

Geographical variation of life cycle in crickets (Ensifera: Grylloidea)

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Grylloidea, crickets, life cycle, geographical variation, diapause, photoperiodism, wing form, selection

Abstract. Crickets are convenient systems for studying life-cycle evolution. They show a considerable diversity in life-cycle types, being homodynamic in some parts of the tropics and heterodynamic with various kinds of diapause and other regulatory responses in the temperate region. Crickets are relatively free from constraints by food supply, because they are omnivorous. Therefore, their geographical variation may clearly reflect climatic selection as exemplified by latitudinal clines in adult size, egg size and ovipositor length. These morphometric clines are closely related to development time, egg diapause and photoperiodic responses, indicating that crickets are highly variable within the framework of their species-specific patterns of life cycle. More fundamental variation is divergence in life-cycle pattern that may be associated with speciation, because closely related species are often different in their life-cycle patterns (e.g., homodynamic versus heterodynamic, or egg overwintering versus larval overwintering). Evolutionary flexibility of life-cycle traits may be assessed by studying cricket populations under special natural or artificial conditions. In Japan, a population of the nemobiine cricket (*Dianemobius mikado*) introduced from a temperate to a subtropical island has almost lost egg diapause presumably in the last 130 years. At volcanic geothermal spots in the northern island (Hokkaido), presumptive relict populations of the nemobiine species *Dianemobius nigrofasciatus* occur and sing in mid-winter, but this cricket retains the photoperiodic response of a southern bivoltine type. In the subtropical nemobiine *D. fascipes*, artificial selection has been effective in changing the incidence and depth of diapause, and strains comparable to the tropical and temperate forms were established. The responsiveness to photoperiod in wing-form determination was also remarkably changed by selection, but this change was not associated with a change in critical photoperiod. Alternated selection in the opposite directions at photoperiods above and below the critical value to be selected was necessary to shift the critical photoperiod.

INTRODUCTION

Life cycle is a temporally coordinated system of development and reproduction. It constitutes the basic adaptation in every organism. In seasonally changing environments, life cycles of insects are characterized by the species-specific arrangement of the active and dormant phases together with the ecophysiological responses switching from one phase to the other.

There is a wide spectrum of life-cycle patterns in insects (Danks, 1987; Tauber et al., 1986). This diversity is a result of evolutionary interactions between environmental factors and species-specific life styles. For understanding the evolutionary process differentiating life-cycle patterns, the responses of life-cycle components to selection pressures should be elucidated. One of the feasible ways of approach is to compare life cycles in different surroundings that exert different selection pressures. The final products of the interaction between such selection pressures and the genetic resources of the species would most commonly be represented by geographical variations. Thus, the adaptive variation in any life-cycle component may be related to some geographical variables such as climatic

factors, seasonal food supply, and predation pressure. Factors of natural selection can be inferred from analysis of such correlates. Geographical variation therefore provides us with rich sources of information on the genetic flexibility of life cycles.

Geographical distribution of every species of organism is a result of dispersal from the original place of the species throughout the evolutionary history. Dispersing species may encounter different environmental conditions as they reach new districts. Insect populations might also experience environmental changes in situ through geological time. Geographical variation in life-cycle traits might therefore demonstrate a profile of the evolutionary history of adaptation to climatic changes in both space and time. Thus, geographical variation would afford important information for understanding the evolution of life cycles in insects.

This mini-review will summarize data on cricket life cycles particularly in relation to their geographical variations, explore responses of populations under special circumstances (immigrant and relict situations), and finally examine life-cycle responses to artificial selection and try to reconstruct geographical clines.

LIFE-CYCLE PATTERNS IN CRICKETS

Nine different patterns of life cycles are known in crickets (Masaki & Walker, 1987; Walker & Masaki, 1989; Fig. 1). These patterns are primarily characterized by the presence of photoperiodically and thermally controlled diapause and developmental responses (heterodynamic) or by the absence of such responses (homodynamic). Homodynamic life-cycles are restricted to the tropical and subtropical regions, where information on cricket life-cycles is scanty (Masaki et al., 1987). It is not known how crickets survive the dry season in seasonally arid tropical districts. The discovery of summer diapause at the early embryonic stage, which is distinct from winter diapause at the later stage, in *Allonemobius fasciatus* (DeGeer) in western North America (Tanaka, 1984), suggests the possibility that a special kind of diapause might have evolved to cope with the hot, dry season in tropical crickets.

In the subtropical regions, some species are homodynamic and others are heterodynamic, and the two types of life-cycles may be intermingled even within a population (Masaki, 1990). In the temperate regions, most species are heterodynamic, and a few of them enter diapause twice in two separate life stages and overwinter twice, e.g., the northern populations of *Nemobius sylvestris* (Bose) pass the first winter as eggs and the second winter as half-grown larvae (Gabbutt, 1959; Brown, 1978). Except for those partivoltine species with generation times of two years, the crickets in temperate regions are commonly univoltine and rarely bivoltine.

Both univoltine and bivoltine crickets overwinter either as eggs or as half-grown larvae, but intraspecific genetic variation in the overwintering stage is not known in the temperate region (Walker & Masaki, 1989). Therefore, there are four major types of life cycle in the temperate species of crickets: univoltine and bivoltine cycles in each of the egg- and larval-overwintering types (Ohmachi & Matsuura, 1951). The occurrence of those types is to some extent related to the climatic conditions, and two geographical tendencies may be perceived.

Bivoltine species tend to be univoltine in the northern cooler areas as commonly observed in many insects, but this is not always the case. Some species fail to establish a

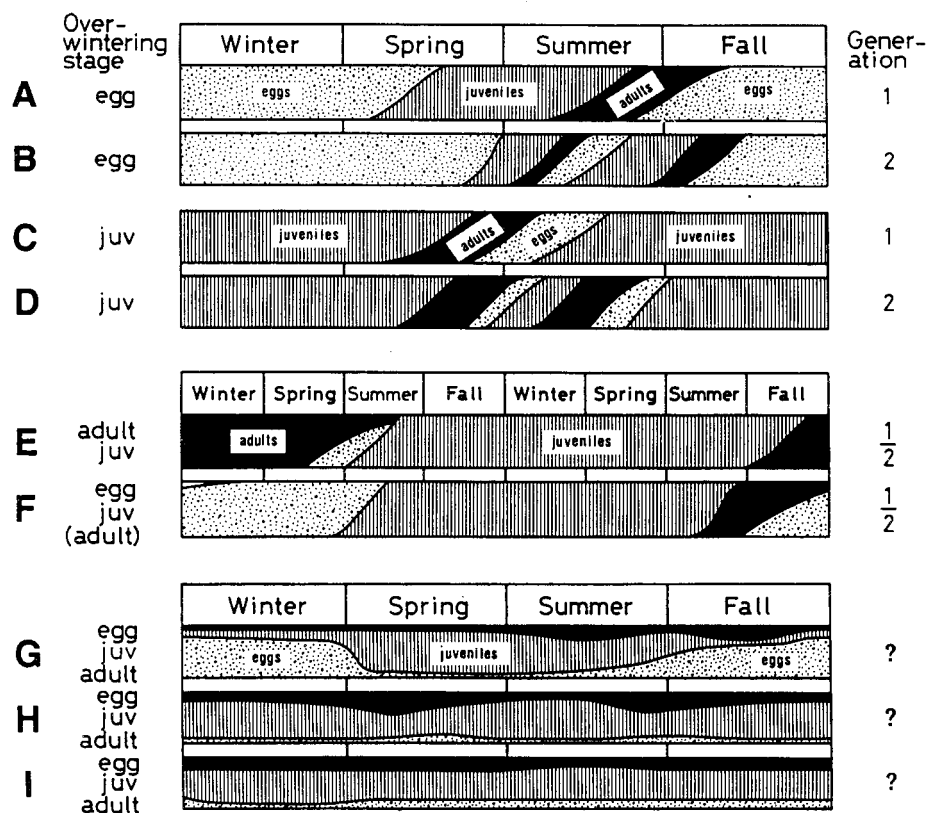


Fig. 1. Life-cycle patterns in crickets. A to F are temperate, heterodynamic life cycles. G is mixture of heterodynamic and homodynamic cycles and may occur in the subtropical regions. H to I are subtropical and tropical homodynamic cycles with different degrees of seasonality. Examples: A – *Teleogryllus emma*, *Gryllus pennsylvanicus*; B – *Dianemobius nigrofasciatus*, southern bivoltine populations; C – *Gryllus campestris*; D – *Teleogryllus occipitalis*, temperate populations; E – *Gryllotalpa fossor*; F – *Nemobius sylvestris*, England; G – *Gryllus firmus*; H – *Dianemobius taprobanensis*, subtropical populations; I – *Gryllus assimilis*. (Modified from Walker & Masaki, 1989.)

