harrison, 1978). The failure of crosses to produce hybrids may also be taken as evidence for their rather remote relationship (Alexander, 1957; Bigelow, 1960a,b). Nevertheless, it is worthwhile to explore the possibility of speciation due to life cycle divergence that results in an effective seasonal isolation.

The partially sympatric distribution of the egg-overwintering (autumn) and nymph-overwintering (summer) forms of *Velarifictorus micado* in Japan illustrates a case in point. Both forms are univoltine and, as far as can be inferred from the singing season, the seasonal isolation is almost complete. There are significant differences between them in the length of ovipositor and the number of file teeth. The summer form has on average a shorter ovipositor and a greater number of file teeth than the autumn form (M. Watanabe, unpublished data). Much more conspicuous differences are found in the egg and nymphal stages (pp. 371, 380, 382; Fig. 10). The summer form is almost free of egg diapause and its nymphs take

a much longer time to mature than those of the autumn form. The latter invariably produces only diapause eggs.

In contrast to the case of *G. pennsylvanicus* and *G. veletis*, the close genetic relationship between the two seasonal forms of *V. micado* is indicated by their interfertility. Since Japanese "micado" may consist of eastern peripheral populations, the possibility cannot be ruled out that these seasonally isolated entities are interconnected by a series of polymorphic populations somewhere on the Asian continent. It is at least certain, however, that they behave as two good species in the Japanese islands because of their distinct adaptations to seasonal changes that effectively isolate them from each other. Were there no such divergence in life cycle, they would not persist as distinct populations, because they are interfertile. Irrespective of whether the initial impetus to speciation arose in allopatry or sympatry, divergence in the seasonal life cycle plays an essential role in maintaining or enhancing the isolation between the two diverging forms. Allochronic speciation is theoretically quite feasible and provides a useful model to approach speciation phenomena. Walker (1974) noted that this model could be applied to the divergence of *Gryllus ovisopis* and *G. fultoni*, but subsequent evidence suggests that *G. ovisopis* is most closely related to *G. firmus*, making allopatric speciation more plausible (Harrison, 1978).

Parallel Divergence of Life Cycles

In the Japanese islands, there are examples suggesting another sort of involvement of life cycle divergence in speciation. In the Ryukyu Arc (about 24–28°N) each of the two northern species of ground crickets is replaced by a closely related subtropical one: *Dianemobius nigrofasciatus* by *D. fascipes*, and *D. mikado* by *D. taprobanensis*. *Dianemobius fascipes* and *D. taprobanensis* occur widely in southeast Asia. Since Chopard identified the temperate Japanese specimens as conspecific to the tropical ones (F. Ohmachi, personal communication), these names have been used for the temperate as well as the subtropical populations. Audiospectrographic analyses of the songs give no clear diagnostic differences between the temperate and subtropical forms in each pair (Matsuura, 1982). Mainly based on the life cycle analyses (nymphal photoperiodic responses, egg diapause, etc.), Masaki (1978*a,b*, 1979*a,b*, 1983) claimed that in each species pair, the temperate and subtropical forms are distinct at the species level, because they are adaptively incompatible with each other. This means that intercrossing between them decreases fitness and they would not form a common gene pool.

The virtual absence of egg diapause and the long-day-type regulation of nymphal development in the subtropical form *D. taprobanensis* contrast sharply with the egg-diapausing and short-day-type nymphal development of the temperate form *D. mikado* (Figs. 13B, 13C). Although the two species are interfertile and the hybrids are fertile, the seasonal regulatory mechanisms are broken down by hybridization. Most hybrid eggs hatch without delay, the expression of the northern diapause character being largely suppressed. Hybrid females develop normally, but their photoperiodic response is intermediate between the parental short-day and long-day types. Growth of hybrid males is remarkably retarded when their mother is subtropical. Conversely, they grow abnormally fast when their mother is temperate. In both cases, the photoperiodic response disappears (Fig. 23). As a result, the male and female hybrids mature in widely separated periods. In F_2 hybrid progeny, there is an outburst of developmental variance in both sexes (Masaki, 1978a).

Crossing the subtropical form *D. fascipes* to the temperate form *D. nigrofasciatus* gives similar results. Differences are the virtual sterility of male hybrids and a slight manifestation of egg diapause in hybrid eggs. However, the overriding result of hybridization is the same, i.e., the photoperiodic regulatory mechanism breaks down. The similarity in this respect is so impressive that one may suspect the existence of the same genetic and physiological mechanisms underlying these abnormalities.

Climatic Speciation Model

Insofar as the northern and southern forms in each pair of these ground crickets are at present parapatric or allopatric, speciation in these cases does not contradict the allopatric model. However, the main difference between the divergent forms resides in the seasonal adaptation, which suggests that the latter is involved in the speciation in an important way. First, these examples show that different climates tend to select for different types of life cycle, the temperate climate an egg-diapausing one and the subtropical climate a nymph-overwintering one.

Since there is an almost linear latitudinal gradient in climatic conditions, the two different types of life cycle have different optimal latitudes. Within a certain range, local adaptations such as those described in the section on geographical speciation can compensate for variation in fitness due to the climatic gradient, and fitness can be maintained. However, near the extremes for this fine tuning, fitness should decrease, limiting the northward distribution of nymph-overwintering populations and the southward distribution of egg-overwintering populations. At some

