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Climatic Adaptation and Species Status in the Lawn Ground Cricket. I. Photoperiodic Response*

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Synopsis The ground cricket, tentatively identified as *Pteronemobius taprobanensis* WALKER, regulates its egg diapause, growth rate, and wing form in response to photoperiod. These responses seem to be physiologically independent of one another, for each of them shows not only a photoperiodic curve, but also a geographic pattern, of its own. Geographic variations in diapause and development indicate at least three different life cycles. (i) A univoltine cycle with egg-overwintering would be prevalent to the north of about 35°N, because the egg enters diapause even in long days (>14 hr), and the nymph controls its growth by a response of short-day type. (ii) A multivoltine cycle with egg-overwintering would be common between 28 and 35°N, because the egg averts diapause in long days, and the long-day retardation of nymphal growth is somewhat reduced. (iii) A multivoltine cycle with nymphal overwintering would occur to the south of about 28°N, because the egg diapause is virtually absent and the nymphal growth is retarded in short days (<14 hr). The last type probably represents a distinct species.

Introduction

Most species of insects adapt themselves in various ways to the seasonally changing environments. Factors involved in this adaptation particularly of their life cycles, such as temperature, daylength, or food supply, vary geographically. Seasonal programming of their life cycles should therefore be adjusted further to expand their existence in a wide variety of climates. The selection pressure in such a case frequently shows a more or less regular geographic gradient, which may be reflected in a well-defined trend of variation as exemplified by photoperiodic clines (BRADSHAW, 1976; BRADSHAW and LOUNIBOS, 1977; DANILEVSKII, 1961). Since the expansion of distribution is a historical event, the adaptation thus established may be suggestive of the response to gradual climatic changes in evolutionary time. Furthermore, various species with various types of life cycle occur in the same climatic gradient. This allows us to conduct comparative studies of their variations, and thereby to draw information about the interaction between endogenous and exogenous factors involved in the climatic adaptation.

In two species of field crickets (*Teleogryllus*), for example, there are physiological clines in diapause intensity of the egg and in development time of the nymph, both

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in parallel to the latitudinal and altitudinal climatic gradients (MASAKI, 1965, 1966, 1967, 1978). Since the development time is positively correlated with the adult size, the latter conforms to the converse of Bergmann's rule (MASAKI, 1967, 1978). Two species of ground cricket (*Pteronemobius*), however, obviously deviate from this rule, showing more complicated geographic trends in adult size (MASAKI, 1973, 1978). This discrepancy can be explained by the different seasonal strategies between the large-sized and small-sized crickets. The former is univoltine. Natural selection has therefore established the intrinsic rates of development and diapause termination inversely proportional to the latitudinal gradient of heat. The latter are variable in voltinism. The heat available per generation varies therefore not only with latitude but also with the number of generations per year.

The response to natural selection by the same environment may indeed be quite different according to the type of life cycle. The interaction of this sort should play an important part in the divergence of life cycle. Comparative studies of climatic adaptations of various species thus provide one of the few feasible ways of approach to the evolution of seasonal strategy. The results of such studies seem also to be informative for further understanding of speciation phenomena, since the significance of life-cycle divergence at various stages of speciation has increasingly been recognized (ALEXANDER, 1968; BUSH, 1969; MASAKI, 1978; MASAKI and OHMACHI, 1967; TAUBER and TAUBER, 1976, 1977; TAUBER *et al.*, 1977; WALKER, 1964, 1974). These are the reasons for undertaking studies on the climatic adaptation of the lawn ground cricket, tentatively identified as *Pteronemobius taprobanensis* WALKER, as well as similar previous studies on other species of crickets. The photoperiodic response, widely known as an efficient timing mechanism among insects (DANILEVSKII, 1961; BECK, 1968; SAUNDERS, 1976), will be dealt with here as Part One of this series.

Materials and Methods

This work was carried out from 1970 to 1976 inclusive. Adults and late-instar nymphs were collected in autumn from lawns or grassy sites in 36 localities between 24 and 44°N of the Japanese Islands (Table 1). The collecting sites were restricted to localities not higher than 200 m above sea level, in order to exclude the complicating effect of altitude. Under room conditions, they were fed on Insect Feed (Oriental Kobo Kogyo) and slices of carrot, and allowed to lay eggs into the cotton-wool plug of a water bottle. The eggs were incubated at 25°C for five weeks, during which nondiapause ones hatched. Diapausing eggs were stored at 10°C for more than three months to terminate diapause and then re-incubated at 25°C. Within three weeks many nymphs hatched.

In most cases, the first progeny thus produced by field-collected adults were used. The method of rearing was almost the same as described previously for *P. fascipes* (MASAKI, 1973). Nymphs and adults were kept in light-proof zinc drums (diam. 40×height 50 cm) fitted with a 6 W white fluorescent lamp and a timer. Each drum could accommodate four rearing jars of 2-litre capacity, and a series of 12 such drums were installed in a constant-temperature room kept at 25°C. Forced ventilation was attempted by a fan, but this was not efficient and the temperature within the drum rose to about 26.5°C during the photophase. In order to test the influence of

Table 1. List of localities where samples of *P. taprobanensis* were collected for the present study.

Island	Locality	Latitude ¹⁾ (°N)	Longitude ¹⁾ (°E)	Mean Temp. ²⁾ (°C)
Hokkaido	Otaru	43°12'	141°04'	8.1
	Sapporo	43°04'	141°19'	7.8
	Hakodate	41°48'	140°46'	8.2
Honsyu	Hirosaki	40°35'	140°29'	10.5
	Odate	40°16'	140°34'	
	Morioka	39°45'	141°08'	9.7
	Akita	39°44'	140°07'	10.9
	Honzyo	39°23'	140°03'	
	Sakata	38°55'	139°50'	11.8
	Murakami	38°13'	139°29'	
	Niigata	37°55'	139°00'	13.0
	Hukushima	37°46'	140°28'	12.3
	Taira	37°03'	140°52'	
	Komatsu	36°25'	136°25'	
	Mito	36°23'	140°27'	13.0
	Amagasaki	34°45'	135°22'	
	Osaka	34°41'	135°39'	15.6
	Matsuyama	33°50'	132°46'	15.4
Sikoku	Asizuri	32°42'	133°01'	17.8
	Hukuoka	33°35'	130°22'	15.7
Kyusyu	Kumamoto	32°49'	130°42'	15.9
	Miyazaki	31°56'	131°25'	16.8
	Kagosima	31°35'	130°33'	17.0
	Nishinomote	30°43'	130°58'	19.0
Tane	Naze	28°25'	129°30'	21.2
Amami	Sinmura	28°14'	129°23'	
	Koniya	28°09'	129°19'	
	Kikai	28°19'	129°57'	
Kikai	Tete	27°53'	128°55'	
	Hetono	27°48'	128°54'	
	Ketoku	27°48'	128°58'	
Okinoerabu	China	27°20'	128°35'	
Okinawa	Naha	26°13'	127°41'	22.3
Miyako	Hirara	24°45'	125°27'	22.9
Yonaguni	Yonaguni	24°28'	123°00'	23.8
Isigaki	Isigaki	24°21'	124°10'	23.3

¹⁾ Determined on 1:50000 maps published by Kokudo Chiri In.