univoltine cycle and their northern distribution might be limited by the sum of heat necessary for completing two generations (Walker & Masaki, 1989). In the Japanese Islands, bivoltine cycles are not found in the northernmost island of Hokkaido and northern Honshu, but several bivoltine species occur in central Honshu and farther south. The mode of overwintering also varies geographically. In the temperate parts of Japan and North America, about 80% of cricket species overwinter as eggs and 20% as larvae (Walker & Masaki, 1989). In the Japanese islands, the frequency of larval overwintering tends to increase southward (Masaki, 1983; Masaki & Walker, 1987).

The life stage for the evolution of diapause seems to be phylogenetically constrained, but this might be mainly due to the general life style of the crickets. Most crickets insert eggs into soil or plant tissue, where they are well protected during the dormant period. For

the same reason, in those species with larvae which burrow into the soil, the larval stage is also suitable for dormancy. Laying eggs deep into protective substrates is adaptively significant behaviour in the tropics and can be regarded as preadaptation to overwintering when crickets reach the temperate region and encounter cold winters (Alexander & Bigelow, 1960; Alexander, 1968).

LIFE-CYCLE REGULATION

Life cycle with egg overwintering

In the temperate region, crickets usually overwinter in the species-specific diapause stage. Diapause is facultative in all the bivoltine species and either obligatory or facultative in the univoltine species irrespective of whether it occurs at the egg stage or the larval stage. Photoperiod is a widely used cue for seasonal regulation of the life cycle (Fig. 2). All the species of crickets hitherto examined respond to photoperiod in various ways. Nemobiine crickets such as *Dianemobius nigrofasciatus* (Matsumura), *D. fascipes* (Walker) and *D. mikado* (Shiraki) show three kinds of photoperiodic responses; the programming of egg diapause, determination of adult wing form, and regulation of larval development (Masaki, 1973, 1979a).

In univoltine egg-overwinterers, the egg diapause is obligatory, but the diapause eggs are more or less sensitive to temperature and diapause termination can be controlled by temperature (Browning, 1952; Hogan, 1960; Masaki, 1960; Rakshpal, 1962; Tanaka, 1987; Masaki & Walker, 1987). In most species of crickets, chilling is not essential for

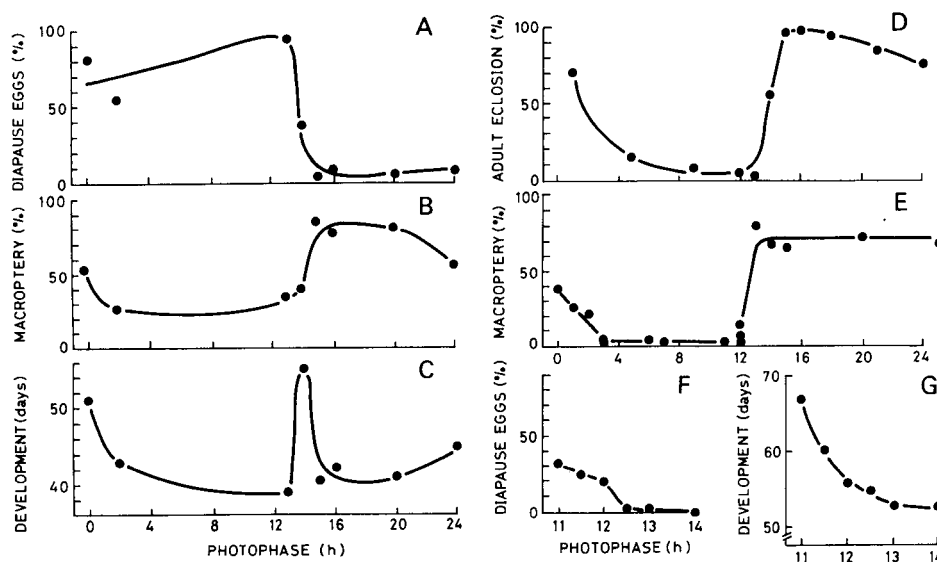


Fig. 2. Various photoperiodic responses in crickets. A – induction of egg diapause; B – determination of wing form; C – duration of larval development in *Dianemobius nigrofasciatus*; D – termination of diapause after short-day exposure in *Pteronemobius nitidus*; E – determination of wing form; F – induction of egg diapause; G – duration of larval development in the subtropical population of *D. fascipes*. (Masaki et al., 1992.)

diapause termination. Although hatching is dispersed over a long period of time, diapause eggs hatch even when they are kept constantly at a high temperature. Therefore, the depth (or intensity) of diapause at a given temperature can be represented by the duration of the egg stage. Photoperiod exerts no or little influence on the duration of egg diapause in univoltine species so far as known (Tanaka, 1992).

Photoperiod has been known to control the rate of larval development. Short photoperiod accelerates, and long photoperiod decelerates, larval development, and this is associated with variation in the number of moults and adult size (Masaki, 1978). The larval response of the egg-overwintering species results in autumn emergence of the adults and appropriate production of diapause eggs before winter as typically represented by *Teleogryllus emma* (Ohmachi & Matsuura), *Velarifictorus micado* (Saussure), *Loxoblemmus campestris* Matsuura and others (Saeki, 1966; Masaki, 1967; Masaki & Ohmachi, 1967) and also the northern populations of *D. nigrofasciatus* and *D. mikado* (Kidokoro & Masaki, 1978; Masaki, 1979a) and *A. fasciatus* (Tanaka, 1986).

The most important regulatory mechanism for bivoltine egg-overwintering crickets is the maternal programming of egg diapause, relying on seasonal cues such as photoperiod and temperature (Fig. 2A; Masaki, 1973; Kidokoro & Masaki, 1978). Such diapause responses are common: long photoperiod and high temperature prevent, and short photoperiod and low temperature induce egg diapause. Diapause tends to be less intense in bivoltine species than in univoltine species. When eggs of *D. mikado* are kept at a high temperature (e.g. 25°C), there is almost no gap in the distribution of the incubation periods between nondiapause and diapause eggs (Masaki, 1979a). However, hatching is clearly bimodal and two peaks appear 3 and 15 weeks after deposition.

Although the bivoltine egg-overwintering cycle is basically moulded by the seasonal programming of egg diapause, the larval response to seasonal cues also plays a role in stabilizing the life cycle against the fluctuating environment. In *D. nigrofasciatus*, for example, the southern bivoltine populations delay larval development in response to the intermediate days of mid-summer, and both the long days in early summer and the short days in autumn accelerate adult emergence (Fig. 2C). The long-day response ensures the completion of a nondiapause generation within a relatively short time before mid-summer, and adult emergence in the next generation is delayed under the intermediate days of mid-summer, so that overwintering eggs are produced in autumn as in the univoltine species. The southern bivoltine populations of *D. mikado*, however, show a response more or less similar to that of univoltine populations. In this species, therefore, the first generation grows larger under long summer days and lays nondiapause eggs, while the next generation matures rapidly under short days and produces diapause eggs (Masaki, 1979a).