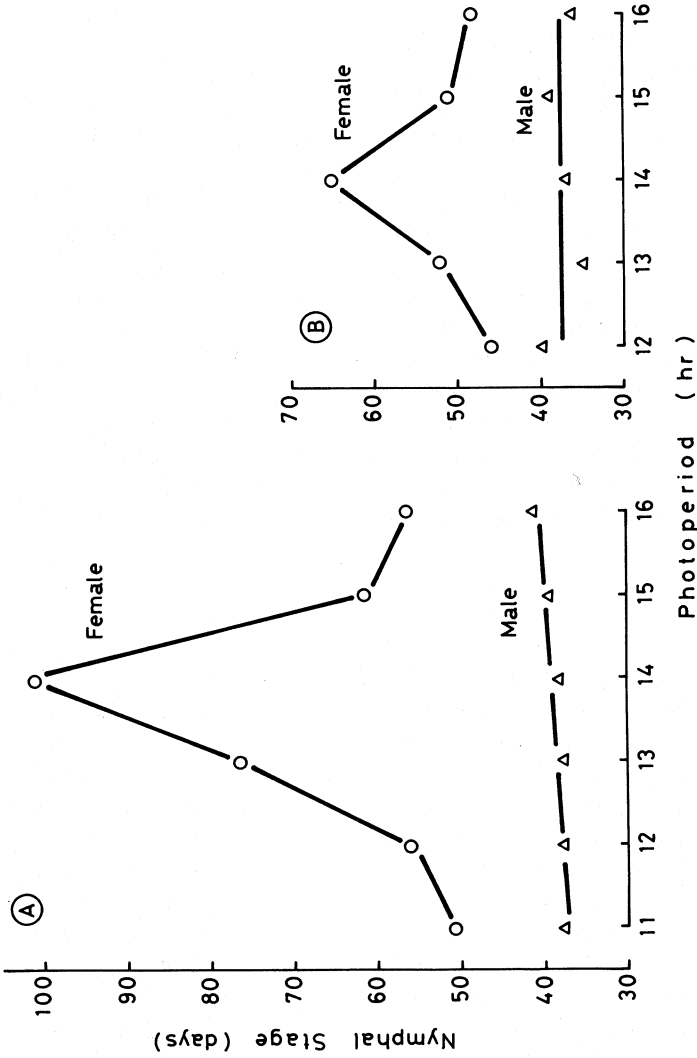


FIG. 23. Nymphal development of F₁ hybrids between *Dianemobius mikado* females and *D. taprobanensis* males. (A) Female parents from central Honshu (35°N). (B) Female parents from Hokkaido (43°N). In both cases male parents are from Tokunoshima (27°N). [From Masaki (1978a and unpublished data).]

point the fitnesses of the two types of life cycle should be equal. To the north of this point selection should favor egg overwintering more than nymph overwintering.

If an egg-overwintering genotype occurs near the northern periphery of a nymph-overwintering population, it may break through the preexisting northern survival limit. As egg-overwinterers advance farther north, they will escape effective gene flow from the nymph-overwintering cohort and be able to evolve by themselves. They can then establish their egg-diapausing life cycle and an adequate photoperiodic response. Since this shift involves reorganization of coadapted subsystems regulating growth, development, and photoperiodism, the newly established genotype becomes more or less adaptively incompatible with the previous one, and can exist only as a distinct biological entity.

If there is a geographical barrier between southern and northern populations, this sort of divergence is facilitated. Even in such a case, however, the geographical isolation itself is not the primary factor triggering speciation. It is the differential selection of the seasonal life cycle by different climates that causes divergence. Therefore, the term climatic speciation may be appropriate to denote this speciation model.

A similar situation is involved in the divergence of a heterodynamic life cycle of any type from a homodynamic life cycle. Such divergence may explain the occurrence of very closely related species pairs, one in lower latitudes and the other in higher latitudes, such as *Teleogryllus oceanicus*/*T. commodus* or *Gryllus bimaculatus*/*G. campestris*. At present more than ten cricket species in Japan are regarded as conspecific to tropical ones (Chopard, 1967, 1968). The model of climatic speciation predicts that they may be distinct from the tropical populations at the species level.

Evolutionary Potential in Life Cycle

The importance of life-cycle divergence in speciation also comes from the fact that the physiological traits molding a life cycle are evolutionarily quite flexible.

Laboratory cultures of crickets are able to respond to artificial selection either by abbreviating or intensifying diapause. Inadvertent selection for rapid maturation and reproduction that tends to occur in rearing successive generations significantly reduces egg diapause within a few generations in *Teleogryllus commodus* (Bigelow and Cochaux, 1962). Selection is effective in eliminating the nymphal diapause from *Gryllus campestris* (Ismail and Fuzeau-Braesch, 1976). Conversely, a subtropical

strain of *D. fascipes* has increased the percentage of egg diapause from about 10% to 60–70% during 15 generations of selection for diapause (Masaki, 1978a, and unpublished data). Similar processes of selection must occur in nature when crickets are exposed to novel environmental conditions. Recent immigration over a great distance into a different climatic area may provide an opportunity to look at this problem.

Teleogryllus commodus is believed to be a native of Australia and has been a pasture pest in northern regions of New Zealand since early European settlement. There is a clear difference in the incidence of diapause at about 30°C between the Auckland (30%) and Nelson (98%) populations (Mason, 1973). This is comparable to the local tendency toward diapause in Australia, i.e., diapause is expressed more strongly in strains from cooler southern localities than in those from warm northern localities (Bigelow and Cochaus, 1962; Hogan, 1965b, 1966). There is a possibility that the local variation in New Zealand is an outcome of selection after European settlement.

The population of *Dianemobius mikado* in the Bonin Islands, located about 900 km south of the main island of Japan, was probably introduced about a century ago. Under the subtropical oceanic climate they seem to grow and reproduce throughout the year, having virtually lost the ability to egg diapause. However, they still retain the morphological characteristics of the temperate form, such as the length of ovipositor and the number of file teeth and also the short-day type of nymphal development (Masaki, 1978a). In the original temperate habitat, the latter response is harmonized with the egg-diapausing cycle (p. 382). Despite the loss of egg diapause, the useless short-day response has survived, probably because the long-day retardation of the nymphal development is not affected at the low latitudes of the Bonin Islands (27°N).

The identity of the Bonin ground cricket is further confirmed by crossing it to the central mainland population. The hybrids show no abnormality in development in either sex and are fertile. Moreover, when crossed to the subtropical *D. taprobanensis*, the Bonin and mainland populations produce similar hybrids characterized by the breakdown of photoperiodic response in male nymphs (p. 409).

A similar loss of diapause is found in the population of *Gryllus firmus* occurring on the isolated island of Bermuda (Kevan, 1980). Since this population shows a minor genetic incompatibility with the Virginian population, the observed divergence is assumed to have evolved prior to human settlement (A.D. 1609).

In view of the ample evidence for the evolutionary flexibility of diapause and photoperiodic responses, it is not surprising that a rather drastic change might occur within a relatively short period of time. The clear

clinal variations in some Japanese species of crickets (see section on geographical adaptations) must indeed have been established within a period shorter than 10,000 years after the last glacial maximum, during which the northern half of the country might not have been habitable for any crickets. The clines are indeed closely correlated with the present climatic gradient.