²⁾ Data from the following sources:

Tokyo Astronomical Station (ed.), 1973. Rikanempyo. Maruzen, Tokyo. Wadati, K. (ed.), 1958. Climate of Japan. Tokyodo, Tokyo. Anonymus, 1954. Climatic Tables. Nogyo Gijutsu Kyokai, Tokyo.

temperature on the photoperiodic response, some groups of crickets were reared in bioclimatic cabinets at 22 or 30°C with programmed light-dark cycles. The effect of a daily cycle of warm (30°C) and cool (20°C) temperatures coupled with a light-dark cycle was also tested in a few cases.

The number of emerging adults were counted every one or two days, and their wing form was recorded. The adults were kept under the same conditions as the nymphs. Eggs laid into moist cotton-wool plugs were collected at weekly intervals over a period of five weeks, and incubated at 25°C to determine the percentage diapause. After collecting egg samples, the surviving adults were killed and preserved in 75 percent methanol for morphometric measurement. As an indicator of the adult size, the head width was measured in both sexes by an ocular micrometer at a magnification of 60 \times , and the length of ovipositor in the female at 30 \times .

Due to the limited space, all the available data cannot be given as diagrams or tables, but they are used as the background information for inferences and arguments made in the text.

Results

Diapause Response. This ground cricket hibernates as an egg (OHMACHI and MATSUURA, 1951) in a state of diapause (MASAKI, 1960). Fig. 1 illustrates the distribution of hatching nymphs from mixed batches of eggs laid under various conditions of photoperiod. In this particular population, there were two distinct peaks of hatch about 20 and 110 days after deposition, respectively. The first one was due to nondiapause eggs and the second to diapause eggs. The egg diapause is thus facultative, which suggests the possibility for a multivoltine cycle. The duration of diapause was highly variable, ranging from about 50 to more than 200 days. Any clear gap was not found between the diapause and nondiapause distributions. The physiological trait controlling diapause would probably vary quantitatively, and eggs would hatch without diapause when it is below a certain threshold. The rate of morphogenesis should also be variable, and the two ranges of variations seem to overlap one another. This made it difficult to distinguish between the two types of eggs. Those eggs that hatched within five weeks were arbitrarily counted as nondiapausing and the rest diapausing.

On this basis, the percentage diapause was determined among eggs laid by 21 local populations at different photoperiods. Unfortunately, the fecundity was not always high under the experimental conditions; many eggs were produced in some cases but not in others. Two points, however, can be made clear. First, the egg diapause is programmed by the parental photoperiod and, second, the photoperiodic response is remarkably variable among geographic populations. Several examples are illustrated in Fig. 2 to show different types of responses.

Some populations showed a consistently high level of diapause in any photoperiod between LD 11:13 (11 hr light: 13 hr dark) and LD 16:8, suggesting a univoltine cycle to be predominant in the field (Fig. 2, a, b). Others responded to photoperiod in an unexpected way, entering diapause in long days (>14 hr) but averting it to a certain extent in short days (<14 hr) (Fig. 2, c). Although the diapause in this case is clearly facultative, this response may also result in a

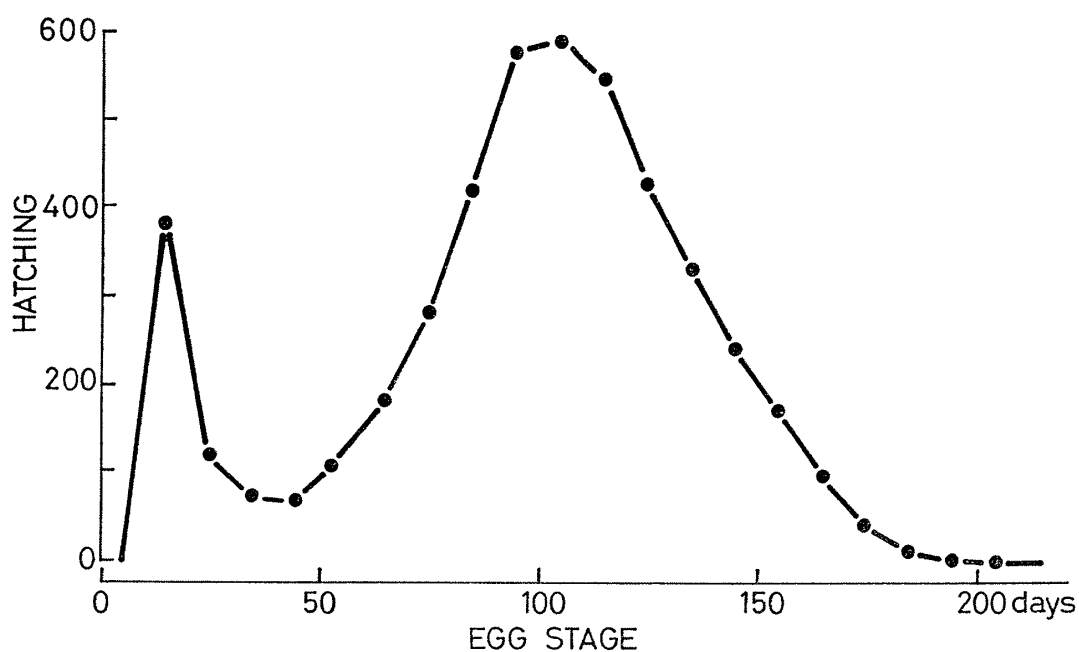


Fig. 1. Distribution of hatching nymphs at 25°C from mixed egg batches produced in different photoperiods (LD 11:13-16:8) by a population of *P. taprobanensis* originated from Osaka (34°41'N). Sample size, 4715.

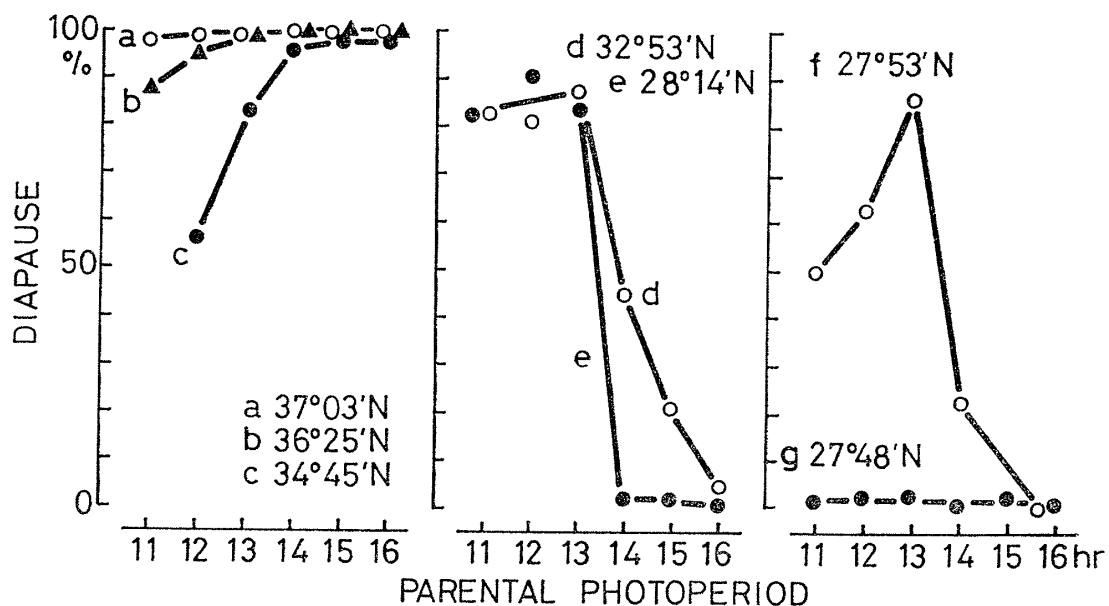


Fig. 2. Effect of parental photoperiod at about 26°C on the incidence of egg diapause in geographic populations of *P. taprobanensis*. Localities (sample size for each symbol): a, Taira (172-560); b, Komatsu (29-542); c, Osaka (192-2380); d, Asizuri (593-2025); e, Sinmura (463-1096); f, Tete (535-1804); g, Hetono (701-3407).