Life cycle with larval overwintering

The life cycles of larval-overwintering crickets are also controlled by the coordinated developmental and diapause responses to photoperiod. In the univoltine larval overwinterer *Pteronemobius nitidus* (Bolivar), the larvae grow faster under short days than under long days until entering diapause, and the number of moults to reach the penultimate instar increases from 6–7 in LD 12 : 12 to 8–11 in LD 15 : 9 at 28°C (Tanaka, 1979). After entering diapause, a change from short to long days terminates diapause more effectively than constant long days (Tanaka, 1983). The diapause-terminating response to photoperiod in this cricket is a mirror image of the diapause-inducing response (compare Fig. 2D with A;

Masaki et al., 1992). In another univoltine larval-overwinterer *Gryllus campestris* DeGeer, a similar photoperiodic response is effected before the penultimate diapause stage (Fuzeau-Braesch, 1963, 1965, 1966; Ismail & Fuzeau-Braesch, 1976).

The bivoltine larval-overwinterer *Modicogryllus* sp. develops without delay in long days (16 h and longer), but development is delayed by about two months in short days (14 h and shorter). At an intermediate daylength of 15 h, the development time is also intermediate between the long-day and short-day levels. As in the univoltine ground cricket, the developmental delay is conspicuously curtailed when a brief period of short days is followed by long days (Masaki & Sugawara, 1992).

GEOGRAPHICAL VARIATION IN ADULT SIZE AND DEVELOPMENT TIME

Simple clines

In univoltine insects, northern populations tend to be smaller in adult size than southern populations, and there are clines that conform to “the converse of the Bergmann principle” (Park, 1949). This trend is based on genetic variation and typically represented by univoltine egg-overwintering species of crickets such as *T. emma* and *T. infernalis* Saussure (formerly *T. yezoemma* [Ohmachi et Matsuura]) (Fig. 3, left; Masaki, 1967, 1978). A similar trend is also found in *Gryllus pennsylvanicus* (Burmeister), *Gryllus veletis* Alexander & Bigelow (Alexander & Bigelow, 1960) and *A. fasciatus* in North America (Tanaka, 1991). In *T. emma*, a multiple regression analysis of local specimens collected from the Japanese islands indicates that the adult body size is inversely correlated with the latitude and altitude of collection site, suggesting that the duration of the growing season or the sum of effective temperatures is the selecting agent.

Adult size is the final result of larval development and varies as a function of development time. Therefore, the converse Bergmann trend might be a side effect of selection on development time by the growing season. In many species of insects, fecundity is positively correlated with body size so that it is also proportional to the development time. However, if the development time is too long, the risk of reproductive failure increases towards the later season because of the increasing probability of frost. Obviously, there is an optimal timing for completing development and starting reproduction in each locality.

Saw-tooth clines

In species with variable voltinism such as *D. mikado* or *D. nigrofasciatus*, the latitudinal size trend is reversed in the transitional zone between univoltine and bivoltine areas (Fig. 3, right). Selection pressure on development time shifts as the number of generations each year varies, for example, from two to one (Masaki, 1978); in the northern univoltine area, the whole growing season is available for development and reproduction of every generation but, in the southern bivoltine area, it is shared by two generations. Therefore, each generation can utilize a longer period for growth and attain a larger adult size in the northern univoltine population than in the southern bivoltine population. In the transitional zone, the populations are heterovoltine (Walker & Masaki, 1989), i.e. univoltine and bivoltine cycles coexist as a polymorphism (Kidokoro & Masaki, 1978). The proportion of the univoltine phenotype increases northward within this zone, hence the mean size of adults increases northward. In the bivoltine area, development time again becomes proportional to the growing season shared by the two generations. This shift in the direction of

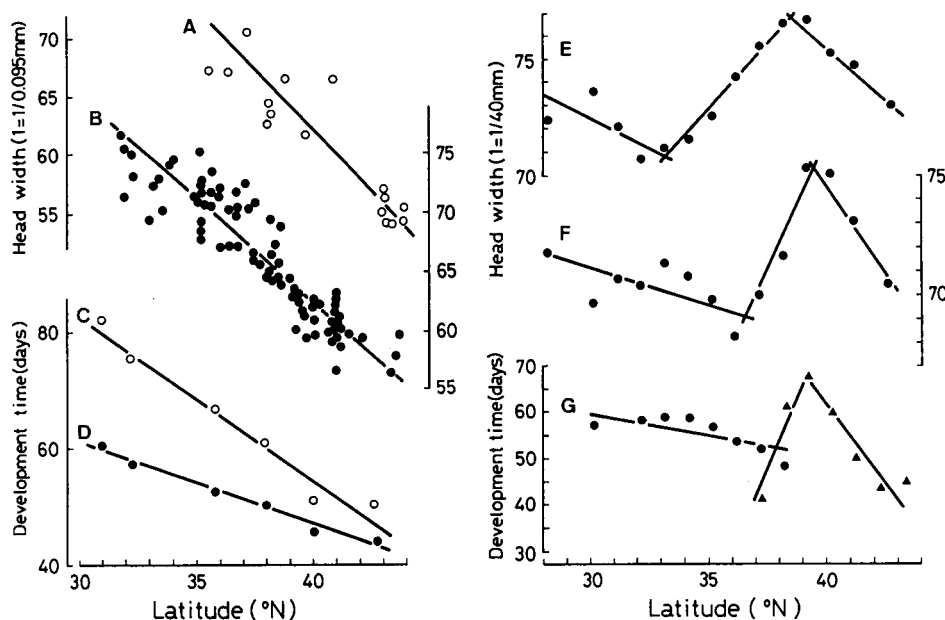


Fig. 3. Adult size and larval development clines in some Japanese crickets. A – *Teleogryllus infernalis*, adult size; B – *T. emma*, adult size; C – *T. emma*, the mean larval stages in LD 16 : 8; D – LD 12 : 12 both at 27°C; E – *Dianemobius mikado*, adult size; F – *D. nigrofasciatus*, adult size; G – *D. nigrofasciatus*, the mean larval stages in LD 14 : 10 for bivoltine populations (circles) and in LD 15 : 9 for univoltine populations (triangles) both at 27°C. All adults for size determination were collected in autumn and the photoperiods for rearing the larvae approximately corresponded to the mean daylength under which autumn adults had grown (15 h in the univoltine area and 14 h in the bivoltine area). (Data from Masaki, 1978.)

selection results in the saw-tooth clines of the bivoltine ground crickets, *D. nigrofasciatus* and *D. mikado* (Fig. 3, right), and the reversed portion of the latitudinal cline reflects the zone of transition, where the bivoltine and univoltine life cycles are intermingled. As described above, this shift of voltinism is associated with a switch in the developmental response to photoperiod from a reversed intermediate-day (bivoltine) type (Fig. 2C) to a short-day (univoltine) type. Similar reversion in latitudinal gradient occurs in the striped ground cricket complex (*Allonemobius*) in North America. The univoltine species *A. fasciatus* shows northward decrease in size; it is largest near the southern limit of distribution at about 39°N. To the south, however, this tendency is replaced by the reversed cline of *Allonemobius socius* Scudder (Tanaka, 1991). In discussing optimal timing for completing development and starting reproduction, Roff (1980) proposed theoretical models for saw-tooth clines.

Egg size and ovipositor length clines

In the two nemobiine species *D. fascipes* and *D. mikado* egg size (length) varies considerably among local populations. It is allometrically correlated with adult size (head width) but this correlation accounts for only a small portion of the total variance. The egg size

significantly increases northward after correction for the regression on adult size. Thus, the northernmost populations produce the largest eggs in both species, although adult size decreases northward within the univoltine area (Masaki et al., 1987). Probably, larger eggs survive better during the longer, colder winter in the north than smaller ones.