Divergence in life cycle may invoke a sequence of changes in other ecological, physiological, behavioral, or morphological traits, because different seasonal arrangements of the life stages result in different selection pressures on each stage. For example, egg-overwintering species of the ground crickets *Dianemobius nigrofasciatus* and *D. mikado* have longer ovipositors than their commonly nymph-overwintering relatives *D. fascipes* and *D. taprobanensis*, respectively (Masaki, 1978a, 1979a). Parallel situations are found in larger field crickets. The ovipositor is longer in *Teleogryllus emma*, which diapauses as an egg, than in *T. occipitalis*, which hibernates as a nymph. As stated before, the egg-overwintering

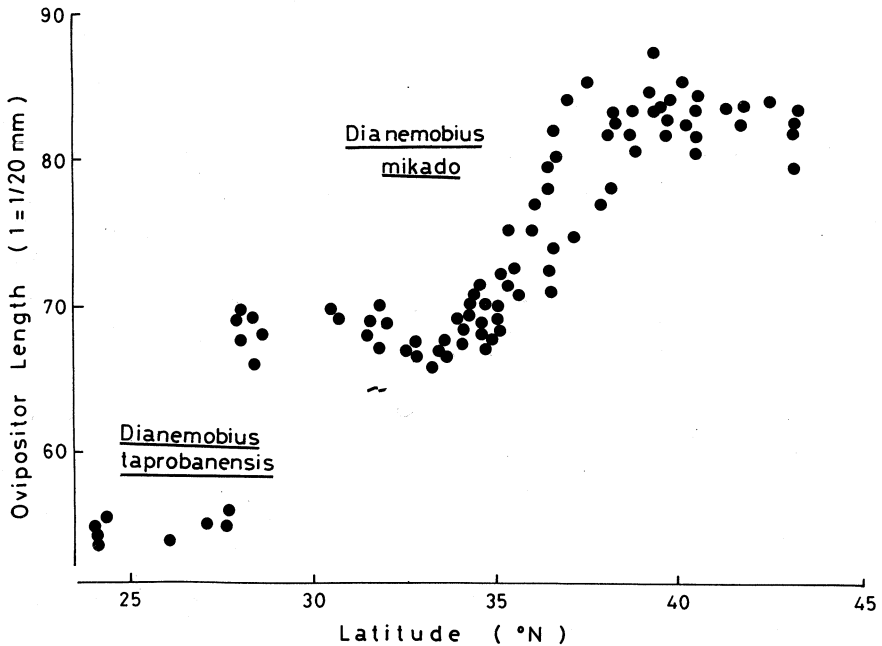


FIG. 24. Latitudinal variation in ovipositor length of *Dianemobius mikado*. Each symbol is the mean for a local sample. Length is given in units of $\frac{1}{20}$ mm. Univoltine populations have longer ovipositors than bivoltine ones. The ovipositor is shortened further in the subtropical relative, *D. taprobanensis*. [Masaki (1979b).]

and the nymph-overwintering forms of *Velarifictorus micado* can be distinguished by ovipositor length. Clearly, the longer ovipositor confers more advantage for egg-overwinterers than for nymph-overwinterers because of the longer period of better protection when eggs are inserted deeper into the soil.

Probably for the same reason, the two egg-diapausing species *D. mikado* and *D. nigrofasciatus* show regular geographical variations in ovipositor length. The ovipositor is longer in the univoltine populations than in the bivoltine populations and also in the northern than in the southern parts of the univoltine area (Fig. 24) (Masaki, 1978a, 1979b, and unpublished data). The ovipositor length is thus correlated with the duration of the egg stage in the field.

The life-cycle type represents one of the most basic features of adaptation and the shift from one type to another is a major change in the way of life that characterizes each species. Speciation may therefore be a natural consequence of divergence in the seasonal life cycle. Since an impetus to such divergence is caused by climatic selection, climatic speciation deserves further serious consideration for understanding evolutionary phenomena in crickets.

REFERENCES

- Alexander, R. D., 1957, The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*), *Ann. Entomol. Soc. Am.* **50**:584–602.
- Alexander, R. D., 1968, Life cycle origins, speciation, and related phenomena in crickets, *Q. Rev. Biol.* **43**:1–41.
- Alexander, R. D., and Bigelow, R. S., 1960, Allochronic speciation in field crickets, and a new species, *Acheta veletis*, *Evolution* **14**:334–346.
- Alexander, R. D., and Thomas, E. S., 1959, Systematic studies on the crickets of the *Nemobius fasciatus* group (Orthoptera: Nemobiinae), *Ann. Entomol. Soc. Am.* **52**:591–605.
- Alexander, R. D., and Walker, T. J., 1962, Two introduced field crickets new to eastern United States, *Ann. Entomol. Soc. Am.* **55**:90–94.
- Arai, T., 1978a, Effects of environmental conditions on the wing form and growth in *Grylloides sigillatus* Walker (Orthoptera: Gryllidae), *Jpn. J. Ecol.* **28**:135–142 [in Japanese].
- Arai, T., 1978b, Effects of group size on the wing form in *Grylloides sigillatus* Walker (Orthoptera: Gryllidae), *Jpn. J. Ecol.* **28**:263–267 [in Japanese].
- Bate, J., 1971, Life history of *Acheta domesticus* (Insecta, Orthoptera, Gryllidae), *Pedobiologia* **11**:159–172.
- Bell, P. D., 1979, Rearing the black horned tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae), *Can. Entomol.* **111**:709–712.
- Bentur, J. S., and Mathad, S. B., 1975, Photoperiodic regulation of reproduction in non-diapausing cricket, *Plebeiogryllus guttiventris* Walker, *Karnatak Univ. J. Sci.* **20**:218–222.

- Bigelow, R. S., 1958, Evolution in the field cricket, *Acheta assimilis* Fab., *Can. J. Zool.* **36**:139–151.
- Bigelow, R. S., 1960a, Developmental rates and diapause in *Acheta pennsylvanicus* (Brumeister) and *Acheta veletis* Alexander and Bigelow (Orthoptera: Gryllidae), *Can. J. Zool.* **38**:973–988.
- Bigelow, R. S., 1960b, Interspecific hybrids and speciation in the genus *Acheta* (Orthoptera, Gryllidae), *Can. J. Zool.* **38**:509–524.
- Bigelow, R. S., 1962, Factors affecting developmental rates and diapause in field crickets, *Evolution* **16**:396–406.
- Bigelow, R. S., and Cochaux, P. S. A., 1962, Intersterility and diapause difference between geographical populations of *Teleogryllus commodus* (Walker) (Orthoptera: Gryllidae), *Aust. J. Zool.* **10**:360–366.
- Brookes, H. M., 1952, The morphological development of the embryo of *Gryllulus commodus* Walker (Orthoptera: Gryllidae), *Trans. R. Soc. Aust.* **75**:150–159.
- Brown, V. K., 1978, Variations in voltinism and diapause intensity in *Nemobius sylvestris* (Bosc.) (Orthoptera: Gryllidae), *J. Nat. Hist.* **12**:461–472.
- Browning, T. O., 1952a, The influence of temperature on the rate of development of insects, with special reference to the egg of *Gryllulus commodus* Walker, *Aust. J. Sci. Res. B Biol. Sci.* **5**:96–111.
- Browning, T. O., 1952b, The influence of temperature on the completion of diapause in the eggs of *Gryllulus commodus* Walker, *Aust. J. Sci. Res. B Biol. Sci.* **5**:112–127.
- Browning, T. O., 1952c, On the rate of completion of diapause development at constant temperatures in the eggs of *Gryllulus commodus* Walker, *Aust. J. Sci. Res. B Biol. Sci.* **5**:344–353.
- Browning, T. O., 1953, The influence of temperature and moisture on the uptake and loss of water in the eggs of *Gryllulus commodus* Walker (Orthoptera—Gryllidae), *J. Exp. Biol.* **30**:104–115.
- Browning, T. O., 1965, Observations on the absorption of water, diapause and embryogenesis in the eggs of the cricket *Teleogryllus commodus* (Walker), *J. Exp. Biol.* **43**:433–439.
- Browning, T. O., 1969a, Permeability to water of the shell of the egg of *Locusta migratoria migratorioides*, with observations on the egg of *Teleogryllus commodus*, *J. Exp. Biol.* **51**:99–105.
- Browning, T. O., 1969b, The permeability of the shell of the egg of *Teleogryllus commodus* measured with the aid of tritiated water, *J. Exp. Biol.* **51**:397–405.
- Browning, T. O., and Forrest, W. W., 1960, The permeability of the shell of *Acheta commodus* Walker (Orthoptera, Gryllidae), *J. Exp. Biol.* **37**:213–217.
- Chauvin, R., 1958, L'action de groupement sur la croissance de grillons (*Gryllus domesticus*), *J. Insect Physiol.* **2**:235–248.
- Chopard, L., 1967, *Orthopterorum Catalogus*. Pars 10, *Gryllides*, pp. 1–211, W. Junk N. V., Gravenhage.
- Chopard, L., 1968, *Orthopterorum catalogus*. Pars 12, *Gryllides*, pp. 213–500, W. Junk N. V., Gravenhage.
- Chopard, L., 1969, *The Fauna of India and Adjacent Countries*. Orthoptera. Vol. 2, *Grylloidea*, Baptist Mission Press, Calcutta.
- Cooper, W. S., and Kaplan, R. H., Adaptive “coin-flipping”: A decision-theoretic examination of natural selection for random individual variation, *J. Theor. Biol.* **94**:135–151.
- Dakshayani, K., and Mathad, S. B., 1973, A comparative study of growth, development and survival of the cricket *Plebeiogryllus guttiventris* Walker reared singly and in groups, *Experimentia* **29**:978–979.

