Res. Popul. Ecol. 37(1), 1995, pp. 119–128.

Special issue:
Dispersal Polymorphism of Insects:
Its Adaptation and Evolution
Papers from a symposium in Okayama, 1994

Variability in Wing Form of Crickets

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Abstract. Loss of functional hindwings is observed in most subfamilies of Japanese crickets. Habitat, behaviour, body size and phylogenetic factors might be involved, but interactions among them may obscure the general trend. Wing dimorphism is common among the relatively small-sized members of Gryllinae, and the two small-sized subfamilies, Nemobiinae and Trigonidiinae. Both environmental cues (e.g. photoperiod) and genetic factors affect the wing form. In *Dianemobius fascipes* (Nemobiinae), the percentage macroptery was drastically changed by selection for macroptery or microptery. Crossing experiments indicated polygenic control of wing form as well as X-chromosomal and maternal effects. Neither the long-winged nor short-winged line bred true after 40 generations of selection. Full-sib families revealed a large genetic variation in frequency of macropterous forms within a population. The genetic determination of the propensity for macropterism did not seem to be directly coupled to the mechanism performing the photoperiodic time-measurement.

Key words: wing forms, crickets, environmental factors, photoperiod, genetic variation, selection.

Introduction

The cricket is believed to have originated from a Permian oedischiid ancestor which had the hindwings suitable for flying and the male forewings specialized for stridulation (Sharov 1968). Many species of crickets, like some other pterygotes, have lost functional hindwings (Roff 1986b, 1990b). This is an intriguing evolutionary problem as the wings are prominent structures and provide the most efficient means of movement by flight. Crickets are especially fascinating experimental animals for the study of this evolutionary problem for several reasons.

Firstly, they are highly variable in wing shape and size. Secondly, they show a very wide range of habitat preferences. Their adaptive radiation in this respect can be seen both at higher (subfamily) and lower (species) taxonomic levels (Masaki 1986; Walker and Masaki 1989), offering opportunities to examine habitat and phylogenetic relationships involved in wing-form variation (Alexander 1968; Walker and Sivinski 1986; Walker and Masaki 1987; Roff 1986b, 1990b). Thirdly, many species of crickets can grow and reproduce under laboratory conditions for generations. For example, we have kept successive generations of *Gryllodes supplicans* (Gryllinae) for 35 years and *Dianemobius fascipes* (Nemobiinae) for 20 years. This easy rearing allows not only physiological and ecological studies of wing form but also selection of different wing forms and genetic analysis.

In this article, we explore first the wing-form variability in the Japanese species of crickets (Grylloidea), and then summarize results of our studies with *D. fascipes* on genetic and environmental factors controlling the wing-form variation. Based on these results, we discuss the interrelation between wing polymorphism (genetic) and polyphenism (environmental).

Spectrum of wing-form variation

In the Japanese Islands there are about 90 species of crickets belonging to 11 subfamilies. Among them, only three small subfamilies (comprising only less than several species) do not show any trend of wing reduction. Four subfamilies are uniformly micropterous or apterous, three of which are relatively small in body size. Other three include dimorphic species and the remaining one is sexually dimorphic, the male being micropterous and the female apterous (Table 1). This taxonomic pattern indicates that wing reduction has evolved in different phylogenetic groups independently of one another. Thus the whole spectrum of wing-forms in the crickets ranges from macroptery with fully developed functional wings to aptery without even rudimentary wings (Fig. 1). Intermediate character states exist between these extremes, suggesting that wing reduction is a gradual rather than abrupt process. This may conform to the polygenic control of wing form (see next section).

In many species, two different forms, one can fly normally and the other cannot, are intermingled probably to cope with the changing (benefit)/(cost) ratio of wings in space and time. A means to minimize the cost of wings can be seen even in macropterous forms. At least some of them restrict the flight activity only in the prereproductive phase of their adult life (Masaki and Walker 1987). The cessation of flying activity may be accompanied by shedding off the hindwings and degeneration of the bulky flight muscles, which in turn may affect the fecundity or egg-laying schedule (Tanaka 1976, 1986b, 1991, 1993; Roff 1984, 1989).

Coexistence of different wing forms within a population may depend on interaction of genetic and environmental factors, and it is difficult, if not impossible, to distinguish between wing polymorphism (genetic) and polyphenism (environmental). Both genetic and environmental effects have been known in Gryllinae, Nemobiinae and Trigonidiinae (Masaki and Walker 1987), and suggest that wing reduction is possible without elimination of the genetic background for macropterous development.