These two species also show more or less similar clinal variations in ovipositor length. The southern bivoltine populations have shorter ovipositors than the northern univoltine populations, and the ovipositor length increases northward in the transitional area (Masaki, 1983). The geographical variation in ovipositor length of *D. mikado* is described by a multiple regression equation,

$$OL = 2.41HW + 1.17N + 0.73E - 168.7 \quad (R^2 = 0.87, P < 0.01),$$

where *HW* is head width, and *N* and *E* are latitude and longitude of the collecting site, respectively (Masaki, 1979b). The ovipositor length shows a significant geographical variation after correction for its regression on body size (head width). Probably, ovipositor length is subject to climatic selection owing to its particular role in protecting eggs by inserting them into the soil or other substrates, and the benefit gained by such a protecting effect might be related to the duration of dormancy under natural overwintering conditions (Masaki, 1986).

GEOGRAPHICAL VARIATION IN THE INTENSITY OF EGG DIAPAUSE

Macrogeographical tendency

Because egg diapause is the widespread means of dormancy in crickets, its origin is the most important episode in the evolutionary history of their northward extension from the tropics. I tried to approach this problem in a species group comprising *D. nigrofasciatus* and *D. fascipes* that had long been regarded as a single species (Masaki, 1983). The latter species occurs widely in the tropical and subtropical regions, and the former in the temperate regions, of East Asia. When eggs of populations originated from the tropical (*D. fascipes*), subtropical (*D. fascipes*) and temperate (*D. nigrofasciatus*) regions are incubated constantly at a high temperature (26°C), they show characteristic hatching patterns (Fig. 4). In all tropical strains (Bogor and Bali in Indonesia, Khaoyai and Doi Pui in Thailand, Cebu in the Philippines) I have examined, most incubated eggs hatch within 4 weeks of incubation with a sharp peak in week 3. A few eggs are delayed, taking 5 to 7 weeks to hatch, in rare cases even 9 weeks. The frequency of such delayed eggs is not affected by the parental photoperiod (Fig. 4, bottom).

In the subtropical population derived from Ishigaki Island (24.5°N), 10 to 15% of the eggs produced by females reared under short-day conditions at 26°C show delayed development, and the maximum duration of the egg stage exceeds 10 weeks (Fig. 4, middle). The incidence of diapause increased at a lower temperature of 20°C (Fig. 2F; see also Masaki et al., 1987), but this egg diapause is opportunistic compared with that in the temperate form. Diapause eggs resume development in response to only a few days of exposure to 26°C or a higher temperature (Masaki, 1990).

Diapause is stable in the temperate form and persists for a longer period than in the subtropical form, although the duration of incubation is highly variable among individuals, ranging from 6 to 30 weeks at 25°C (Fig. 4, top). A few eggs laid by short-day females

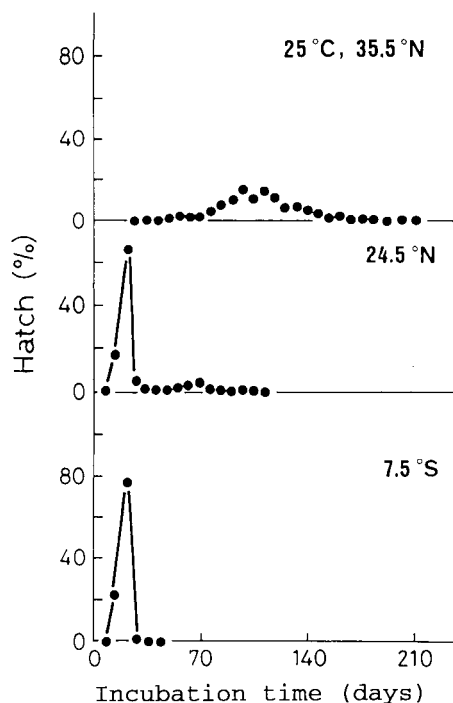


Fig. 4. Duration of development in eggs laid by females of *Dianemobius* species collected from different climatic regions and reared under LD 12 : 12 at 25°C. The latitude of collecting site is given on the right in each panel. Top, *D. nigrofasciatus* from central Honshu; middle, *D. fascipes*, the subtropical form from Ishigaki Island; bottom, *D. fascipes*, the tropical form from Java.

tropical-subtropical species *D. taprobanensis*. In this species group, however, the subtropical populations lack the ability to programme egg diapause in response to seasonal cues, but larval development is controlled by a long-day-type response that would increase the possibility of larval overwintering (Masaki, 1979a).

The temperate species with diapause and the tropical species without diapause in each of the genera *Teleogryllus* and *Loxoblemmus* undoubtedly are phylogenetically related. Egg diapause in many species of crickets in the temperate region might have evolved in various species groups independently of one another during the processes of northward extension or in situ change in climatic conditions at certain latitudes. This assumption is supported by crossing the two temperate species, *T. emma* and *T. infernalis*. Hybrid eggs failed to enter diapause normally, and many of them hatched much earlier than those of either parent species (Ohmachi & Masaki, 1964). Diapause was not expressed at all in some eggs. These results suggest different genetic backgrounds for diapause in the two species.

may avert diapause, but even at a temperature as high as 30°C most eggs hatch only after a period of diapause.

Three different patterns of egg development thus occur in this species group of ground crickets, corresponding to different climatic regions: predominantly nondiapause in the tropics, opportunistic diapause (see Masaki, 1990) in the subtropics, and stable diapause in the temperate region.

Geographical origin of egg diapause

Many temperate species of crickets with stable egg diapause are very closely related to predominantly nondiapause tropical and/or subtropical species. The species complex mentioned above is one of such examples. The temperate species *D. nigrofasciatus* with egg diapause formerly had been regarded as conspecific to the tropical form of *D. fascipes* that lacks photoperiodic programming of diapause and produces only a very few delayed eggs without regard to photoperiod. The tropical species extends into the subtropical area where it has evolved a physiological system to programme an egg diapause in response to photoperiod, although this diapause is opportunistic as already described (Masaki, 1990).

A similar situation occurs in the species group of ground crickets comprising the temperate species *D. mikado* and the

Either set of diapause genes would not be expressed properly in the heterozygous state. The crickets seem to have a physiological and genetic potential to evolve egg diapause easily. Egg diapause has been established repeatedly and independently in many taxa.

Intraspecific variation

Extensive data on diapause duration are available for *T. emma* collected from about 40 localities in the temperate region. They show a simple linear cline in diapause duration decreasing from south to north (Fig. 5; Masaki, 1965). This gradient appears to conflict with the macrogeographical trend of diapause intensity across the tropical, subtropical and temperate regions. However, a multiple regression analysis suggests that the cline reflects adaptation to the climatic gradient within the framework of univoltine adaptation (Masaki, 1965). The egg diapause then becomes more intense southwards because the risk of untimely development before winter is larger in warmer southern districts than in cooler northern districts. Had eggs terminated diapause and resumed development and hatched before winter in response to temporary warm weather, they would fail to overwinter. The probability of such risks would be proportional to the sum of effective temperatures remaining after the reproductive season of the parent generation. Therefore, a relatively intense diapause would be selected in the warmer south as long as a univoltine life cycle is maintained. Presumably, when *T. emma* invaded the Japanese islands via the Korean Peninsula, it already had a univoltine cycle with a stable egg diapause. As this species extended north and south, the optimal diapause intensity was selected by the climatic gradient.

IMMIGRANT ISLAND POPULATIONS

Geographical differentiation of life cycle might be understood better if we can follow the dynamic process of the life-cycle change over time. Such opportunities might be afforded by immigrant populations introduced from a climatically distinct area. Immigrant

populations are subject to different selection pressures they have not experienced previously, and their life cycles might be modified (Masaki & Walker, 1987). In the Japanese Islands, three presumptive cases of immigrant populations of ground crickets have been found.