univoltine cycle in the field, because the short days prevail only in the cool season and the low temperature may favour the incidence of diapause. Still other populations demonstrated responses of long-day type commonly observed in many other species of insects (Fig. 2, d, e). A slightly modified response of this type was also found, in which the incidence of diapause clearly decreased at either side of LD 13:11 (Fig. 2, f). Variation in the incidence of diapause manifested itself in a most drastic way by the virtual absence of diapause as shown in Fig. 2g, in which only less than 3 percent of the eggs persisted more than five weeks of incubation at any photoperiod.

The diapause response of this ground cricket is thus highly variable among geographic populations. In one extreme diapause is prevalent at any photoperiod, in the other it is virtually absent, and different types of photoperiodic effects are found between them. The relative importance of the nymphal and adult photoperiods for these responses has not been elucidated.

Development Response. The nymphs also were directly responsive to photoperiod, for their development time varied with photoperiod. In the example presented in Fig. 3, the nymphs matured much faster and more uniformly at LD 11:13 than at LD 16:8. The difference in the mean development time between the two groups was as large as 50 days. This long-day retardation was due to general decrease in the rates of growth and morphogenesis, but not to any arrested development.

Geographic populations were variable in this development response as illustrated by several examples in Fig. 4, which are selected from the tested 31 populations. The left panel of this figure represents responses of short-day type in that the development is promoted by short days and delayed by long days. The development time in photoperiods of LD 13:11 or shorter was less variable, being about 40 days, while it was remarkably different among the populations in LD 15:9 or 16:8. Other eight populations collected between 34 and 40°N showed similar responses at 30°C, indicating little or no modifying effect of the high temperature. In the middle panel of Fig. 4, however, the retarding photoperiod is shifted to LD 14:10 as the temperature rises from about 26° to 30°C. The two curves (d, e) are based on different but very close populations on the island of Amami, and probably indicate the modifying action of temperature. A few other populations from this island were also examined. They tended to be retarded slightly more at LD 15:9 than at LD 16:8 at 26°C, but conspicuously more at LD 14:10 than at LD 15:9 or 16:8 at 30°C. The response at 30°C can therefore be described as an intermediate type rather than a short-day one. A response making a sharp contrast to the short-day type is given in Fig. 4f, in which the nymphal development is prolonged by short days but accelerated by long days. This type of response persisted either at 22 or 30°C. A daily cycle of warm (30°C) and cool (20°C) temperatures combined with LD 12:12 neither mitigated nor enhanced the short-day retardation. The expression of this long-day type response seemed to

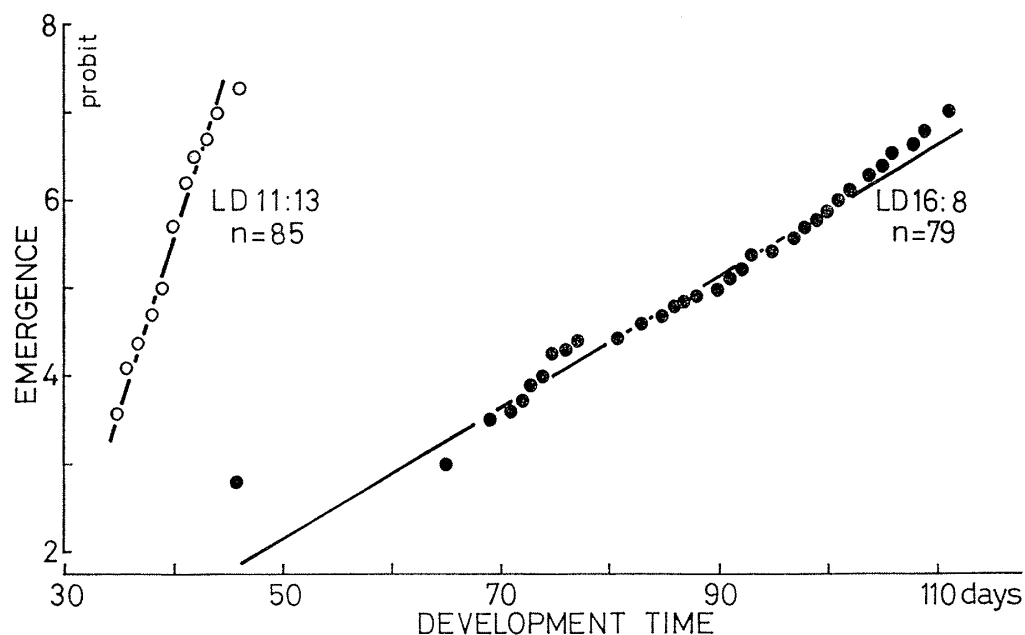


Fig. 3. Effect of photoperiod on adult emergence at about 26°C in a population of *P. taprobanensis* originated from Osaka (34°41'N).