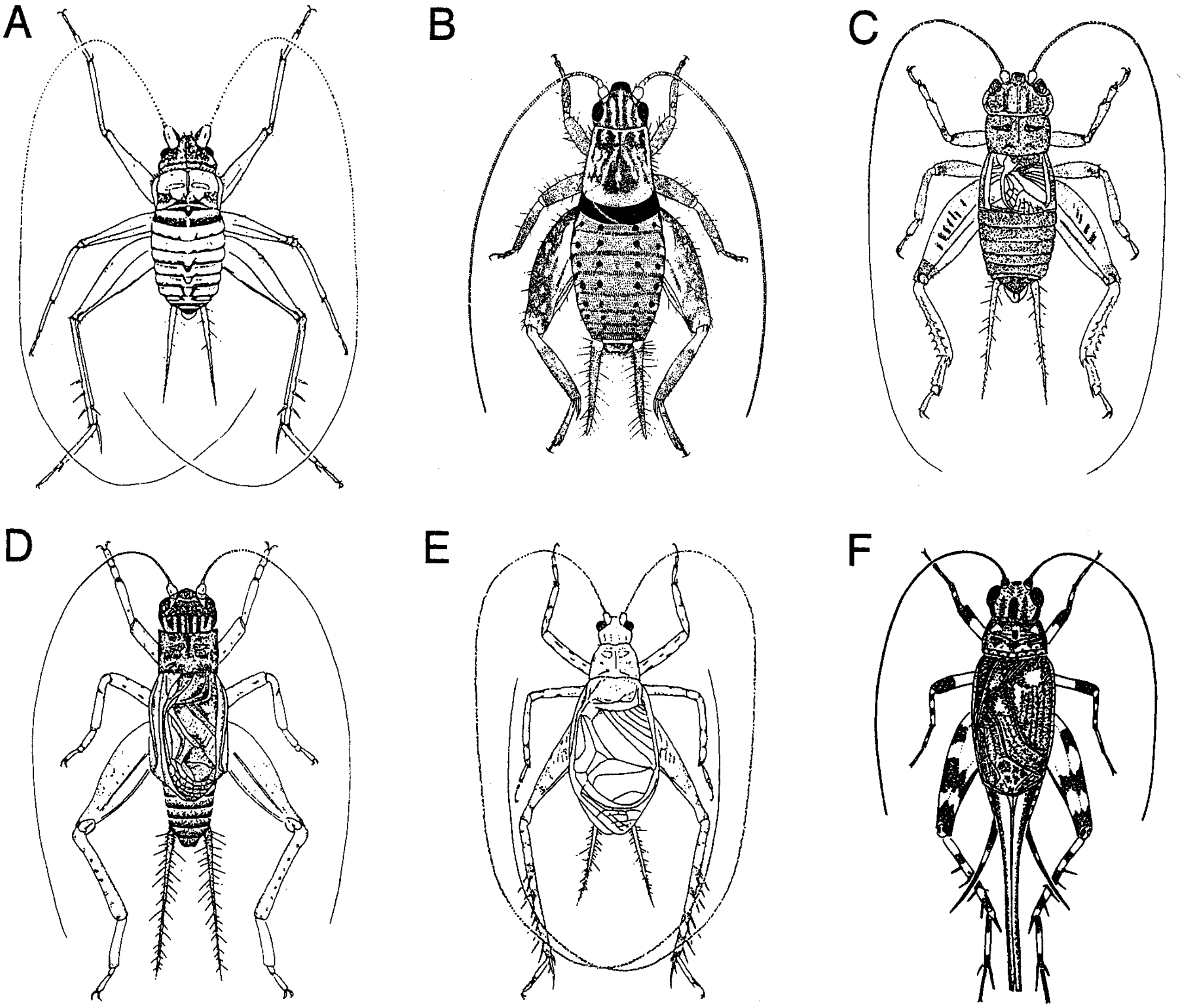

Fig. 1. Examples of various wing forms in Japanese crickets. A, *Parapteronemobius takarai*, Nemobiinae (from Ôshiro 1990a); B, *Tubarama iriomotejimana*, Mogoplistinae (from Yamasaki 1985); C, *Duolandrevus yaeyamensis*, Pteroplistinae (from Ôshiro 1988); D, *Velarifictorus ryukyuensis*, Gryllinae (from Ôshiro 1990b); E, *Phaloria ryukyuensis*, Eneopterinae (from Ôshiro 1985); F, *Dianemobius fascipes*, Nemobiinae. (Not to scale)

In Mogoplistinae, the females are entirely apterous while the males retain very small forewings with only acoustic function. A special sex-linked system must have evolved for the differential control of wing morphogenesis between the sexes under the selection pressure imposed by the mating success of stridulating males. In mute species, wing reduction can reach the extreme state in both sexes. Examples are *Goniogryllus sexspinosus*, inhabiting litters on forest floor (Ichikawa 1987), *Parapteronemobius sazanami* and related shore crickets (Furukawa 1970; Ôshiro 1986, 1990a, c), cavernicolous *Caconemobius* species (Gurney and Rentz 1978) and ant-nest crickets *Myrmecophilus sapporoensis* and related species.

It is clear that the characteristic acoustic behaviour of crickets constrains the evolutionary reduction of their wings. Some species were successful to overcome the constraint, but others stayed at a certain compromising state. So far as the forewings persist as a sound producing organ, the female also has to retain them or evolve a special sex-linked system to suppress wing development. Morphogenetic correlations between the fore- and hindwings might be another constraining factor. In wing dimorphic crickets, the female forewing length is clearly shorter in the micropterous than in the macropterous form (Shimizu and Masaki 1993b).