Immigrants in the Bonin Islands

About 1,000 km south of Tokyo in the Pacific Ocean are the isolated Bonin Islands (27°N), well known for their endemic biota. The climate is oceanic and subtropical, with extremes of monthly mean temperature of 17.3°C (January) and 27.3°C (August). The warm climate would allow continuous growth and reproduction if food supply is not seasonally limited. Among several

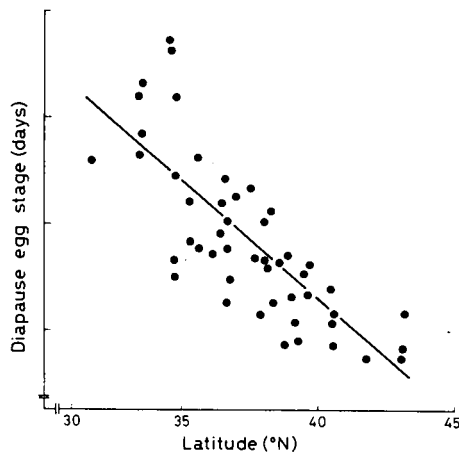


Fig. 5. Duration of diapause egg stage at 25°C as a function of original latitude in Japanese populations of *T. emma*. (Masaki, 1965, modified.)

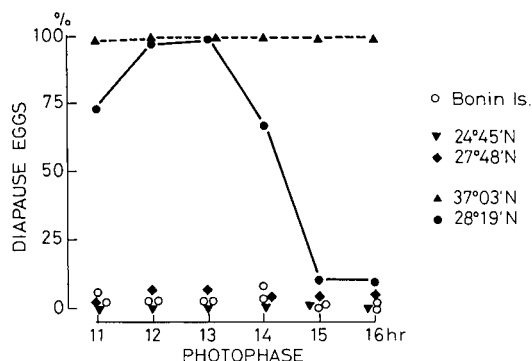


Fig. 6. Percentage of diapause in eggs in response to photoperiod in the Bonin population of *Dianemobius* (open circles), northern (triangles) and southern (solid circles) strains of *D. mikado* and, two strains (diamonds and inverted triangles) of *D. taprobanensis*. Note the virtual absence of egg diapause in the Bonin population.

species of crickets occurring on these islands is a ground cricket which cannot be morphologically distinguished from *D. mikado*. This cricket is heard singing and both adults and larvae were collected even in winter (T. Arai, pers. commun.). In the laboratory, eggs deposited under short-day conditions hatch without diapause within a few weeks at 26°C except for a few delayed ones (Fig. 6; Masaki, 1978). In this respect, the Bonin ground cricket is similar to the subtropical Ryukyu populations of *D. taprobanensis* occurring in similar latitudes and climatic conditions, although the two island groups are separated from

each other by more than 1,300 km of sea. The eggs of *D. mikado* in the main islands of Japan enter diapause in short days, so that the Bonin eggs are quite distinct from them.

Unexpectedly, however, the larval developmental response to photoperiod is similar to the short-day type of *D. mikado* (Masaki, 1979a) and the ovipositor is longer than that of *D. taprobanensis*, falling within the range of variation in *D. mikado*. From these observations, I concluded that the Bonin cricket was introduced from a temperate district of Japan and inferred that it probably originated from about 35°N, based on the geographical variation in the larval development time under various photoperiodic conditions.

This conclusion was supported by abnormal hybrids produced by crossing the Bonin and Ryukyu strains. The hybrid females showed a developmental response intermediate between the parents while male hybrids developed unusually fast and lost the photoperiodic response altogether. In contrast, hybrid larvae between the Bonin and Honshu (the main island) populations did not show any sex-linked abnormality in development.

The earliest possible introduction of *D. mikado* from the main island of Japan is about 130 years ago when agricultural exploitation started on the Bonin islands and seedlings and nursery trees with soil were brought in. Diapause eggs in the soil could have tolerated the long journey. The subtropical conditions in these islands allowed development and reproduction all year round, and natural selection might have eliminated egg diapause, because it lowered fitness by delaying reproduction. The delay of larval development at long-days (short-day type response) has persisted, because it is not expressed under the daylength at the low latitude of the islands and escaped natural selection.

Immigrants in the Ryukyu Islands

In the Japanese Islands, the southern limit of distribution of *D. nigrofasciatus* is about 30°N, Yakushima Island off the southern coast of Kyushu. The subtropical sibling species *D. fascipes* occurs on Ishigaki, Iriomote and Yonaguni Islands at about 24°N. Neither of the two sibling species had been recorded on islands between Yakushima and Ishigaki Islands. In 1972, however, I found *D. nigrofasciatus* within a very limited area of the

Ogamiyama Park in Naze City on Amami-Oshima Island (28.5°N) but nowhere else in the island. I revisited the island in 1975, and found *D. nigrofasciatus* again only at the same collecting site as three years before. This restricted habitat was close to the lawns planted around the monument erected in commemoration of the end of U. S. occupation in 1953.

Although the climate in Amami-Oshima is subtropical with extreme monthly means of 14.2°C (January) and 28.3°C (July), a high proportion of the progeny entered egg diapause under short days at 26°C as did the northern mainland populations. Larval developmental responses to photoperiod and adult morphometrical traits, particularly the relative ovipositor length, were all similar to specimens of *D. nigrofasciatus* occurring in southern Kyushu but quite distinct from *D. fascipes* populations inhabiting Ishigaki and adjacent Islands. All lines of evidence suggested that the Ogamiyama population belonged to *D. nigrofasciatus* derived from the north, probably from Kyushu where the lawn grass had been shipped out.

The ground crickets collected in 1975 laid a lower proportion of diapause eggs under short days than those collected in 1972 (51% versus 99%). It is as yet uncertain whether this is a result of response to selection by the subtropical climate over three years or whether it is due to sampling or other errors. If this is really an immigrant population and still exists, it would be another example of natural selection now going on. However, the possibility is not entirely ruled out that this restricted population has not been founded by recent arrivals, because *D. mikado* of the temperate type with egg diapause occurs widely and abundantly in Amami-Oshima Island.

Another immigrant population of *D. nigrofasciatus* was found in October, 1988, at a more southerly locality, Oppadake, in Okinawa Island (26.5°N), around a recently established viewing spot on a hillside. The ground around the hut was covered with lawns shipped from Kyushu a few years ago. This population, like the immigrants in Amami-Oshima, produced progeny with egg diapause in short days, while *D. taprobanensis* collected at the same site produced mostly nondiapause eggs. Unfortunately, the immigrant population of *D. nigrofasciatus* seems to have become extinct. In November, 1991, I could neither find nor hear this species singing at Oppadake.

PRESUMPTIVE RELICT POPULATION AT GEOTHERMAL SPOTS

In unusual habitats in Hokkaido, *D. nigrofasciatus* is heard singing in the snowy mid-winter when the air temperature consistently falls below 0°C. Ground crickets are active on geothermal spots of volcanic origin where green herbs form "islets" in the "sea" of snow. The temperature on the soil surface under the leaf litter or moss growth where crickets were singing ranged from 25 to 30°C in December when the air temperature was -3°C and the temperature under the leaf litter in the surrounding forest floor was about 1°C (N. Ichijo, unpublished).

One might expect that these unique island situations would have evolved a homodynamic life cycle of the tropical type. We collected adults and larvae of *D. nigrofasciatus* in December 1992 and again in January 1994 and analyzed the life-cycle characteristics of the offspring (S. Masaki & N. Ichijo, unpubl.). We found that the geothermal populations have the ability to programme egg diapause in response to short photoperiods with a critical length of 14.5 h. Therefore, they are clearly heterodynamic. The primary reason for their continuous activity during winter might be the direct (phenotypical) response to the

ground heat, because diapause eggs can hatch at constant high temperatures without preliminary chilling and their hatching time is much less at 30°C than at 25°C (Fig. 7).

In spite of the "equatorial" climate, the geothermal population thus retains egg diapause. If genetic variation in the diapause trait had been eroded in the northernmost island, the selection pressure to eliminate diapause would not have been effective. We tested this possibility by selecting nondiapause eggs under short-day conditions through 10 generations, and found that the percentage nondiapause increased from 15% in the 1st generation to 65% in the 10th generation. Thus the population could respond to selection for nondiapause. Therefore, there should be a factor or factors intercepting the selection pressure in the geothermal site. Gene flow from the surrounding populations might be one such factor.