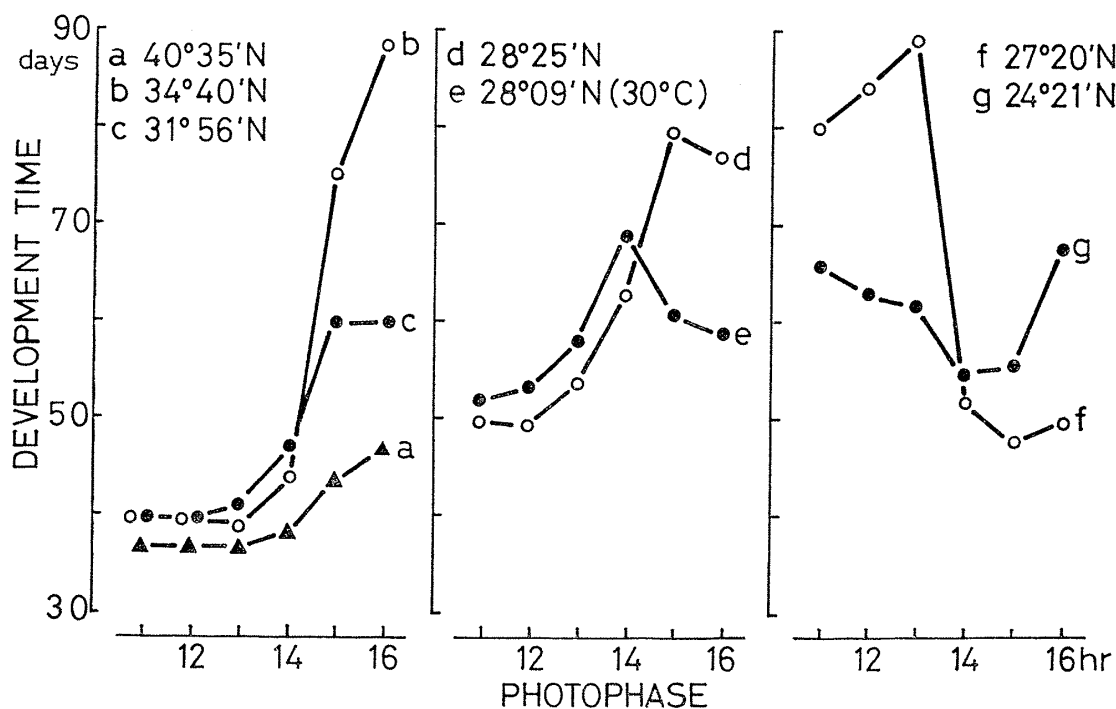


Fig. 4. Nymphal photoperiodic responses at about 26°C (except for e) in geographic populations of *P. taprobanensis*. Localities (sample size for each symbol): a, Hirosaki (81–117); b, Osaka (38–93); c, Miyazaki (49–84); d, Naze (58–89); e, Koniya (70–101); f, Okinoerabu (52–113); g, Isigaki (64–81).

be geographically variable, and a population with a less obvious response is represented in Fig. 4g.

This ground cricket is thus highly variable in the development response as well as the diapause response to photoperiod. At least two basically different types, short-day and long-day types, can be recognized in the development response. Moreover, each type of response varies among geographic populations. In either type, there was a general tendency that the variance of the development time was larger at the retarding photoperiods than expected from the increased mean.

Size Response. Probably as a consequence of the development response, there were photoperiodic variations in the adult size; that is, the body size varied as a function of the development time. In many populations, therefore, the development response was reflected in the adult size. In Figs. 5A and B, the development response of short-day type resulted in smaller adult size in short days than in long days. Although many other populations of the short-day type showed similar tendencies, there were clear differences in adult size among them as well as between the sexes. The northern adults were larger than the southern ones, and the females were larger than the males. The ovipositor length varied not only in proportion to the head width, but also among populations. The northern females had longer ovipositors than the southern ones.

The size response to photoperiod was obscure only in the populations occurring at about 28°N (Fig. 5B, left). Three others derived from the vicinity of this latitude all showed similarly dubious size responses, although the nymphal development was clearly of the short-day type (Fig. 4d). The size response again became obvious in populations near 27°N, but in an exactly inverted way. The short-day adults were larger than the long-day ones. This was obviously a result of the longer time for development in short days. This shift of response was accompanied by a remarkable decrease in the length of ovipositor (Fig. 5B).

Shape Response. Like many other members of the nemobiine crickets, this species is dimorphic in the shape of wing. The macropterous form with well-developed hind wings can fly, while the micropterous form has only atrophied wings and its tegmina too are somewhat shortened in the female. The macropters were scarce in the field, but many of them emerged under crowded experimental conditions. Crowding seemed to be essential, but not the only factor responsible for the appearance of macropters. A very clear effect of photoperiod, especially of its change, on the wing development has been reported (TANAKA *et al.*, 1976).

The incidence of macropters was generally higher in the female than in the male, but in otherwise the two sexes responded in similar ways. In Figs. 6A and B, therefore, the mid-values between the male and female percentages of macropters are plotted. As in the other criteria of photoperiodic response, there is a geographic variation in the shape response. The northern populations tended to produce more macropters in long days than in short days (Fig. 6, a, b). This type of response was also found in other five populations derived from about 39 to 43°N.

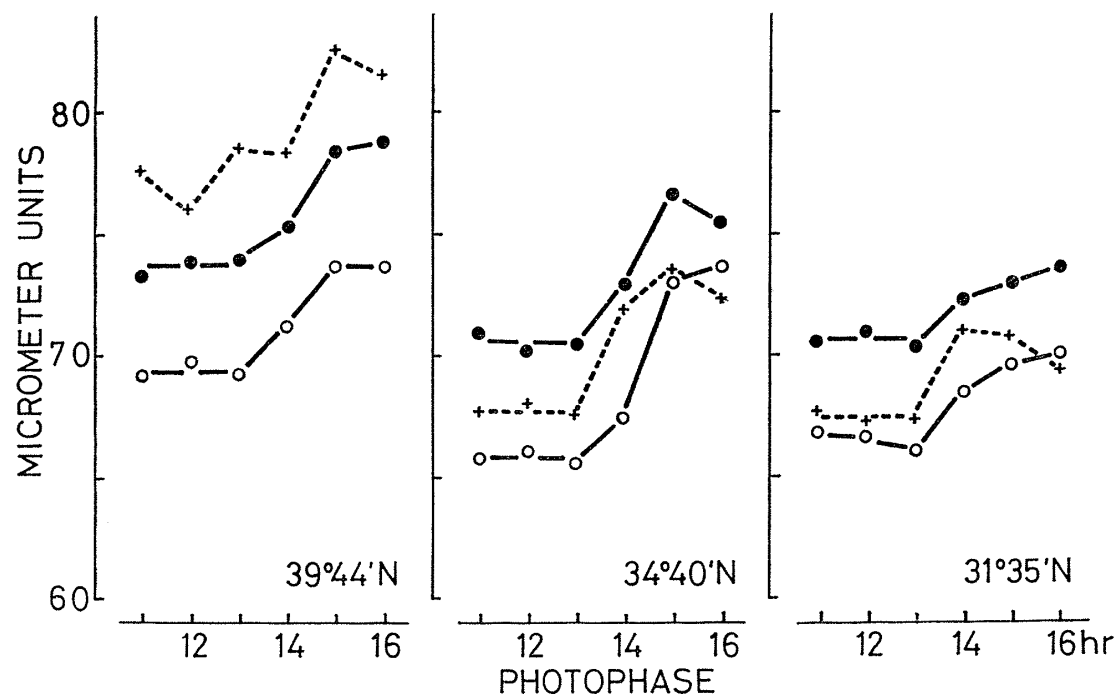


Fig. 5A. Effects of photoperiod on adult head width (open circle for male, closed circle for female, $1=1/40$ mm) and ovipositor length (cross, $1=1/20$ mm) in geographic populations of *P. taprobanensis*. Localities (sample size for each symbol) from left to right: Akita (σ^7 21-55, ϕ 16-35), Osaka (σ^7 15-54, ϕ 18-58), Kagosima (σ^7 33-49, ϕ 35-44).