- Dakshayani, K., and Mathad, S. B., 1975, Life-history of the cricket, *Plebeigrillus guttiventris* Walker, *Karnatak Univ. J. Sci.* **20**:240-243.
- Denlinger, D. L., 1986, Dormancy in tropical insects, *Annu. Rev. Entomol.* **31**:239-264.
- Forrest, T. G., 1986, Oviposition and maternal investment in mole crickets (Orthoptera: Gryllotalpidae): Effects of season, size and senescence, *Ann. Entomol. Soc. Am.*, **79**:918-924.
- Fulton, B. B., 1915, The Tree Crickets of New York: Life History and Bionomics, Technical Bulletin New York Agricultural Experiment Station No. 42.
- Fulton, B. B., 1931, A study of the genus *Nemobius* (Orthoptera: Gryllidae), *Ann. Entomol. Soc. Am.* **24**:205-237.
- Fulton, B. B., 1951, The seasonal succession of orthopteran stridulation near Raleigh, North Carolina, *J. Elisha Mitchell Soc.* **67**:87-95.
- Fuzeau-Braesch, S., 1963, Ajustment du cycle de vie avec les saisons chez un insecte univoltin, *C. R. Acad. Sci. Paris* **256**:792-794.
- Fuzeau-Braesch, S., 1965, Hibernation de *Gryllus campestris* L. (Orthopteres, Gryllides): Analyse de la stabilité et des exigences de la diapause, *C. R. Seances Soc. Biol.* **159**:1048-1052.
- Fuzeau-Braesch, S., 1966, Etude de la diapause de *Gryllus campestris* (Orthoptera), *J. Insect Physiol.* **12**:449-455.
- Fuzeau-Braesch, S., 1972, Pigments and color changes, *Annu. Rev. Entomol.* **17**:403-424.
- Fuzeau-Braesch, S., 1975, Cycle de vie et évolution larvaire d'un grillon d'Algérie, *C. R. Acad. Sci. Paris D* **281**:1385-1388.
- Fuzeau-Braesch, S., and Ros, A.-M., 1965, Effet de groupe et température dans la croissance d'un insecte: *Gryllus bimaculatus* (Orthopteres, Gryllides), *C. R. Acad. Sci. Paris* **260**:987-990.
- Gabbutt, P. D., 1959a, The bionomics of the wood cricket, *Nemobius sylvestris* (Orthoptera: Gryllidae), *J. Anim. Ecol.* **28**:15-42.
- Gabbutt, P. D., 1959b, The instars of the wood cricket *Nemobius sylvestris* (Bosc.) (Orthoptera: Gryllidae), *Proc. R. Entomol. Soc. Lond. A* **34**:37-43.
- Ghouri, A. S. K., and McFarlane, J. E., 1957, Reproductive isolation in the house cricket (Orthoptera: Gryllidae), *Psyche* **64**:30-36.
- Ghouri, A. S. K., and McFarlane, J. E., 1958a, Observations on the development of crickets, *Can. Entomol.* **90**:158-165.
- Ghouri, A. S. K., and McFarlane, J. E., 1958b, Occurrence of a macropterous form of *Grylodes sigillatus* (Walker) (Orthoptera: Gryllidae) in laboratory culture, *Can. J. Zool.* **36**:837-838.
- Grellet, P., 1971, Analyse expérimentale de l'absorption d'eau dans l'oeuf de *Scapsipedeus marginatus* (Orthoptere, Gryllide), *J. Insect Physiol.* **17**:1533-1553.
- Harrison, R. G., 1978, Ecological parameters and speciation in field crickets, in: *Ecological Genetics: The Interface* (P. F. Brussard, ed.), Springer-Verlag, New York.
- Harrison, R. G., 1979, Flight polymorphism in the field cricket *Gryllus pennsylvanicus*, *Oecologia* **40**:125-132.
- Harrison, R. G., 1980, Dispersal polymorphism in insects, *Annu. Rev. Ecol. Syst.* **11**:95-118.
- Harrison, R. G., and Arnold, J., 1982, A narrow hybrid zone between closely related cricket species, *Evolution* **36**:535-552.
- Hayslip, N. C., 1943, Notes on biological studies of mole crickets at Plant City, Florida, *Fla. Entomol.* **26**:33-46.
- Hogan, T. W., 1960a, The onset and duration of diapause in eggs of *Acheta commodus* (Walk.) (Orthoptera), *Aust. J. Biol. Sci.* **13**:14-29.