However, this is not the whole story. There is evidence suggesting the unique evolutionary situation of the geothermal population. In general, *D. nigrofasciatus* is univoltine in Hokkaido, producing a high proportion of diapause eggs even under long days. As already mentioned, the geothermal population mostly averts diapause in long days at 25°C like the southern bivoltine populations (Fig. 2A). Although singing in winter can be ascribed to a direct response to the geothermal conditions, the population seems to have adapted better to a warmer climate than the present cool climate of Hokkaido.

In this connection, the occurrence of univoltine *V. micado* around the geothermal area should be noted. This cricket had not previously been recorded anywhere else in Hokkaido, and the Tsugaru Strait has been believed to delimit the northern distribution of this species. This isolated and restricted occurrence suggests that *V. micado* around the geothermal spots is a relict population. The species might have once spread over a much wider range in Hokkaido when the climate was much warmer than it is today. After the last glaciation there was the hypsithermal period (the "Jomon" period) during which the annual mean temperature was considerably higher than it is today (Udvardy, 1969, p. 321) and the climate in some parts of Hokkaido might have been comparable to that in the bivoltine area. It is then possible that the geothermal spots have been refuges for the southern type bivoltine population of *D. nigrofasciatus* as well as for *V. micado* when the

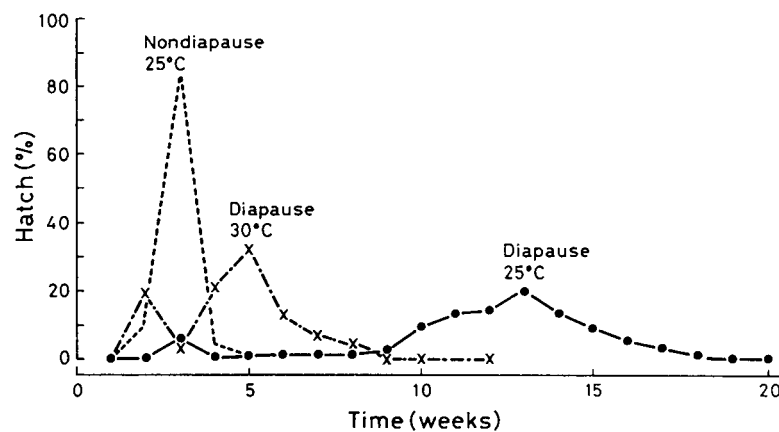


Fig. 7. Time for egg hatch in a population of *D. nigrofasciatus* inhabiting a geothermal spot (43°N) in Hokkaido. Diapause eggs were produced by females reared in LD 12 : 12 and nondiapause eggs by those reared in LD 16 : 8, both at 25°C.

hypothermal period ended and the southern forms retreated from the general area in Hokkaido. The isolated populations of *D. nigrofasciatus* might have thus survived as relicts only around the geothermal spots and retained the ancestral bivoltine life cycle, and some eggs deposited near the geothermal centre may hatch and mature in winter. This hypothesis should be tested by further comparative study and genetic analysis of those populations in the geothermal and adjacent areas.

RESPONSE TO ARTIFICIAL SELECTION

Incidence and intensity of egg diapause

The immigrants noted above were transported from north to south. However, because the crickets originated in the tropics (Alexander, 1968), the main stream of their life-cycle evolution was the establishment of diapause and photoperiodism as southern ancestral populations expanded north into the temperate region. This evolutionary process may be reconstructed by artificial selection. For more than 20 years I have repeatedly selected eggs from the lagging tails of hatching distributions in several tropical strains of *D. fascipes* collected from southeast Asia. In those strains at 25°C, hatching peaks occur in week 3 after oviposition, but a few eggs may hatch in weeks 6 to 9. If such delayed hatch is controlled genetically, these eggs might serve as an initial step in the evolution of egg diapause. However, all attempts to increase the proportion of delayed eggs failed owing to the scarce and inconsistent occurrence of developmental delay, biased sex ratio, inbreeding depression, etc. The possibility cannot be ruled out that the delayed hatch is due to nongenetic physiological or pathological factors.

In view of these difficulties, I finally switched to a subtropical population of *D. fascipes* derived from Ishigaki Island in the southwestern corner of the Ryukyu Arc (Masaki & Nagase, 1992). This population has an ability of maternal photoperiodic programming of egg diapause. However, as mentioned before, its diapause is characteristically opportunistic. The incidence as well as the intensity of diapause is much less than in the temperate form *D. nigrofasciatus*. Even when the parent generation was reared in a typical short day of LD 12 : 12 at 25°C, only 15% of the eggs had a period of diapause (Masaki, 1990). The subtropical specimens are morphologically similar to the tropical ones and distinct from the temperate species.

I established five lines at LD 12 : 12, 25°C and selected eggs hatching after different periods of incubation. For convenience, these lines are designated by the number of weeks closest to the mid point of the selected range, i.e. W3, W5, W8, W15, and W22, respectively. W3 represents selection for nondiapause. Since the maximum duration of the egg stage in the founder population was about 15 weeks, W22 could not be isolated at the start of experiments. With the progress of selection, the diapause incidence and duration increased and, after several generations of selection, some eggs in W15 took more than 22 weeks so that W22 could be started. For other details of the selection procedure, see Masaki & Nagase (1992).

As shown in Figs 8 and 9, selection was highly effective in modifying the incidence and duration of diapause. In W3, the percentage diapause decreased rapidly and reached almost zero after several generations. In the other lines, both the incidence and duration of diapause increased, and the differences in selection pressure were reflected in their different profiles of hatching distribution (Fig. 10). In W8, the incidence of diapause was more

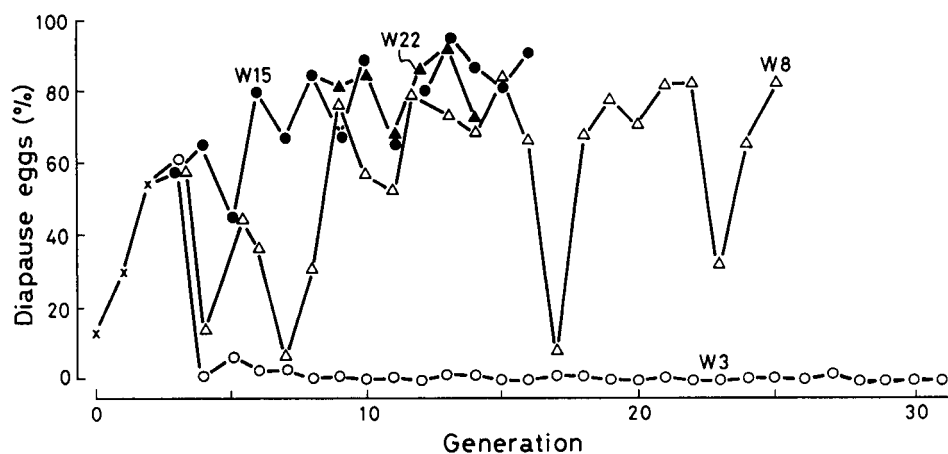


Fig. 8. Changes in the incidence of diapause under different selection pressures in the Ishigaki population of *D. fascipes* kept in LD 12 : 12 at 25°C. The first three generations were selected for diapause lasting more than 60 days, and then four strains (designated as W3, W8, W15 and W22) were isolated and eggs hatching in about 3, 8, 15 and 22 weeks, respectively, were selected in each generation.