Various selecting forces might be involved in the wing reduction as extensively surveyed by Roff (1990b). Hindwing reduction in crickets was probably triggered as they shifted their life style from arboreal to terrestrial in the Permian. In Japan, as in North America (Alexander 1968; Walker and Sivinski 1986), wing reduction may be more common among crickets found in more stable habitats such as forests and rocky seashore than among those in pioneer associations such as grassland or abandoned fields. However, this tendency can not be confirmed because of the small number of cricket species in Japan. It is not easy, moreover, to determine which of the two factors, the habitat permanency itself or the behavioural characteristic of the species is more important. For example, bark crickets of *Duolandrevus* and several other related genera are all micropterous (Otte 1988), but together with their flat body, the wing reduction may be an adaptation to living in crevices under bark. The apterous forest cricket, *Goniogryllus sexspinosus*, is strictly nocturnal, and burrows into the leaf litter during the daytime (Ichikawa 1987). The loss of wings might be favoured by this behaviour as well as by the stable habitat conditions.

For those species living on tall herbs or trees, flight is a highly efficient means of movement from a plant stem or twig to another, avoiding a long up-and-down surface trip. Thus, tree crickets (Oecanthinae) are all macropterous. In contrast, Mogoplistinae commonly living in bushes and trees are flightless as mentioned above. Since some members of this subfamily such as *Tubarama iriomotejimana* (Fig. 1B) live in forest leaf litters, the possibility is not excluded that this subfamily became flightless before the present arboreal life, and the universal loss of flight ability might be ascribed to the phylogenetic constraint.

Phenotypically, wing reduction looks like a process of going down a hill, but it is probably creation of an elaborate genetic system to shut off the normal channel, or switch between the alternative channels, of wing development. It is not surprising therefore that an extremely micropterous form such as the female of *Gryllodes supplicans* may still retain a complete set of genes to form at least morphologically perfect wings. If macroptery is not expressed under the normal ecological conditions, it might escape from the force of natural selection and persist as a concealed genetic trait. Such a possibility is suggested also by *Chizuella bonneti* (Tettigoniidae). Although all the specimens collected in the field were micropterous with only rudimentary wings, a few macropterous adults appeared in the laboratory (T. Arai and M. Higaki, personal communication).

Wing polymorphism: Genetic variation

One of the strategies to cope with the fluctuating balance between the cost and benefit of functional wings is to mix fliers and non-fliers in optimal proportions. Wing dimorphism is thus not uncommon in crickets, and in most, if not all, of those cases the difference in wing form is at least partly based on genetic variation. Therefore, wing dimorphism not only poses an interesting problem of adaptation by itself, but also provides a clue to solve the problem of wing-form evolution.

Evidence for the genetic control of wing form may be obtained by comparing geographic populations of the same species with different frequencies of long- and short-winged adults under constant laboratory conditions. Such comparisons in *Dianemobius nigrofasciatus*, *D. fascipes*, *D. mikado* and *D. taprobanensis* (Masaki 1973, 1979; Masaki et al. 1987) indicated that the observed interpopulation variations are genetic. More compelling evidence is obtained by selection and cross breeding between various selected lines. Studies along this line were made in *Gryllus firmus* (Roff 1986a, 1990a), *G. rubens* (Walker 1987) and *D. fascipes* (Masaki and Seno 1990; Shimizu and Masaki 1993a). Heritability was estimated in *G. rubens* (Walker 1987), *G. firmus* (Roff 1986a, 1990a) and *D. fascipes* (Shimizu and Masaki 1993a).

In our experiments with *D. fascipes*, three lines designated as L, S, and C have been maintained for more than 40 generations over a period of about 10 years. The L line is selected for long-winged under a short daylength, the S line for short-winged under a long daylength, and the