- Hogan, T. W., 1960b, The effects of subzero temperatures on embryonic diapause of *Acheta commodus* (Walk.) (Orthoptera), *Aust. J. Biol. Sci.* **13**:527–540.
- Hogan, T. W., 1961, The action of urea on diapause in eggs of *Acheta commodus* (Walk.) (Orthoptera: Gryllidae), *Aust. J. Biol. Sci.* **14**:419–426.
- Hogan, T. W., 1962a, The absorption and subsequent breakdown of urea by diapausing eggs of *Acheta commodus* (Walker) (Orthoptera: Gryllidae), *Aust. J. Biol. Sci.* **15**:362–370.
- Hogan, T. W., 1962b, The effect of ammonia on the rate of termination of diapause in eggs of *Acheta commodus* (Walker) (Orthoptera: Gryllidae), *Aust. J. Biol. Sci.* **15**:538–542.
- Hogan, T. W., 1964, Further data on the effect of ammonia on the termination of diapause in eggs of *Teleogryllus commodus* (Walk.) (Orthoptera: Gryllidae), *Aust. J. Biol. Sci.* **17**:752–757.
- Hogan, T. W., 1965a, Changes in pH associated with the application of ammonia and potassium hydroxide to diapausing eggs of *Teleogryllus commodus* (Walk.) (Orthoptera: Gryllidae), *Aust. J. Biol. Sci.* **18**:81–87.
- Hogan, T. W., 1965b, Some diapause characteristics and interfertility of three geographic populations of *Teleogryllus commodus* (Walk.) (Orthoptera: Gryllidae), *Aust. J. Zool.* **13**:455–459.
- Hogan, T. W., 1966, Physiological differences between races of *Teleogryllus commodus* (Walker) (Orthoptera: Gryllidae) related to a proposed genetic approach to control, *Aust. J. Zool.* **14**:245–251.
- Hogan, T. W., 1967, The influence of diapause on the resistance to desiccation of eggs of *Teleogryllus commodus* (Walk.) (Orthoptera: Gryllidae), *R. Soc. Victoria* **80**:37–42.
- Hogan, T. W., 1971, An evaluation of a genetic method for population suppression of *Teleogryllus commodus* (Walk.) (Orth., Gryllidae) in Victoria, *Bull. Entomol. Res.* **60**:383–390.
- Ibrahim, R., and Walker, T. J., 1980, Diapause and nondiapause eggs laid daily by individual *Gryllus firmus* females (Orthoptera: Gryllidae), *Fla. Entomol.* **63**:510–512.
- Ingrisch, S., 1977, Das Stridulationsorgan der Käfergrille *Trigonidium cicindeloides* (Orthoptera: Gryllidae: Trigoniniinae) und Beobachtungen zur Eidonomie und Ethologie, *Entomol. Germ.* **3**:324–332.
- Ingrisch, S., 1978, Zur Anatomie der Hinterflügel bei Grillen (Saltatoria, Gryllidae), *Entomol. Z.* **88**:1–6.
- Irie, K., Suzuki, K., and Miya, K., 1979, Change of carbohydrate content during ovarian and embryonic development in Emma field cricket, *Teleogryllus emma*, *Appl. Entomol. Zool.* **14**:278–284.
- Ismail, M. S., and Fuzeau-Braesch, S., 1972a, Analyse du déterminisme de la diapause larvaire de *Gryllus campestris* (Orthopteres): Suppression de la diapause par sélection génétique, *C. R. Acad. Sci. Paris D* **275**:1007–1009.
- Ismail, M. S., and Fuzeau-Braesch, S., 1972b, Action du photopériodisme sur le nombre de stades larvaires, la diapause et la morphogénèse chez *Gryllus campestris* (Orthoptere), *C. R. Acad. Sci. Paris D* **275**:2535–2538.
- Ismail, M. S., and Fuzeau-Braesch, S., 1976, Programmation de la diapause chez *Gryllus campestris*, *J. Insect Physiol.* **22**:133–139.
- Kevan, D. K. McE., 1980, The taxonomic status of the Bermuda beach cricket (Orthoptera: Gryllidae), *Syst. Entomol.* **5**:83–95.
- Kidokoro, T., and Masaki, S., Photoperiodic response in relation to variable voltinism in the ground cricket, *Pteronemobius fascipes* Walker (Orthoptera: Gryllidae), *Jpn. J. Ecol.* **28**:291–298.
- Liebermann, J., 1955, Bioecología y sistemática del grillo Argentino de hábitos subterráneos, *Anurogryllus muticus* (de Geer) (Orthop., Ensifera, Grylloidea, Gryllidae), *Natur* **1**:147–156.

- Logan, J. A., Wollkind, D. J., Hoyt, S. C., and Tanigoshi, L. K., 1976, An analytic model for description of temperature dependent rate phenomena in arthropods, *Environ. Entomol.* **5**:1133–1140.
- Love, R. E., and Walker, T. J., 1979, Systematics and acoustic behavior of scaly crickets (Orthoptera: Gryllidae: Mogoplistinae) of eastern United States, *Trans. Am. Entomol. Soc.* **105**:1–66.
- MacFarlane, J. R., and Drummond, F. H., 1970, Embryonic diapause in a hybrid between two Australian species of field cricket, *Teleogryllus* (Orthoptera: Gryllidae), *Aust. J. Zool.* **18**:265–272.
- MacFarlane, J. R., and Hogan, T. W., 1966, Free amino acid changes associated with diapause in the egg of the field cricket, *Teleogryllus*, *J. Insect Physiol.* **12**:1265–1278.
- Masaki, S., 1960, Thermal relations of diapause in the eggs of certain crickets (Orthoptera: Gryllidae), *Bull. Fac. Agric. Hirosaki Univ.* **6**:5–20.
- Masaki, S., 1961, Geographic variations of diapause in insects, *Bull. Fac. Agric. Hirosaki Univ.* **7**:66–98.
- Masaki, S., 1962, The influence of temperature on the intensity of diapause in the eggs of the Emma field cricket (Orthoptera: Gryllidae), *Kontyû* **30**:9–16.
- Masaki, S., 1963, Adaptation to local climatic conditions in the Emma field cricket (Orthoptera: Gryllidae), *Kontyû* **31**:249–260.
- Masaki, S., 1965, Geographic variation in the intrinsic incubation period: A physiological cline in the Emma field cricket (Orthoptera: Gryllidae: *Teleogryllus*), *Bull. Fac. Agric. Hirosaki Univ.* **11**:50–90.
- Masaki, S., 1966, Photoperiodism and geographic variation in the nymphal growth of *Teleogryllus yezoemma* (Ohmachi et Matsuura) (Orthoptera: Gryllidae), *Kontyû* **34**:277–288.
- Masaki, S., 1967, Geographic variation and climatic adaptation in a field cricket (Orthoptera: Gryllidae), *Evolution* **21**:725–741.
- Masaki, S., 1972, Photoperiodism in seasonal life cycles of crickets, in: *Problems of Insect Photoperiodism and Diapause*, Leningrad University, Leningrad [in Russian].
- Masaki, S., 1973, Climatic adaptation and photoperiodic response in the band-legged ground cricket, *Evolution* **26**:587–600.
- Masaki, S., 1977, Seasonal rhythm in crickets, *Iden* **1**:46–52 [in Japanese].
- Masaki, S., 1978a, Seasonal and latitudinal adaptations in the life cycles of crickets, in: *Evolution of Insect Migration and Diapause* (H. Dingle, ed.), pp. 72–100, Springer-Verlag, New York.
- Masaki, S., 1978b, Climatic adaptation and species status in the lawn ground cricket. II. Body size, *Oecologia* **35**:343–356.
- Masaki, S., 1979a, Climatic adaptation and species status in the lawn ground cricket. I. Photoperiodic response, *Kontyû* **47**:48–65.
- Masaki, S., 1979b, Climatic adaptation and species status in the lawn ground cricket. III. Ovipositor length, *Oecologia* **43**:207–219.
- Masaki, S., 1983, Climatic speciation in Japanese ground crickets, *GeoJournal* **7**:483–490.
- Masaki, S., 1984, Unity and diversity in insect photoperiodism, in: *Photoperiodic Regulation of Insect and Molluscan Hormones* (Ciba Foundation Symposium 104), pp. 7–25, Pitman, London.
- Masaki, S., 1986, Significance of ovipositor length in life cycle adaptations of crickets, in: *The Evolution of Insect Life Cycles*, pp. 20–34, Springer-Verlag, New York.
- Masaki, S., and Ohmachi, F., 1967, Divergence of photoperiodic response and hybrid development in *Teleogryllus* (Orthoptera: Gryllidae), *Kontyû* **35**:83–105.
- Masaki, S., and Oyama, N., 1963, Photoperiodic control of growth and wing-form in *Nemobius yezoensis* Shiraki (Orthoptera, Gryllidae), *Kontyû* **31**:16–26.