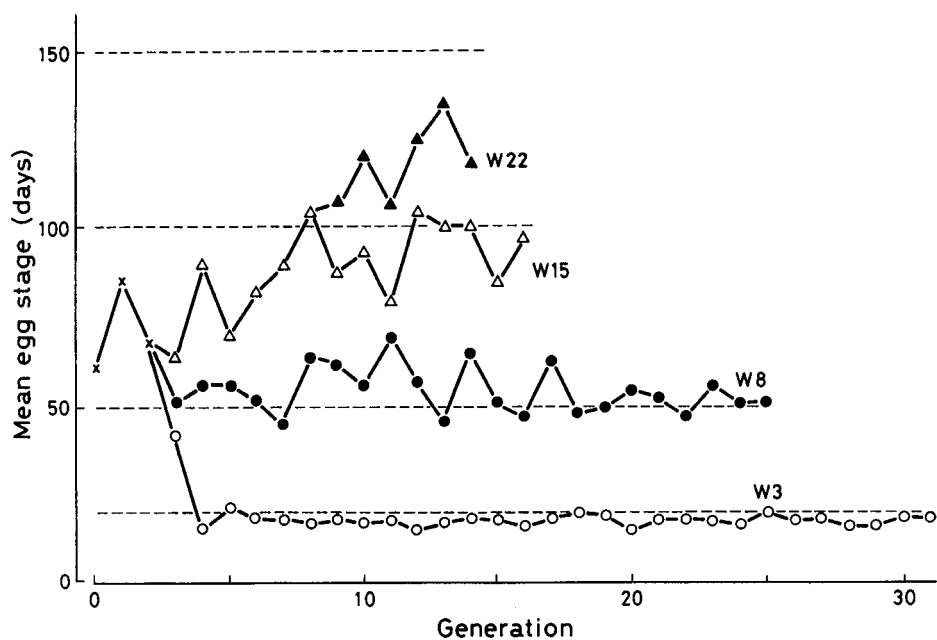


Fig. 9. Changes in the mean duration of diapause egg stage in the W8, W15 and W22 lines selected from the Ishigaki population of *D. fascipes* (see caption for Fig. 8). For the W3 line, means of all eggs are given. The broken horizontal lines are selection goals.

variable from generation to generation than in the long diapause lines (W15 and W22). In the latter lines, the maximum duration of incubation period far exceeded the limit observed in the founder stock, and was even greater than in the temperate species *D. nigrofasciatus*. The maximum egg stage hitherto recorded was 277 days at 25°C. Egg diapause is therefore highly responsive to selection. It is adaptively a highly flexible trait. The heritability of the duration of the diapause egg stage at 25°C was 0.46 as estimated by the parent-offspring regression, using the first and second offspring generations of crickets newly collected on Ishigaki Island in 1992 (S. Masaki, unpublished).

The mode of response to selection indicates that both the incidence and intensity of egg diapause are quantitative traits controlled by polygenic systems. The changes in the diapause traits were gradual. Cross breeding tests between the different selection lines indicate involvement of both autosomal and sex-chromosomal factors (S. Masaki & T. Shibuta, unpubl.). Although strict stabilizing selection has been performed for many generations, nondiapause phenotypes were not excluded in any of the diapause-selected lines (W8, W15, W22). Furthermore, there was no gap in hatching distribution between the nondiapause and diapause eggs (Fig. 10). Selection for a longer egg stage raised the upper limit of diapause duration but not the lower limit. As a result, the phenotypic variance in the egg stage became larger with the progress of selection for a longer diapause which should have reduced the genetic variance. This paradoxical situation might be related to some unknown physiological mechanism involved in diapause.

I could not establish any diapause strain that bred true in respect to the diapause incidence even after more than 33 (W8), 21 (W15) or 13 (W22) generations of selection,

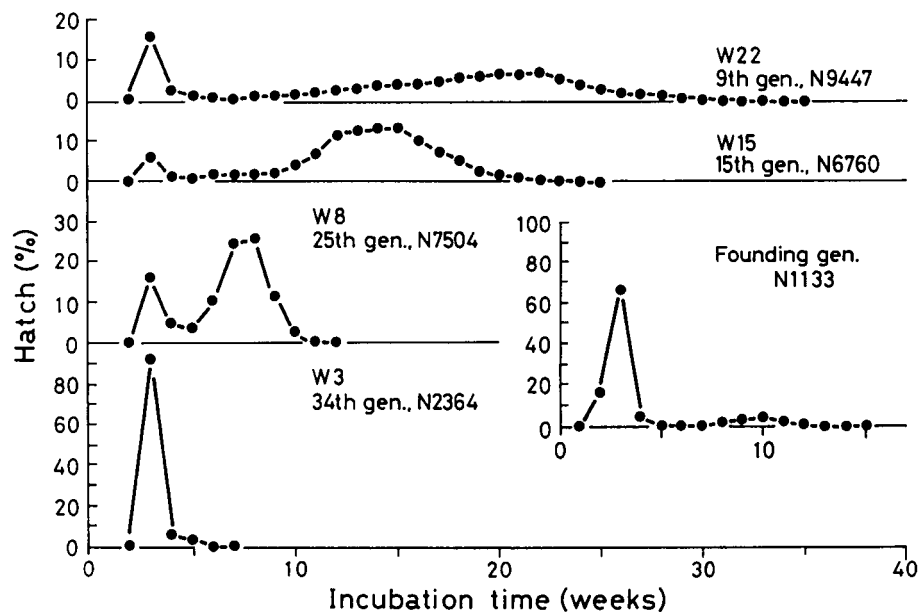


Fig. 10. Distribution of hatching eggs in the founding Ishigaki population (inset) and four selected lines (W3–W22) of *D. fascipes*, all kept at LD 12 : 12 and 25°C.

although the percentage diapause increased from 15% in the founding population to 80–90% in the later generations of W15 and W22.

Photoperiodic response controlling wing form

The classic works by Danilevskii and his colleagues amply demonstrate the existence of regular geographical clines in the critical photoperiod in many species of moths and other insects (Danilevskii, 1965). Many more examples are cited in later reviews on the seasonal adaptation, dormancy and photoperiodism in insects (Beck, 1980; Saunders, 1982; Tauber et al., 1986; Danks, 1987). Photoperiodic clines are common products of climatic selection for the optimal timing of switch from the active to dormant phases in the life cycle. However, only a few studies have examined the variability of the critical photoperiod within a population that provides genetic resources for the evolutionary response to natural selection (Sauer et al., 1986; Cambell & Bradshaw, 1992; Hard et al., 1993).

We tried to assess the intra-population variation in the critical photoperiod, and also to select strains with different levels of photoperiodic response and those with different critical photoperiods. In crickets, the genetic and environmental control of wing form seems to be widespread (Tanaka, 1978; Roff, 1986, 1990, 1994; Walker, 1987; Masaki & Simizu, 1995). For our purpose, therefore, we used the wing-form response in the Ishigaki strain of *D. fascipes* (Masaki & Seno, 1990; Shimizu & Masaki, 1993), in which the adult wing form is determined by the larval photoperiod under crowded and warm conditions in a way similar to the diapause programming (Figs 2B,D; Masaki & Watari, 1989), and the response can be assessed in a much shorter time than for the diapause response. Thus, 24 isofemale lines were separated from the offspring of crickets collected in the field, and the responses to photoperiods between 11 and 16 h were determined for each family (Fig. 11; Shimizu & Masaki, 1993).