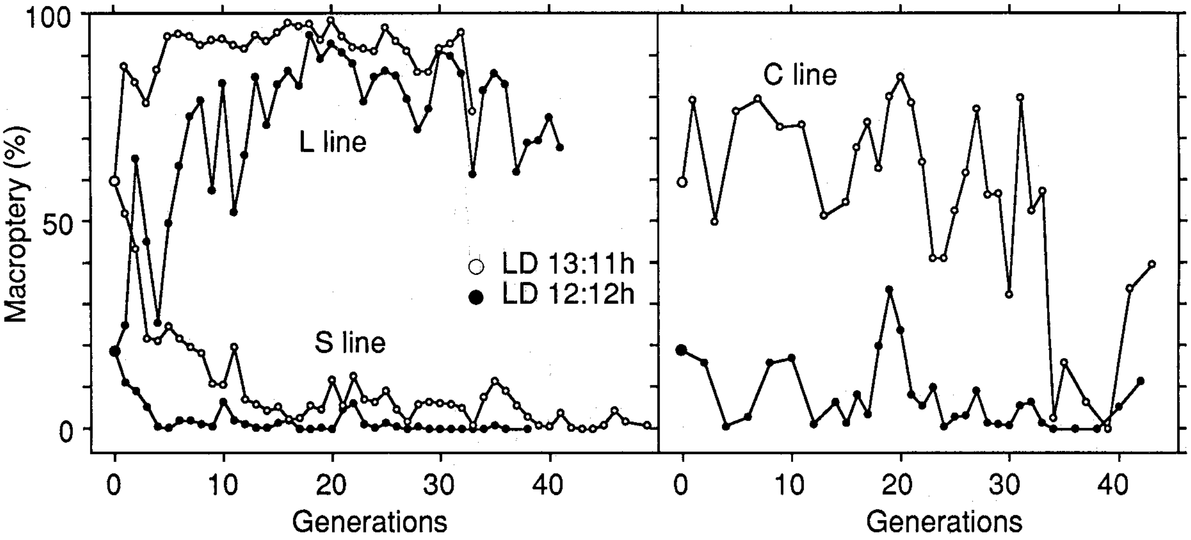

Fig. 2. Profiles of responses to selection over 40–50 generations for long-winged form under short photoperiod (L line) and short-winged form under long photoperiod (S line). Control (C line) was selected for short-winged under short photoperiod and long-winged under long photoperiod in alternate generations (Masaki and Seno 1990 and unpublished data).

C line for long-winged under a long daylength and for short-winged under a short daylength in alternate generations (Fig. 2; see the next section for the photoperiodic control of wing form). For unknown reason, the C line suffered bottle necks of population depression, which might have caused fluctuations in the percentage macroptery. The difference between the L and S lines was consistently maintained and the C line was generally intermediate between them. Despite the long-continued selection, however, neither the long-winged nor the short-winged crickets bred true. Similar situations were found in selection experiments with *Gryllus firmus* (Harrison 1979; Roff 1986) and *G. rubens* (Walker 1987). Roff (1994) simulated truncated selection of a threshold trait and showed that, when more than several loci were involved and the environmental variance (stochasticity) was maintained at a certain level, the selected form was hardly fixed within 20 generations.

Since the retrogressive evolution of wings took place in various lineages of crickets independently of one another (Table 1), it is not surprising that the genetic background for the wing-form determination is variable among different subfamilies and even different species of the same genus. Thus, the results of reciprocal crosses of long-wing and short-wing selected lines of *Gryllus rubens* indicated a primary or sole control by an *X*-chromosomal locus (Walker 1987), while crossing an isofemale line to the long-winged line implicated two alleles with dominance of the short-winged over the long-winged (Zera, cited by Walker 1987). In *Gryllus firmus*, on the other hand, there is no evidence for the *X*-linkage of wing-form alleles (Roff 1986a). The *X*-linkage may be masked by other determinants, depending on the genetic constitutions of the stocks used for crossing (Walker 1987).

We crossed in all possible combinations between the 11th generation of the L line and the 13th generation of the S line of *D. fascipes* (Fig. 3). The percentage macroptery among the progeny is generally proportional to the rate of the genes derived from the L lines (Masaki and Seno 1990). Probably, polygenes are involved. A partial

Table 1. Wing-form distribution among subfamilies of crickets in Japan (tentatively compiled from various sources and unpublished observations).

Subfamily[a]	Approx. no. of species	M	M′	m	A	M′–m	m–A
Gryllinae	25	+	+	+	+	+	+
Scleropterinae	1			+			
Pteroplistinae	3–4			+			
Oecanthinae	5	+					
Phalangopsinae	1		+				
Eneopterinae	10	+		+		?	
Nemobiinae	18			+	+	+	
Trigonidiinae	13	?		+		+	
Mogoplistinae	7						+
Myrmecophilinae	3				+		
Gryllotalpinae	1	+					

[a] As adopted by Alexander (1968).

M, macropterous, the hindwings extend beyond the forewings and are retained for life; M′, ditto but the hindwings are normally shed; m, micropterous; the hindwings are completely hidden beneath the forewings; A, apterous; M′–m, dimorphic, M′ and m occur in each sex; m–A, the male is micropterous and the female apterous.