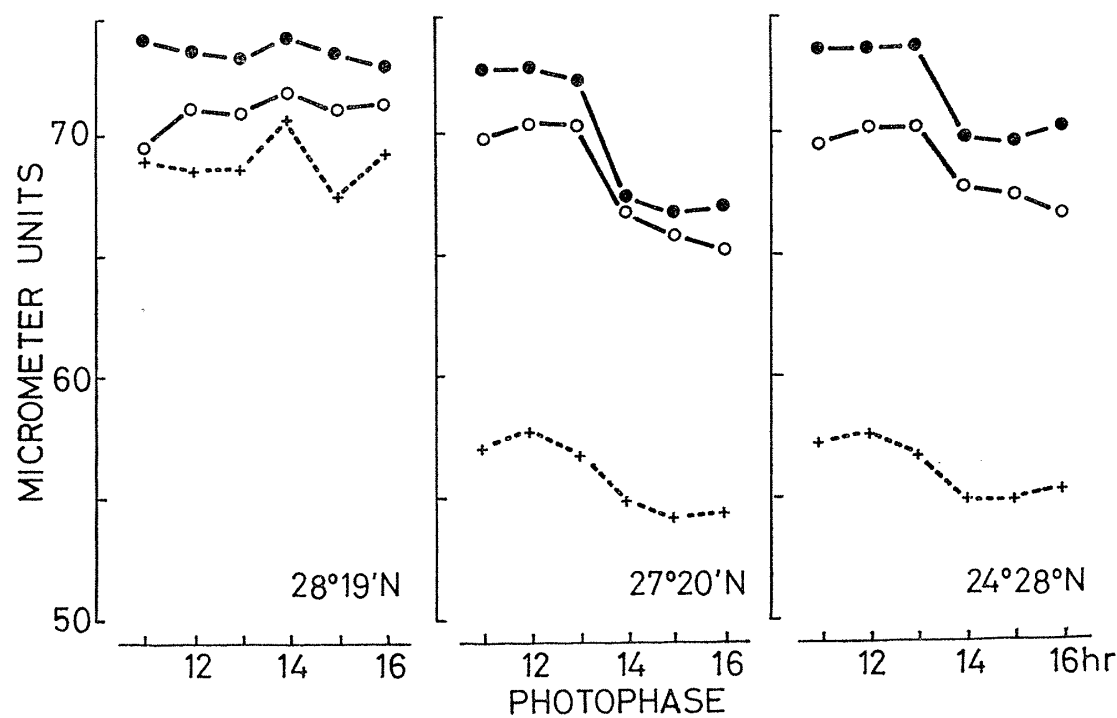


Fig. 5B. The same as Fig. 5A. Kikai (σ^7 15-44, ϕ 10-52), Okinoerabu (σ^7 10-44, ϕ 17-43), Yonaguni (σ^7 8-46, ϕ 10-39).

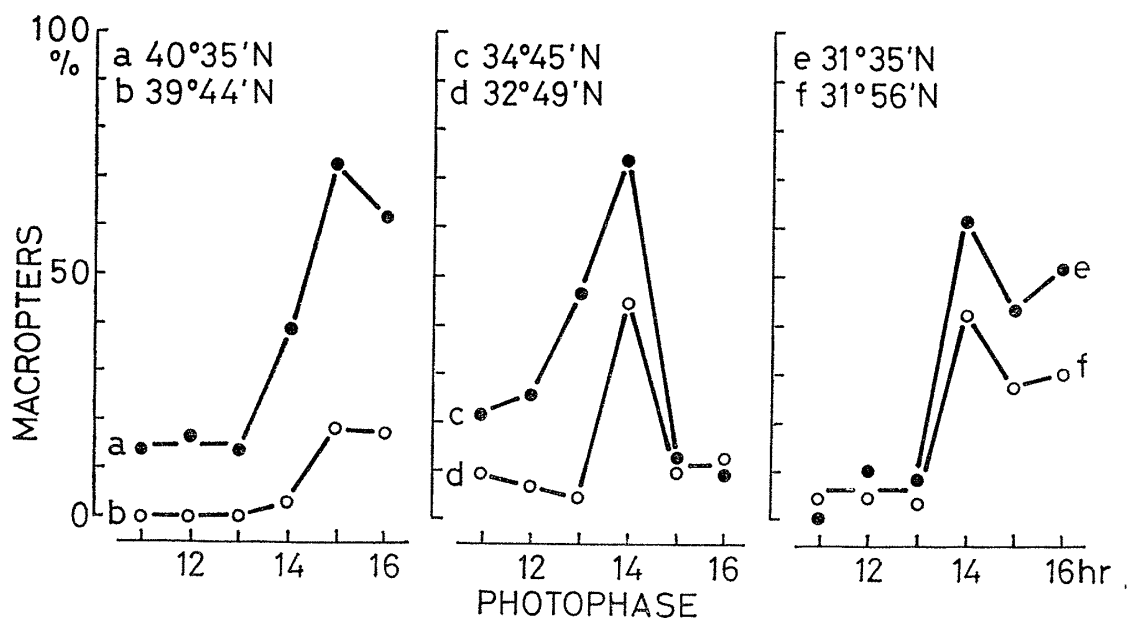


Fig. 6A. Effect of photoperiod on the incidence of macropters in geographic populations of *P. taprobanensis*. Localities (sample size for each symbol): a, Hirosaki (67-93); b, Akita (66-95); c, Amagasaki (87-102); d, Kumamoto (70-94); e, Kagosima (71-96); f, Miyazaki (66-84).

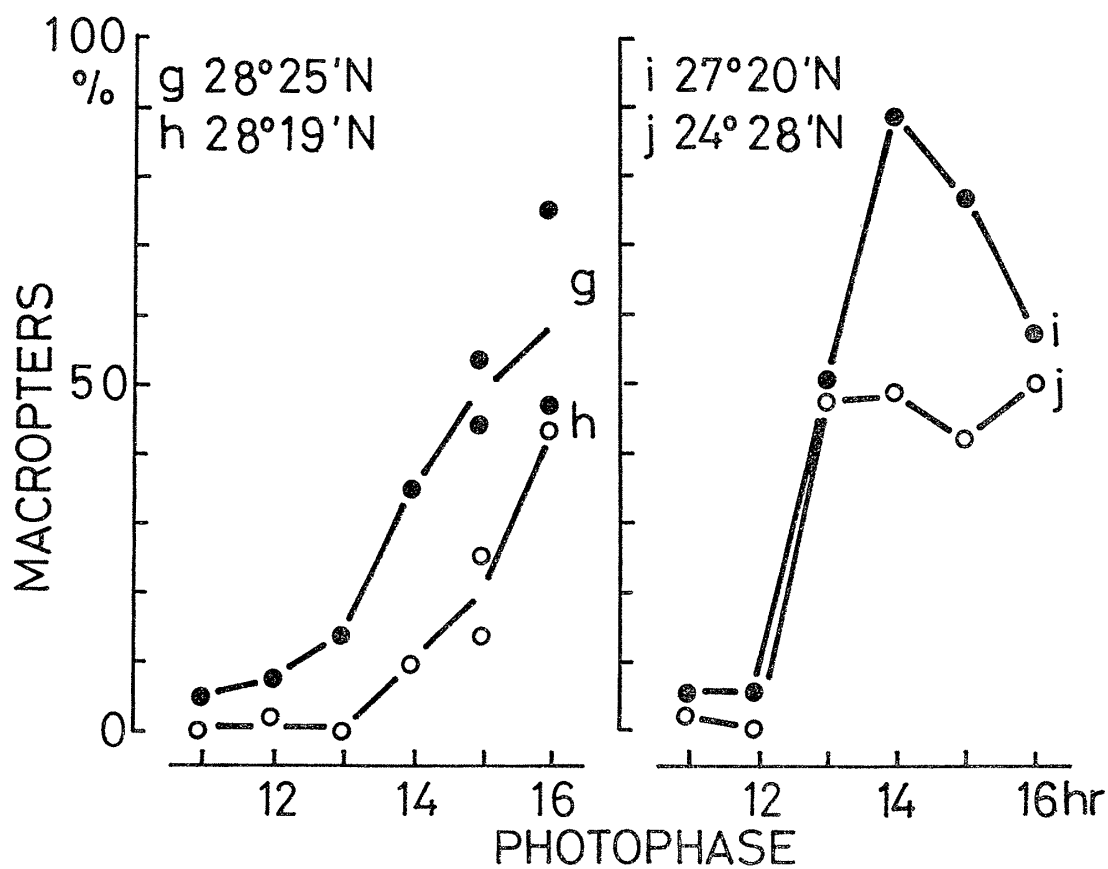


Fig. 6B. The same as Fig. 6A. g, Naze (57-73); h, Kikai (26-74); i, Okinoerabu (52-113); j, Yonaguni (64-93).