- Masaki, S., Ando, Y., and Watanabe, A., 1979, High temperature and diapause termination in the eggs of *Teleogryllus commodus* (Orthoptera: Gryllidae), *Kontyû* 47:493–504.
- Mason, P. C., 1973, Differences in diapause characteristics between Auckland and Nelson populations of *Teleogryllus commodus* (Orthoptera: Gryllidae), *N. Z. Entomol.* 5:178–181.
- Mathad, S. B., and McFarlane, J. E., 1968, Two effects of photoperiod on wing development in *Grylloides sigillatus* (Walk.), *Can. J. Zool.* 46:57–60.
- Matsuura, I., 1976, Japanese crickets (1), *Kontyu to Shizen* 11(5):9–13.
- Matsuura, I., 1977a, Japanese crickets (2), *Kontyu to Shizen* 12(9):16–19.
- Matsuura, I., 1977b, Japanese crickets (3), *Kontyu to Shizen* 12(10):23–27.
- Matsuura, I., 1978a, Japanese crickets (4), *Kontyu to Shizen* 13(2):17–22.
- Matsuura, I., 1978b, Japanese crickets (5), *Kontyu to Shizen* 13(12):19–24.
- Matsuura, I., 1979a, Japanese crickets (6), *Kontyu to Shizen* 14(8):13–17.
- Matsuura, I., 1979b, Japanese crickets (7), *Kontyu to Shizen* 14(11):17–21.
- Matsuura, I., 1982a, Japanese crickets (8), *Kontyu to Shizen* 17(10):42–45.
- Matsuura, I., 1982b, Japanese crickets (9), *Kontyu to Shizen* 17(11):26–29.
- Matsuura, I., 1982c, Japanese crickets (10), *Kontyu to Shizen* 17(12):26–29.
- McFarlane, J. E., 1962, Effect of diet and temperature on wing development of *Grylloides sigillatus* (Walk.) (Orthoptera: Gryllidae), *Ann. Entomol. Soc. Quebec* 7:28–33.
- McFarlane, J. E., 1964a, Interaction between two species of crickets reared together, *Can. J. Zool.* 42:689–691.
- McFarlane, J. E., 1964b, Factors affecting growth and wing polymorphism in *Grylloides sigillatus* (Walk.): Dietary protein level and a possible effect of photoperiod, *Can. J. Zool.* 42:767–771.
- McFarlane, J. E., 1966a, Studies on group effects in crickets. I. Effect of methyl linolenate, methyl linoleate, and vitamin E, *J. Insect Physiol.* 12:179–188.
- McFarlane, J. E., 1966b, Studies on group effects in crickets. II. A temperature and concentration effect on *Acheta domesticus* (L.), *Can. J. Zool.* 44:1013–1016.
- McFarlane, J. E., 1966c, Studies on group effects in crickets. III. Wing development of *Grylloides sigillatus* (Walk.), *Can. J. Zool.* 44:1017–1021.
- McFarlane, J. E., 1976, Vitamin K: A growth factor for the house cricket (Orthoptera: Gryllidae), *Can. Entomol.* 108:391–394.
- McFarlane, J. E., and Kennard, C. P., 1960, Further observations on water absorption by the eggs of *Acheta domesticus* (L.), *Can. J. Zool.* 38:77–85.
- McFarlane, J. E., Ghouri, A. S. K., and Kennard, C. P., 1959, Water absorption by the eggs of crickets, *Can. J. Zool.* 37:391–399.
- McFarlane, J. E., Alli, I., and Steeves, E., 1984, Studies on the group effect in *Acheta domesticus* (L.) using artificial diets, *J. Insect Physiol.* 30:103–107.
- McIntyre, M. E., 1978, Some aspects of diapause in the field cricket *Pteronemobius nigrovus* and *P. bigelowi* (Orthoptera: Nemobiinae), with notes on their ecology, *Mauri Ora* 6:3–10.
- Mello, A. M. L. T., Neto, S. S., and Parra, J. R. P., 1980, Tabela de fertilidade e esperanca de vida de *Gryllus assimilis* (Fabricius, 1775) (Orthoptera, Gryllidae) em laboratorio, *An. Soc. Entomol. Brasil* 9:133–141.
- Merkel, G., 1977, The effect of temperature and food quality on the larval development of *Gryllus bimaculatus* (Orthoptera, Gryllidae), *Oecologia* 30:129–140.
- Moiseff, A., Pollack, G. S., and Hoy, R. R., 1978, Steering response of flying crickets to sound and ultrasound: Mate attraction and predator avoidance, *Proc. Natl. Acad. Sci. USA* 75:4052–4056.
- Morris, G. K., and Fullard, J. H., 1983, Random noise and congeneric discrimination in