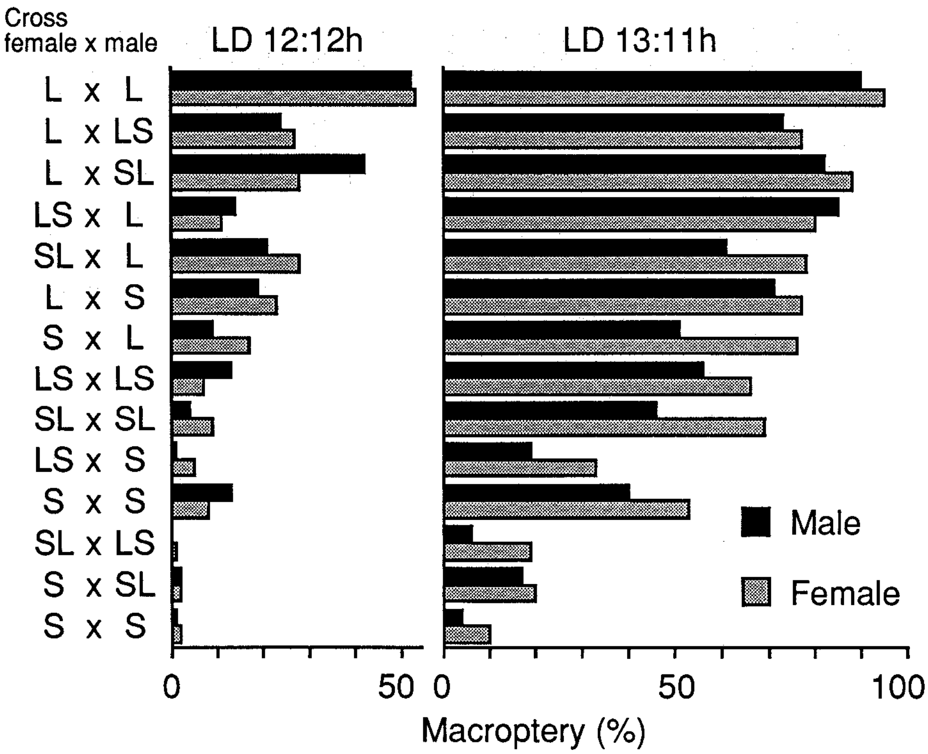

Fig. 3. Frequencies of macropterous adults in F_1 and F_2 produced by reciprocal crosses between the L and S lines and backcrosses under short-day (left) and long-day (right) conditions. Crosses are arranged in the descending order of gene doses derived from the L line (Masaki and Seno 1990).

maternal effect is indicated by the multiple regressions of the male (*Om*) and female (*Of*) offspring on the female (*Pf*) and male (*Pm*) parents. Thus,

$$Om=0.64\ Pf+0.35\ Pm-7.02\ (R^2=0.87),$$

$$Of=0.61\ Pf+0.41\ Pm-4.24\ (R^2=0.87).$$

The partial regression coefficient on the female parent is consistently larger than that on the male parent. The involvement of an *X*-chromosomal locus was indicated by the results of reciprocal crosses that gave similar frequencies of macroptery in the female progeny but clearly different frequencies in the male progeny (Fig. 3; see also Shimizu and Masaki 1993a). Wing-form determination may not be a simple process, comprising many component responses each of which is controlled by a unique set of genes.

Wing polyphenism: Response to environmental factors

Although wing form may ultimately be determined by genes in most wing dimorphic species of crickets, it can be controlled by various environmental factors such as rearing density (McFarlane 1966; Saeki 1966a; Nakamura 1968; Arai 1978a, b; Zera and Tiebel 1988; Shimizu and Masaki 1993a), nutrition (McFarlane 1964), temperature (Arai 1978a; Nakamura 1968; McFarlane 1962; Shimizu and Masaki 1993a), photoperiod (Masaki and Oyama 1963; Saeki 1966b; Mathad and McFarlane 1968; Masaki 1973, 1979; Tanaka 1976, 1978, 1986a; Tanaka et al. 1976; Arai 1978a; Masaki and Watari 1989; Masaki and Sugahara 1992; Shimizu and Masaki 1993a) and stresses (Shimizu and Masaki 1993b). Environmental cues signalling habitat deterioration (crowding) or the favourable season for flying activities (long daylengths) induce macropterous development. However, the responses to these factors vary from species to species or from population to population probably according to the characteristics of the life style and habitat conditions. Thus, *Gryllus rubens* tends to be brachypterous under crowded and macropterous under isolated conditions (Zera 1988), although the reverse is true in most other species such as *Gryllodes supplicans* (Arai 1978b), *Velarifictorus micado* (Saeki 1966a) and nemobiine species (Shimizu and Masaki 1993a). These opposite responses suggest that crowding can act as a token stimulus like photoperiod, and it does not directly affect the process of wing morphogenesis.