At middle latitudes between 32 and 37°N, macropters occurred most frequently in intermediate days (=14 hr), but they were scarce in either the short or long days (Fig. 6, c, d). Similar responses were obtained in other five populations from the same range of latitudes. In the populations near the southern tip of Kyusyu, the maximum incidence was also observed at LD 14:10, but there was no conspicuous decrease in the longer photoperiod. The population from the southwestern corner of Sikoku also belonged to this type. The incidence of macropters in long days increased again further south at about 28°C (Fig. 6, g, h). As already noted, the development response changed from the short-day type to the long-day type to the south of 28°N, but there was no corresponding change in the shape response (Fig. 6, i, j). The critical photoperiod for the induction of macropters was, however, clearly shorter than in the north, and even a short photoperiod of LD 13:11 favoured the development of long wings.

In each type of response represented in Figs. 6A and B, two populations are selected to show high and low levels of incidence of macropters. There was a large variation in the incidence of macropters in each type, and it was as yet difficult to conceive any clear geographic trend in the competence to develop into the macropterous form.

Geographic Profile of Egg Diapause. From the foregoing accounts, it is clear that this ground cricket is responsive to photoperiod in several different ways, and also that the responses are highly variable among the geographic populations. These variations would be expected to show definite geographic trends, if they are products of natural selection by the climatic gradient. In the following paragraphs, the geographic profiles of only the egg diapause and nymphal development are explored, and morphometric variations will be reserved for the next part of this series.

As mentioned before, the egg production was very poor in some cases so that the precise geographic profile of variation in the incidence of diapause could not be given for each photoperiod. The percentage diapause was therefore calculated for pooled egg samples in photoperiods of LD 13:11 and shorter, or of LD 14:10 and longer. The short-day and long-day plots thus obtained roughly indicate the geographic variation in the incidence of egg diapause (Fig. 7).

To the north of about 35°N, diapause was prevalent in either the short or long days; therefore, a univoltine cycle would be prevalent. From 35 to about 28°N, diapause was induced by short days but not by long days; the life cycle would possibly be multivoltine with egg-overwintering. To the south of 28°N, the egg diapause was virtually absent in either the long or short days; the life cycle would therefore be quite different from the northern ones.

Geographic Profile of Nymphal Development. As shown in Fig. 4, nymphs of most populations developed at more or less similar rates in short photoperiods of LD 11:13 to 13:11. The mean durations of short-day development were therefore plotted together in Fig. 8 to show the geographic profile of the variation

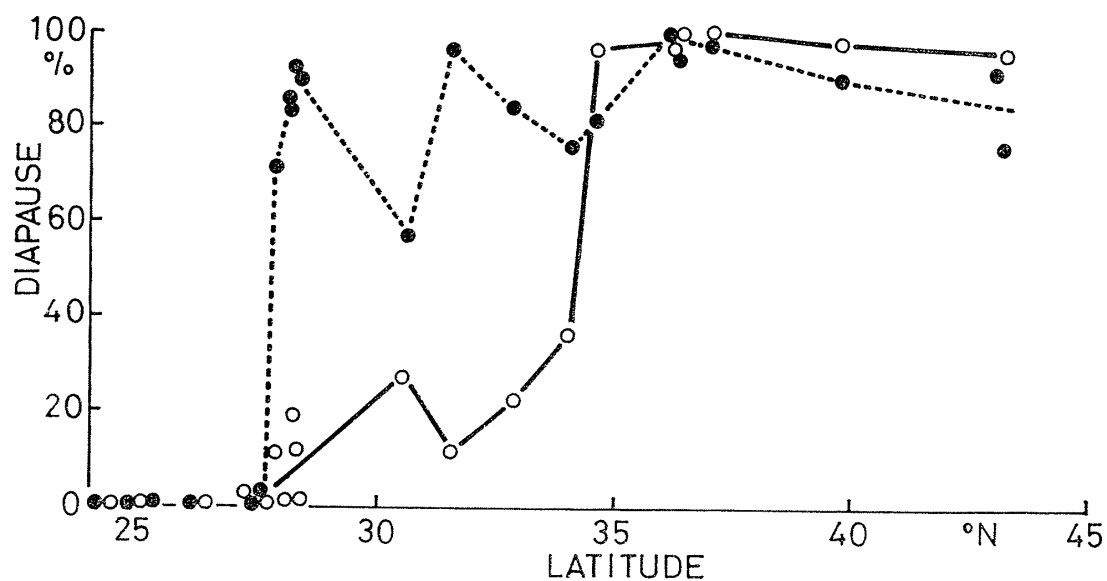


Fig. 7. Geographic profile of the incidence of egg diapause under long-day (LD 14:10-16:8, open circles) and short-day (LD 11:13-13:11, closed circles) conditions at about 26°C. Sample size for each symbol ranges from 197 to 10132 with a mean of 2860.