In mass rearing at 28°C, many adults are long-winged in long days but short-winged in short days, the critical photoperiod being consistently close to 12.5 h. The inbred lines

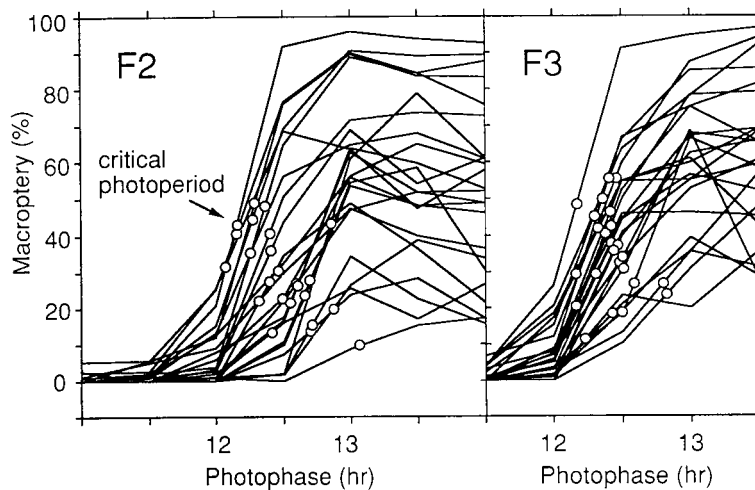


Fig. 11. Photoperiodic responses in percentage macroptery at 28°C in the 2nd and 3rd generations of 24 isofemale lines established from the Ishigaki population of *D. fascipes*. (Shimizu & Masaki, 1993.)

showed, however, considerable variation in the photoperiodic response particularly in the maximum proportion (the saturated incidence) of long-winged adults in the long photoperiods. In the short photoperiods, the incidence of long-winged adults was consistently low and the differences among the families were much less than in the long photoperiods. If we define the critical photoperiod by the mid-point between the upper and lower saturation levels of the response, the critical photoperiod varied to a considerable extent, ranging from 12 to 13 h. We determined the critical photoperiod also in the offspring of each parent family, and the heritability was estimated to be 0.36 by the regression method (Shimizu & Masaki, 1993).

Simple selection either for long-winged forms at a short photoperiod of 12 h or for short-winged forms at a long photoperiod of 13 h remarkably modified the wing-form response to photoperiod (Fig. 12), but the change mainly occurred in the saturation level and amplitude of the response. No shift in the critical photoperiod as defined by the midpoint between the lower and upper saturation level in the response curve was discernible. Therefore, the critical photoperiod and the wing-form determination are based on different genetic backgrounds.

Then special selection regimens were applied to create strains with different critical photoperiods. We selected long-winged forms at a photoperiod A in one generation and short-winged forms at a photoperiod B in the next generation ($A > B$) and this alternated selection was continued. A critical photoperiod between A and B would be selected by this method. We made selection in regimens of $A = 12$ h and $B = 11$ h and also $A = 14$ h and $B = 13$ h. The resulting shift in the critical photoperiod was not clear, probably because of the unavoidable effect of selection on the general physiological background for wing development. Because the critical photoperiod was originally between 12 and 13 h, selection for long-winged adults at a 12 h photoperiod in a regimen of $A = 12$ h and $B = 11$ h might exert an enhancing effect, and selection for short-winged adults at 13 h photoperiod in a

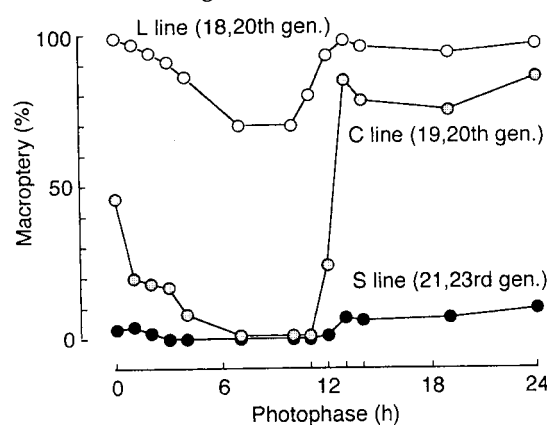


Fig. 12. Photoperiodic responses in percentage macroptery in three lines from the Ishigaki population of *D. fasciipes* selected for long wing in LD 12 : 12 (L line), short wing in LD 13 : 11 (S line) and control (C line) alternately selected for long wing in LD 13 : 11 and short wing in LD 12 : 12. (Shimizu & Masaki, 1993.)

regimen of $A = 14$ h and $B = 13$ h might have a suppressing effect, on long-wing development. At least in one line, however, the percentage macroptery in 12 h photoperiod increased while it remained at a low level in 11 h photoperiod, suggesting a decrease in the critical photoperiod.

Thus, the life-cycle components, the incidence and duration of diapause and critical photoperiod for wing-form determination can be modified by selection. All these results suggest the high evolutionary flexibility of life cycle in crickets.

CONCLUDING REMARKS: LIFE CYCLE AND SPECIATION

Crickets share regulatory responses to seasonal changes with most other insects: division of the life cycle into active and dormant phases, the control of both diapause programming and development time depending on seasonal cues such as photoperiod and temperature, and characteristic thermal requirements for diapause termination. Natural selection would coordinate and optimize these ecophysiological functions within the framework of the species-specific pattern of life cycle in each habitat. The differential local selection is reflected by the geographical variations in life-cycle components such as critical photoperiod, diapause intensity, development time, and adult size. Although crickets are highly variable, the previously established patterns of life cycle and other aspects of their ways of life constrain the shift of their life-cycle pattern to a basically different one. This constraint is indicated by the species-specificity in the life stage for overwintering in the temperate region.

Under subtropical conditions, however, some species of crickets seem to be released from this constraint. They may develop and reproduce all year round, although other species such as *Cardiodactylus novaeguineae* Haan enter a firm obligatory egg diapause (Oshiro et al., 1981). In the Yaeyama group of the Ryukyu Islands located at about 24°N, different patterns of life cycle may coexist as an ecophysiological polymorphism. Under short days, for example, adults of *D. fascipes* produce some diapause eggs at a low temperature and larvae require more time to mature than under long days (Figs 2F, G). Therefore, diapause eggs, larvae and adults coexist during winter, and the life-cycle pattern may be similar to that of *Gryllus firmus* Scudder in Florida (Fig. 1G; Ibrahim & Walker, 1980). On the other hand, *D. taprobanensis* collected from near the northern limit of distribution at about 27°N of the Ryukyu Islands has virtually no egg diapause and responds to short days by a conspicuous delay in larval development (Masaki, 1979a), making a sharp contrast with its temperate sibling *D. mikado* overwintering as eggs and growing faster in short days than in long days.

The egg- and larval-overwintering life cycles require contrasting types of regulatory responses; adult emergence is accelerated by short days in the egg-overwintering species but by long days in the larval-overwintering species. These two types of life cycle cannot coexist in the same gene pool in the temperate region where a severe dormant season regularly occurs. Disharmonized combination of life-cycle traits, e.g. an egg diapause combined with a short-day delay of larval development, or a larval diapause induced by long days, is maladapted and can not survive. Moreover, the different overwintering stages may result in seasonal isolation. Thus, Alexander & Bigelow (1960) tried to explain speciation of *G. pennsylvanicus* overwintering as eggs and *G. veletis* overwintering as larvae by allochronic isolation resulting from the divergence in the overwintering stage. Unfortunately, these two species are genetically not closely related, so that the allochronic speciation model has not been supported by later works (Lim et al., 1973).

However, speciation associated with life-cycle divergence should be taken into consideration more seriously to explain the occurrence of closely related species with different modes of seasonal adaptation. Such species may be sympatric, allopatric or parapatric, depending on the adaptability of the different life cycles to the climatic gradient. The geographical relationship between the two closely related species is variable so that allochronic isolation is not the only factor in speciation triggered by life-cycle divergence.

V. micado overwintering as an egg and its “summer form” (probably conspecific to *V. ryukyuensis* Oshiro) overwintering as a larva are partly sympatric. *D. mikado* with egg diapause and *D. taprobanensis* with short-day delay of larval development are parapatric. The temperate species *D. nigrofasciatus* enters a firm egg diapause and shows a short-day or reversed intermediate-day type developmental response (Fig. 2C), the subtropical form of *D. fascipes* is characterized by an opportunistic egg diapause and long-day type developmental response (Fig. 2F,G), and the tropical form of the “same” species is homodynamic (Fig. 4). These allopatric forms are genetically incompatible to one another as indicated by sterility, decreased fecundity or developmental delay in hybrids (Masaki, 1983; unpubl.). The mode of climatic adaptation in life cycles seems to be important in triggering speciation in these cases, hence the term “climatic speciation” has been proposed (Masaki, 1972, 1983).

Thus, study of geographical variation not only contributes to an understanding of the evolution of life cycles but also throws light on the speciation problem in crickets.

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