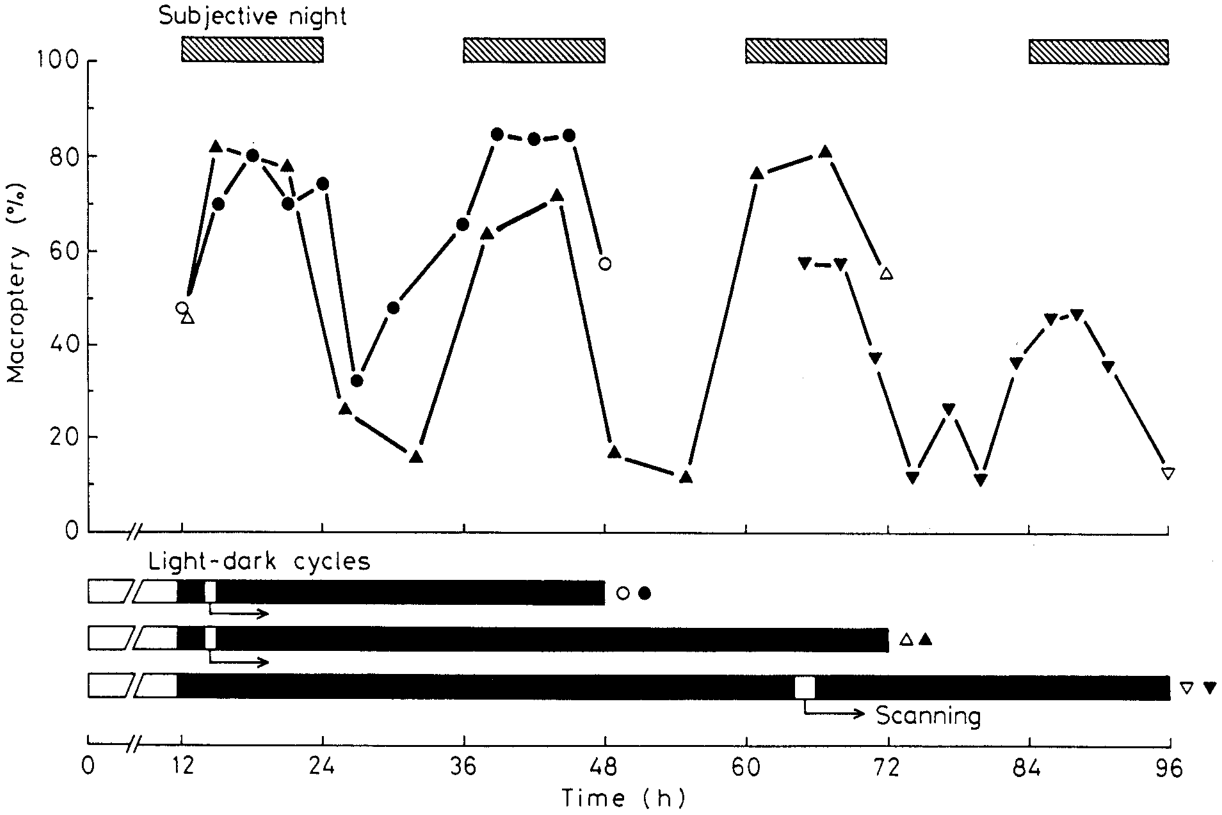

Fig. 4. Circadian periodicity in the wing-form response to photoperiod in *Dianemobius fascipes* as revealed by Bünsow protocols. A light period of 12 h was followed by 36, 60 or 84 h dark periods, which were systematically interrupted by 1 h light pulse at various times (horizontal axis) after lights-off (Masaki et al. 1992).

Photoperiod is the most reliable seasonal cue as evidenced by its universal influence on diapause programming in insects (Danks 1987). The consistent wing-form responses to photoperiod among various species of crickets might be consequences of natural selection for microptery in the cool short-day season that is less favourable than the warm long-day season for flying, particularly nocturnal, activities. The photoperiodic control of wing form in *D. fascipes*, *D. nigrofasciatus*, *D. mikado*, *D. taprobanensis* and *Pteronemobius nitidus* is very similar to that of diapause induction in various species of arthropods, and the clearly defined critical photoperiod is based on the photoperiodic time-measuring system in both responses (Fig. 6C).

The kinetics of the wing-form "photoperiodic clock" has been analyzed by means of special light-dark cycles known as Bünsow and Nanda-Hamner protocols. The results are very similar to those of the diapause "photoperiodic clocks", suggesting the involvement of a circadian system in both cases (Fig. 4; Masaki and Watari 1989; Masaki et al. 1992). More data in other species should be accumulated before making any generalization, but the clear effect of photoperiod on wing-form determination implies that wing polyphenism at least in some species of crickets has evolved as a component of seasonal adaptation.

Variation within a population

Intrapopulation variation provides a starting point for the response to selection, and thus may lead to divergence in adaptation. Assessment of intrapopulation variation is therefore important in understanding the wing-form evolution.

For this purpose, we isolated 24 full-sib families in the second laboratory generation of *Dianemobius fascipes* originated from Ishigaki Island (24°N in the Ryûkyûs) and determined the percentage macroptery over a range of ecologically meaningful photoperiods (11–14 h). They showed a large variation in percentage macroptery as represented by the height of photoperiodic response curves of individual families (Fig. 5; Shimizu and Masaki 1993a). The variability somewhat decreased in the next inbred generation, but the regression of the offspring on parent was clear and the heritability (h^2) was as high as 0.7