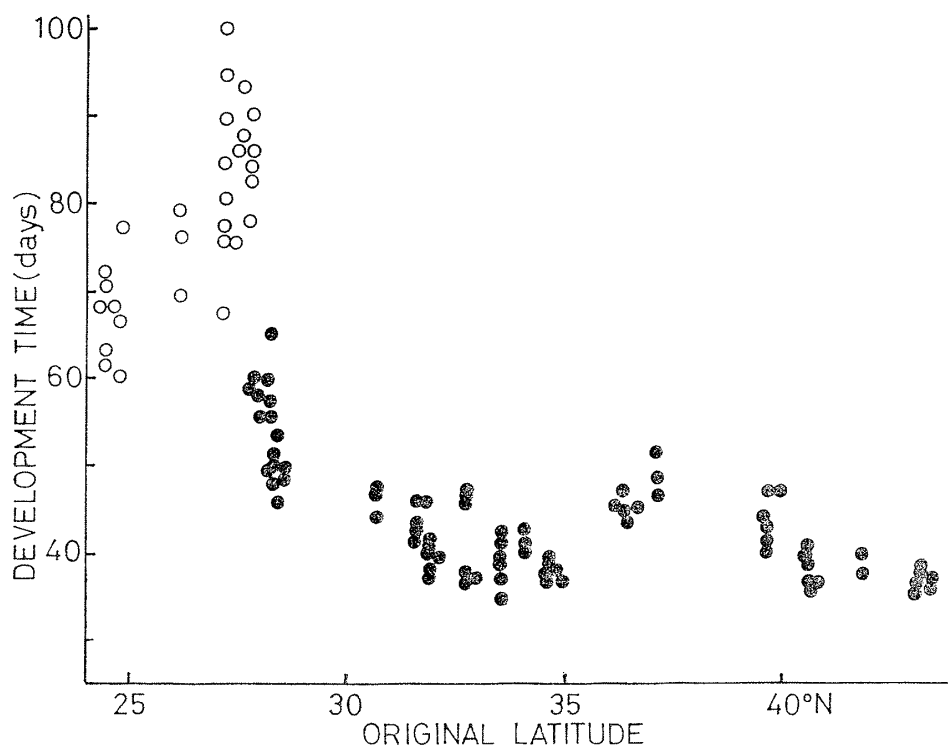


Fig. 8. Geographic profile of nymphal development time at short photoperiods (LD 11:13-13:11) and 26°C in *P. taprobanensis*. Open symbols indicate the long-day type and closed ones the short-day type. Sample size for each symbol ranges from 33 to 203 with a mean of 76.

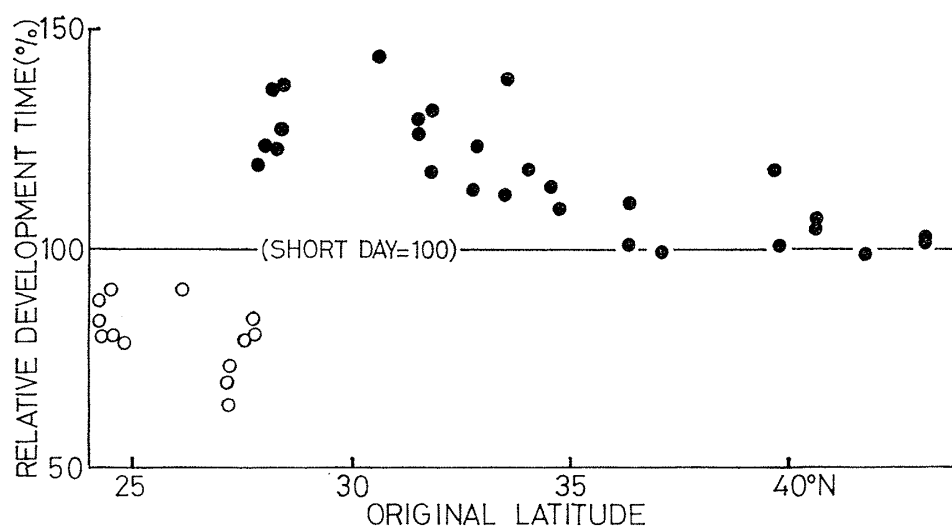


Fig. 9. Geographic profile of development time at LD 14:10 and about 26°C relative to that at LD 11:13 in *P. taprobanensis*. Open symbols, the long-day type; closed symbols, the short-day type. Sample size for each symbol ranges from 36 to 130 with a mean of 74.

over the whole stretch of the Japanese Islands. The northernmost populations at about 43°N matured on the average in less than 40 days. The development time slightly increased southward, reached its peak at about 38°N, then decreased to about 35°N, and increased southward again. At about 28°N, it became considerably longer than in the north, ranging from about 50 to 60 days. A further drastic increase in development time occurred at about 27°N (open circles). As shown below, this was due to the shift in the type of response from the short-day to long-day one. Further south, there was again a decreasing tendency for the development time.

The data presented in Fig. 4 suggest that geographic populations are variable in both the type and magnitude of response to photoperiod. These two aspects of variation can be expressed simultaneously by plotting the ratios of the development time in any photoperiod to that in a certain standard photoperiod. Since LD 11:13 consistently gave the shortest development in most populations inhabiting to the north of 28°N, it was chosen as the standard photoperiod. At LD 14:10, the northernmost populations developed at a rate similar to that at the short photoperiod, and the relative development time increased southward down to about 28°N (Fig. 9). To the south of this latitude, the response was suddenly switched to the long-day type, and the nymphs were accelerated to mature at LD 14:10 instead of retarded. A much more remarkable variation was found in a long photoperiod of LD 15:9 or 16:8 (Fig. 10). The retarding effect of long days was not great in the northernmost populations, but increased sharply southward to about 35°N, where the long-day development lasted about twice as long as the short-day development. Although there was again a decreasing tendency

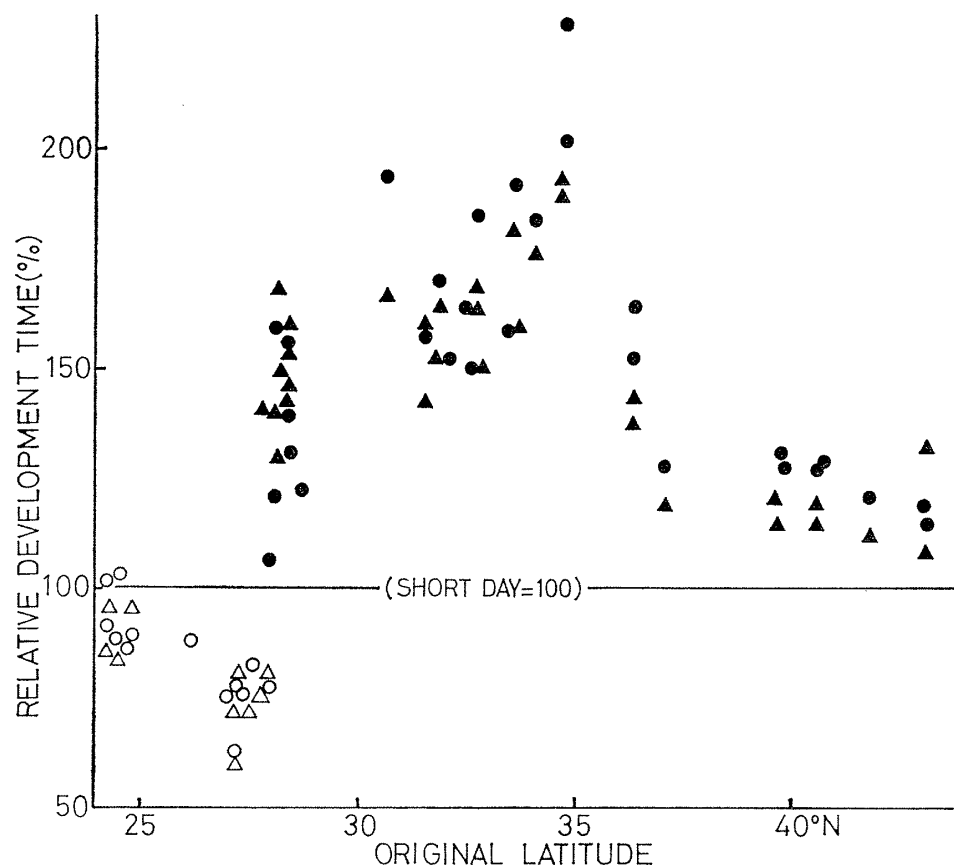


Fig. 10. Geographic profile of development time in LD 15:9 (triangle) and LD 16:8 (circle) both at about 26°C relative to that at LD 11:13 in *P. taprobanensis*. Open symbols indicate the long-day type and closed ones the short-day type. Sample size for each symbol ranges from 30 to 115 with a mean of 70.

further south, the long-day retardation was still clear at the southern limit of the short-day type, making a contrast to the response of the southern adjacent populations of the long-day type. The accelerating effect of long days on the long-day type decreased southward.