- Conocephalus* (Orthoptera: Tettigoniidae), in: *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (D. T. Gwynne and G. K. Morris, eds.), pp. 73–96, Westview Press, Boulder, Colorado.
- Nakamura, K., 1968, The wing-form in a cricket, *Grylloides sigillatus* Walker (Orthoptera: Gryllidae), *Jpn. J. Ecol.* **18**:186–192 [in Japanese].
- Nielsson, R. J., and Bass, M. H., 1967, Seasonal occurrence and number of instars of *Nemobius fasciatus*, a pest on white clover, *J. Econ. Entomol.* **60**:699–701.
- Ngo, Dong, and Beck, H. W., 1982, Mark–release of sound-attracted mole crickets: Flight behavior and implications for control, *Fla. Entomol.* **65**:531–538.
- Nolen, T. G., and Hoy, R. R., 1984, Initiation of behavior by single neurones: The role of behavioral context, *Science* **226**:992–994.
- Nowosielski, J. W., and Patton, R. L., 1965, Life-tables for the house cricket, *Acheta domesticus* L., and the effect of intra-specific factors on longevity, *J. Insect Physiol.* **11**:201–209.
- Ohmachi, F., 1932, Miscellaneous notes on crickets (3), *Kontyû* **6**:175–180 [in Japanese].
- Ohmachi, F., and Kioku, M., 1935, Nymphal development of *Loxoblemus doenitzi*, *Oyo-Dobutsugaku Zasshi* **7**:151–154 [in Japanese].
- Ohmachi, F., and Masaki, S., 1964, Interspecific crossing and development of hybrids between the Japanese species of *Teleogryllus* (Orthoptera: Gryllidae), *Evolution* **18**:405–416.
- Ohmachi, F., and Matsuura, I., 1951, Observations and experiments on four types in the life history of the Gryllodea, *J. Appl. Zool.* **16**:104–110 [in Japanese].
- Ohmachi, F., and Yamashita, Z., 1938, Nymphal development in *Homeogryllus japonicus* with special reference to the wing and genital organ, *Oyo-Dobutsugaku Zasshi* **10**:199–203 [in Japanese].
- Okamoto, D., Akino, K., and Sasaki, M., 1956, Bionomics and control by aldrin of *Grylotalpa africana* Palisot de Beauvois, *Nogyo Oyobi Engei* **31**:569–572 [in Japanese].
- Oshiro, Y., and Gaja, K., 1979, Studies on the singing insects in the Ryukyu Islands. Part 2. Life history of the Suzumushi cricket, *Homoeogryllus japonicus* Haan in Okinawa Island, *Okinawa Nogyo* **15**:39–47 [in Japanese].
- Oshiro, Y., and Tamashiro, I., 1985, Studies on the singing insects in the Ryukyu Islands. Part 7. Life history of the Matsumushi cricket, *Xenogryllus marmoratus* Haan (Orthoptera, Gryllidae) in Okinawa Island, *Biol. Mag. Okinawa* **23**:17–24 [in Japanese].
- Oshiro, Y., Sakai, T., and Oshiro, T., 1981, Studies on the singing insects in the Ryukyu Islands. Part 5. Life history of the spotted tree cricket, *Cardiodactylus novaeguineae* Haan (Orthoptera: Gryllidae) in Okinawa Island, *Biol. Mag. Okinawa* **19**:25–32 [in Japanese].
- Otte, D., and Alexander, R. D., 1983, The Australian crickets (Orthoptera: Gryllidae), *Acad. Nat. Sci. Phila. Monogr.* **22**:1–477.
- Ragge, D. R., 1972, An unusual case of mass migration by flight in *Gryllus bimaculatus* De Geer, *Bull. Inst. Fondam. Afr. Noire A Sci. Nat.* **34**:869–878.
- Rakshpal, R., 1962a, Morphogenesis and embryonic membranes of *Gryllus assimilis* (Fabricius) (Orthoptera: Gryllidae), *Proc. R. Entomol. Soc. Lond. A* **37**:1–12.
- Rakshpal, R., 1962b, Morphological development of the embryo in diapause and post-diapause eggs of *Gryllus pennsylvanicus* Burmeister (Orthoptera: Gryllidae) and a comparison with non-diapause species of the genus *Gryllus*, *Zool. Anz.* **168**:46–53.
- Rakshpal, R., 1962c, Respiratory metabolism during embryogenesis of *Gryllus veletis* (Alexander and Bigelow) (Orthoptera: Gryllidae), *Physiol. Zool.* **35**:47–51.
- Rakshpal, R., 1962d, The effect of cold on pre- and post-diapause eggs of *Gryllus pennsylvanicus* Burmeister (Orthoptera: Gryllidae), *Proc. R. Entomol. Soc. Lond. A* **37**:117–120.

- Rakshpal, R., 1962e, Diapause in the eggs of *Gryllus pennsylvanicus* Burmeister (Orthoptera: Gryllidae), *Can. J. Zool.* **40**:179–194.
- Rakshpal, R., 1962f, Respiratory metabolism during embryogenesis of a diapause species of field cricket, *Gryllus pennsylvanicus* Burmeister (Orthoptera, Gryllidae), *J. Insect Physiol.* **8**:217–221.
- Rakshpal, R., 1963, Effects of freezing temperatures on the eggs of *Gryllus pennsylvanicus* Burmeister and *Nemobius allardi* Alexander and Thomas (Orthoptera: Gryllidae), *Ind. J. Entomol.* **24**:199–204.
- Rakshpal, R., 1964, Diapause in the eggs of *Nemobius allardi* Alexander and Thomas (Orthoptera: Gryllidae: Nemobiinae), *Zool. Anz.* **173**:282–288.
- Richards, T. J., 1952, *Nemobius sylvestris* in S. E. Devon, *Entomologist* **85**:83–87, 108–111, 136–141, 161–166.
- Rivnay, E., and Ziv, M., 1963, A contribution to the biology of *Gryllus bimaculatus* deG. in Israel, *Bull. Entomol. Res.* **54**:37–43.
- Roff, D. A., 1984, The cost of being able to fly: A study of wing polymorphism in two species of crickets, *Oecologia* **63**:30–37.
- Roubaud, E., 1922, Etude sur le sommeil d'hiver pré-imaginal des muscides, *Bull. Biol. Fr. Belg.* **54**:455–544.
- Saeki, H., 1966a, The effect of the population density on the occurrence of the macropterous form in a cricket, *Scapsipedus aspersus* Walker (Orthoptera, Gryllidae), *Jpn. J. Ecol.* **16**:1–4 [in Japanese].
- Saeki, H., 1966b, The effect of the day-length on the occurrence of the macropterous form in a cricket, *Scapsipedus aspersus* Walker (Orthoptera: Gryllidae), *Jpn. J. Ecol.* **16**:49–52 [in Japanese].
- Smith, A. G., and Harrow, K. M., 1971, Black field cricket survival factors, *N. Z. J. Agric.* **122**:52–54.
- Tanaka, S., 1971, A record of growth and development of a small cricket, *Pteronemobius taprobanensis*, *Insectarium* **8**:212–213 [in Japanese].
- Tanaka, S., 1976, Wing polymorphism, egg production and adult longevity in *Pteronemobius taprobanensis* Walker (Orthoptera, Gryllidae), *Kontyû* **44**:327–333.
- Tanaka, S., 1978a, Effects of changing photoperiod on nymphal development in *Pteronemobius nitidus* Bolivar (Orthoptera, Gryllidae), *Kontyû* **46**:135–151.
- Tanaka, S., 1978b, Photoperiodic determination of wing form in *Pteronemobius nitidus* Bolivar (Orthoptera, Gryllidae), *Kontyû* **46**:207–217.
- Tanaka, S., 1979, Multiple photoperiodic control of the seasonal life cycle in *Pteronemobius nitidus* Bolivar (Orthoptera: Gryllidae), *Kontyû* **47**:465–475.
- Tanaka, S., 1983, Seasonal control of nymphal diapause in the spring ground cricket, *Pteronemobius nitidus* (Orthoptera: Gryllidae), in: *Diapause and Life Cycle Strategies in Insects* (V. K. Brown and I. Hodek, eds.), pp. 35–53, W. Junk, The Hague.
- Tanaka, S., 1984, Seasonal variation in embryonic diapause of the striped ground cricket, *Allonemobius fasciatus*, *Physiol. Entomol.* **9**:97–105.
- Tanaka, S., Matsuka, M., and Sakai, T., 1976, Effect of change in photoperiod on wing form in *Pteronemobius taprobanensis* Walker (Orthoptera: Gryllidae), *Appl. Entomol. Zool.* **11**:27–32.
- Townsend, B. C., 1980, A taxonomic study of two similar species of *Teleogryllus* (Orthoptera: Gryllidae), *J. Nat. Hist.* **14**:153–162.
- Tsuji, H., 1951, *Duolandrevus coulonianus* in the northern Izu Peninsula, *Shin-Kontyû* **4**(6):15–22 [in Japanese].
- Umeya, Y., 1950, Studies on embryonic hibernation and diapause in insects, *Proc. Jpn. Acad.* **26**(6):1–7.