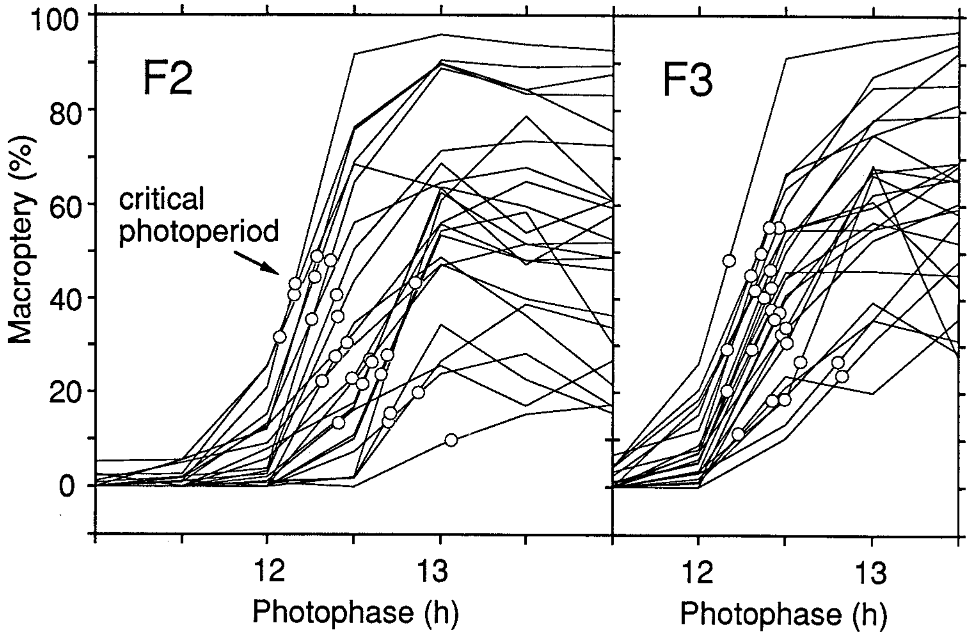

Fig. 5. Photoperiodic responses of 24 full-sib families of *Dianemobius fascipes* in the 2nd and 3rd laboratory generations under 28°C and crowded conditions. Circles indicate the critical photoperiod defined as the midpoint photoperiod between the upper and lower saturation levels of percentage macroptery (Shimizu and Masaki 1993a).

at a photoperiod of 13 h or longer. At photoperiods shorter than the critical length (12.5 h), the heritability tended to be smaller and decreased to about 0.3 at a short photoperiod of 11.5 h.

Since short photoperiod suppressed macroptery, it is natural that the variance among the families was more clearly expressed in a longer photoperiod that enhanced macroptery. The critical photoperiod varied with the height of the response curve, if we defined it to be the photoperiod corresponding to the mid point between the upper and lower saturation levels of macroptery. The heritability of the critical photoperiod thus defined was 0.48.

Interaction between polymorphism and polyphenism

Although the three selected lines L, S, and C of *Dianemobius fascipes* (see Fig. 2) are clearly different in the incidence of long-winged adults, they showed basically similar patterns of the photoperiodic response, i.e., macroptery was relatively suppressed by the short photoperiods between 6 and 12 h and enhanced by the longer photoperiods (Fig. 6; Shimizu and Masaki 1993a). Thus, the photoperiodic polyphenism is still manifested after about 20 generations of selection. However, the response amplitude varied greatly among the three lines. The responsiveness to photoperiod was remarkably lowered from the original high level in both the L and S lines but generally maintained in the C lines. Therefore, the response curves represent the interaction between polymorphism and polyphenism.

This interaction can be interpreted by the threshold response model (Falconer 1989). In this model, the propensity to be short-winged (or long-winged) is a quantitative character, and it is determined by both genetic

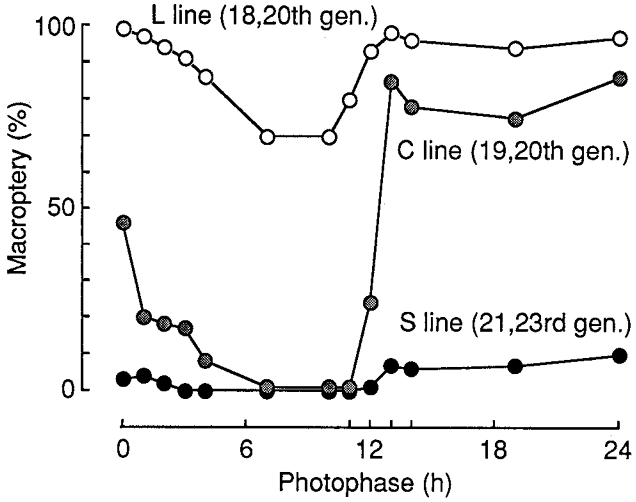

Fig. 6. Photoperiodic response curves of the L, S, and C lines (see Fig. 2) under 28°C and crowded conditions (Shimizu and Masaki 1993a).