To summarize, populations with the response of short-day type occur between about 28 and 43°N and those with the response of long-day type to the south of about 28°N. Within the range of each type, the magnitude of response varies from one population to another.

Discussion

The sensitivity to photoperiod of this ground cricket is thus manifested by several different criteria, the egg diapause, adult emergence, adult size, and wing form. All these responses should be integral parts of the climatic as well as the

seasonal adaptation. In order to maintain successive generations in the temperate regions, the egg has to enter diapause before winter, the adult has to emerge in autumn, and the macropterous form has to appear at an appropriate time of the year when the external conditions favour migration by flight or when the population density tends to be high.

Except for a few populations at around 28°N, the adult size varies as a function of the nymphal development (Figs. 4 and 5), and so they are probably different expressions of the same photoperiodic effect. The diapause, development, and shape responses seem, however, to be physiologically independent of one another, since each reveals its own photoperiodic curve. On the one hand, populations sharing the same short-day type of development may be different from one another in their shape responses and, on the other hand, those with contrasting types of development may show similar shape responses (Figs. 4 and 6). Moreover, variations in the diapause response are not consistently accompanied by parallel variations in either the development or shape responses (Figs. 2, 4, 6). It is therefore difficult to assume that the three photoperiodic responses are different expressions of a single physiological process involved in the photoperiodic time measurement. They seem to be controlled by some mechanisms more or less independent of one another. This inference leads to a further assumption that each of them has its own genetic basis. Each response could, therefore, have been a target of natural selection.

Nevertheless, the egg diapause and nymphal development work together to mould the seasonal life cycle, so that the evolutionary response to natural selection would apparently have been determined by their interaction. As judged from the prevalence of diapause eggs in long days as well as in short days, the life cycle would mainly be univoltine in the area to the north of about 35°N. This is probably associated with the southward increase in the long-day retardation on the nymphal development. If diapause eggs are to be laid in autumn, the development time of nymphs should be adjusted to the available heat or the duration of the growing season (Table 1). From 35°N south to about 28°N, the egg diapause is less stabilized and effectively prevented by long days. Obviously, this response would result in an alternation of diapause and nondiapause generations, i.e., a bivoltine cycle. Although the nymphal response to photoperiod is the short-day type similar to that of the univoltine populations, the retarding effect of long-days tends to be decreased in this area, despite the greater amount of heat units. This is undoubtedly due to natural selection favouring a shorter development time when the growing season is shared by two or more generations. As will be discussed later on, however, the shift in voltinism is not a very clear phenomenon, and there might be a broad transitional zone where univoltine and bivoltine cycles coexist. The distribution of the two types of life cycle might be complicated further by microgeographic conditions of climate.

The disruption of developmental cline due to variation in voltinism has also

been found in *P. fascipes*. There is, however, an interesting difference between the two species. In *P. fascipes* the bivoltine cycle is controlled by the response of intermediate type, i.e., the development time is prolonged by intermediate days (about 14 hr) but by neither long nor short days (MASAKI, 1973). In *P. taprobanensis* a similar response was observed only at 30°C in the populations at about 28°N. At this latitude, however, the longest days slightly exceed 14 hr so that the nymphal development in the field would not differ substantially from the short-day type.

The difference in the nymphal photoperiodic response would cause a phenological difference between the two species in the bivoltine area. The first nymphal development in the long days of early summer would be retarded in *P. taprobanensis* but not in *P. fascipes*. In the last week of June, 1975, many adults of the latter were heard singing on the campus of Nagoya University (about 35°N) but those of *P. taprobanensis* were very few, although nymphs were abundant. This delay in the first appearance of adults is probably compensated for in the next generation, because the later it begins to develop, the shorter is the daylength and so the less is the retarding effect on the nymphal development. Owing to this feedback effect, both species similarly mature in autumn to lay diapause eggs.

Yet an important consequence of their different photoperiodic responses should be pointed out. In a typical bivoltine cycle of *P. fascipes*, the first egg-laying period mainly coincides with the long-day season (June-July) and the second with the short-day season (September-October), the adult emergence being prevented by intermediate days during the intervening period. Under such circumstances, any uncertainty in the diapause determination would be avoided, since the egg diapause is influenced by the daylength only during the late-nymphal and adult stages (KIDOKORO and MASAKI, 1978). Owing to its persistent short-day type response, on the other hand, the first reproductive period of *P. taprobanensis* is more variable and extends to later dates, and subsequently there would be a higher possibility to encompass daylengths around the critical range. The developmental fate of eggs may therefore be less stabilized, some undergo diapause and others do not. So far as the seasonal programming concerns, the univoltine and bivoltine cycles in this species seem to be less differentiated than in the other species.

Some ecological, physiological or evolutionary factors may be responsible for this slight but meaningful difference between the two species, which may be accounted for by various hypotheses. The two species, for example, prefer different types of habitats, and therefore are exposed to different sets of physical conditions. If this results in different rates of seasonal mortality at any particular stage, different seasonal arrangements of the life-cycle stages would be selected for. *P. fascipes* usually occurs at such sites as sparsely covered with short grasses, where the temperature at the soil surface may be extremely high on sunny days. This may be a great risk for eggs laid in the soil at the hottest season, hence the evolution of the response of intermediate type to prevent adult emergence in the hazardous period. Such a risk may be smaller in *P. taprobanensis* which prefers more densely

covered sites. In order to support this hypothesis, the exact sites of oviposition should be made clear in the field.

Another hypothesis, not mutually exclusive with the above, may be related to the different origins of bivoltinism between the two species. The persistence of short-day type in *P. taprobanensis* might have been due to the ancestral univoltine cycle when the species reached this island chain for the first time. A bivoltine cycle might have been evolved simply by abbreviating the egg diapause in response to temporally or geographically increasing heat units. The ancestral population of *P. fascipes*, on the other hand, might have already had a well-moulded bivoltine cycle with a characteristic response of intermediate type, from which a univoltine cycle might have been derived as the species extended northward. This hypothesis seem to be possible even if the geographic origins of the two species in this country are the same, because the intrinsic rate of growth is higher in *P. fascipes* than in *P. taprobanensis* so that the former is able to establish a bivoltine cycle in an area where the latter fails to do so.

Much more drastic than the variation in voltinism are the virtual disappearance of egg diapause and the simultaneous inversion of the development response from the short-day to long-day type at around 27–28°N. In all probability, this response confers on the subtropical population a higher chance to encounter winter in the nymphal stage rather than the egg stage—a seasonal strategy basically different from the northern ones. As each species of organism can be defined by its unique way of adaptation, such a basic difference in climatic adaptation implies that there are two distinct biological entities in this nominal species. From the climatic ranges of their adaptation, they have been called the temperate and subtropical forms, respectively (MASAKI, 1978). The two forms should be distinguished at the species level. This view is supported by a clear difference in the length of ovipositor between them (Fig. 5). Further data to test this hypothesis will be given in forthcoming parts of this series.

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