- Utida, S., 1957, Developmental zero temperature in insects, *Jpn. J. Appl. Entomol. Zool.* **1**:46–53 [in Japanese].
- Vannini, M., and Chelazzi, G., 1978, Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 17. Description of a new species of intertidal cricket, *Speonemobius litoreus*, with notes on its ecology and behaviour, *Monit. Zool. Ital. N. S. Suppl.* **11**:1–13.
- Walker, T. J., 1962, The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). I. The genus *Neoxabea* and the *niveus* and *varicornis* groups of the genus *Oecanthus*, *Ann. Entomol. Soc. Am.* **55**:303–322.
- Walker, T. J., 1963, The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). II. The *nigricornis* group of the genus *Oecanthus*, *Ann. Entomol. Soc. Am.* **56**:772–789.
- Walker, T. J., 1969a, Systematics and acoustic behavior of United States crickets of the genus *Orocharis* (Orthoptera: Gryllidae), *Ann. Entomol. Soc. Am.* **62**:752–762.
- Walker, T. J., 1969b, Systematics and acoustic behavior of United States crickets of the genus *Cyrtoxipha* (Orthoptera: Gryllidae), *Ann. Entomol. Soc. Am.* **62**:945–952.
- Walker, T. J., 1972, Deciduous wings in crickets: A new basis for wing dimorphism, *Psyche* **79**:311–313.
- Walker, T. J., 1973, Systematics and acoustic behavior of U. S. and Caribbean short-tailed crickets (Orthoptera: Gryllidae: *Anurogryllus*), *Ann. Entomol. Soc. Am.* **66**:1269–1277.
- Walker, T. J., 1974, *Gryllus ovisopsis* n. sp.: A taciturn cricket with a life cycle suggesting allochronic speciation, *Fla. Entomol.* **57**:13–22.
- Walker, T. J., 1977, Re-examination of monopterous and “micropterous” house crickets (*Acheta domesticus*), *Ann. Entomol. Soc. Am.* **70**:602.
- Walker, T. J., 1980a, Mixed oviposition in individual females of *Gryllus firmus*: Graded proportions of fast-developing and diapause eggs, *Oecologia* **47**:291–298.
- Walker, T. J., 1980b, Reproductive behavior and mating success of male short-tailed crickets: Differences within and between demes, *Evol. Biol.* **13**:219–260.
- Walker, T. J., 1984, Biology of pest mole crickets: Systematics and life cycles, *Univ. Fla. Agric. Exp. Sta. Bull.* **846**:3–10.
- Walker, T. J., 1986, Stochastic polyphenism: Coping with uncertainty, *Fla. Entomol.* **69**:46–62.
- Walker, T. J., 1987, Wing dimorphism in *Gryllus rubens*, *Ann. Entomol. Soc. Am.* **80**: (in press).
- Walker, T. J., and Fritz, G. N., 1983, Migratory and local flights in mole crickets, *Scapteriscus* spp. (Gryllotalpidae), *Environ. Entomol.* **12**:953–958.
- Walker, T. J., and Nation, J. L., 1982, Sperm storage in mole crickets: Fall matings fertilize spring eggs in *Scapteriscus acletus*, *Fla. Entomol.* **65**:283–285.
- Walker, T. J., and Sivinski, J. M., 1986, Wing dimorphism in field crickets (Orthoptera: Gryllidae: *Gryllus*), *Ann. Entomol. Soc. Am.* **79**:84–90.
- Walker, T. J., and Whitesell, J. J., 1982, Singing schedules and sites for a tropical burrowing cricket (*Anurogryllus muticus*), *Biotropica* **14**:220–227.
- Walker, T. J., Reinert, J. A., and Schuster, D. J., 1983, Geographical variation in flights of mole crickets, *Scapteriscus* spp. (Orthoptera: Gryllotalpidae), *Ann. Entomol. Soc. Am.* **76**:507–517.
- Weaver, J. E., and Sommers, R. A., 1969, Life history and habits of the short-tailed crickets, *Anurogryllus muticus*, in central Louisiana, *Ann. Entomol. Soc. Am.* **62**:337–342.
- West, M. J., and Alexander, R. D., 1963, Sub-social behavior in a burrowing cricket *Anurogryllus muticus* (deGeer), *Ohio J. Sci.* **63**:19–24.

- Wheeler, W. M., 1900, The habits of *Myrmecophila nebrascensis* Bruner, *Psyche* **9**:111–115.
- Woodring, J. P., Roe, R. M., and Clifford, C. W., 1977, Relation of feeding, growth and metabolism to age in the larval female house cricket, *J. Insect Physiol.* **23**:207–212.
- Woodring, J. P., Clifford, C. W., and Beckman, B. R., 1979, Food utilization and metabolic efficiency in larval and adult house crickets, *J. Insect Physiol.* **25**:903–912.