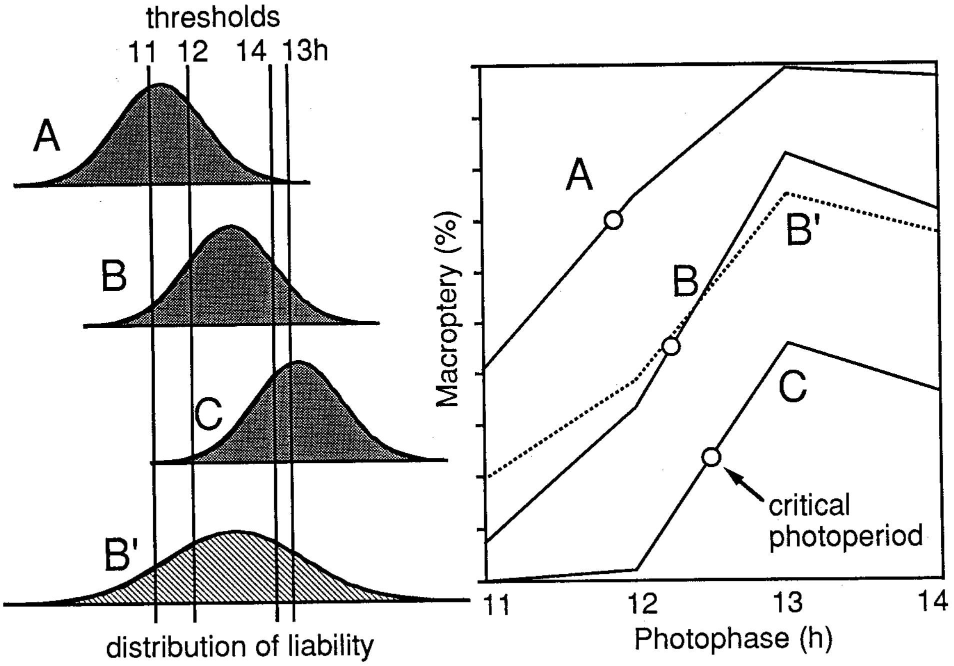

Fig. 7. Threshold response model for the photoperiodic and genetic determination of wing form in *Dianemobius fascipes*. The continuously distributed propensity for macroptery (or microptery) is genetically and photoperiodically determined. A threshold divides the population into the two dichotomous wing forms. In this panel, the photoperiodically induced change in propensity is expressed by shifting the threshold lines for different photoperiods. These propensity distributions in relation to the threshold give photoperiodic response curves as shown in the right panel (Shimizu and Masaki 1993a).

and environmental factors. Individuals with propensity values exceeding the threshold would be short-winged (or long-winged) and the rest long-winged (or short-winged). Given certain environmental conditions (photoperiod, temperature, density, etc.) that set the threshold at a certain point in the propensity distribution, the population would be wing polymorphic. With a shift of environmental conditions, the distribution of propensity varies and results in changed frequencies of the two wing forms—a situation regarded as polyphenism. Selection for a particular wing phenotype shifts the propensity distribution and accordingly modifies the photoperiodic response curve at least within the ecologically significant range of photoperiod (Fig. 7, right panel).

Photoperiodic response in general is a threshold response and the response curve around the critical point represents the cumulative distribution of individual critical photoperiods. In *D. fascipes*, however, we have as yet no evidence for any genetic correlation between the photoperiodic threshold and the wing-form propensity. Although the selection resulted in a large difference in percentage macroptery between the L and S lines and also in responsiveness to photoperiod between the C and L or S lines, the shift from the lower to the upper saturation levels of long-winged frequency occurred only within a very narrow range of photoperiod between 11 and 13 h, within which, however, the critical photoperiod decreased as the percentage macroptery increased by selection. The basic pattern of the photoperiodic response was thus retained.

In order to shift the critical photoperiod, a special selection scheme is necessary, in which long-wing selection in a long photoperiod is alternated with short-wing selection in a short photoperiod. Under such conditions, the selected line would be expected to acquire a critical photoperiod between these two photoperiods. By choosing the two photoperiods in this selection scheme, one may increase or decrease the critical photoperiod. Contrary to the clear response to selection for wing forms, the effect of this selection scheme was limited. We could shorten the critical photoperiod slightly but failed to lengthen it (Shimizu and Masaki 1993a). Thus, our wing-form selection made little change in the time-measuring system underlying the photoperiodic response.

Since photoperiod is the most reliable seasonal cue and exerts a dramatic effect on the wing-form determination, it is one of the important factors in the evolution of wing dimorphism. How was the photoperiodic time measuring system coupled with the wing dimorphism? To answer this question should be crucial step to understand the evolution of wing dimorphism.

Acknowledgments: We sincerely thank Y. Ôshiro for Figs. 1A, C, D, E, and T. Yamasaki for Fig. 1B; the Entomological Society of Japan, the Japanese Society of Systematic Zoology, and the Kyoto Entomological Society for permission to reproduce these figures; anonymous reviewers for improvements; and F. Nakasuji for giving us impetus to write this paper. Experimental works described in this paper were partly supported by a grant (03660037) from the Ministry of Education, Science and Culture, Japan. This is contribution No. 127 from the Laboratory of Entomology, Hirosaki University.

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Received 4 November 1994; Accepted 1 March 1995