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Environmental and Genetic Control of Wing Morph Determination in Three Subtropical Populations of a Cricket, *Modicogryllus confirmatus* (Orthoptera: Gryllidae)

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Abstract The effects of photoperiod and temperature on the relative frequency of short-winged (SW) and long-winged (LW) morphs of a cricket, *Modicogryllus confirmatus* WALKER, were examined in three subtropical populations (Naha: 26.1°N; Yonaguni: 24.3°N and Ishigaki: 24.2°N) from Okinawa Prefecture, Japan. The genetic basis of wing morph determination was also studied by crossing different wing morphs of crickets recently collected or selected over 30 generations with respect to wing length. The frequency of SW adults was relatively high at a short photoperiod (12L–12D) and low at longer photoperiods (13L–11D to 16L–8D) in the Naha and Yonaguni populations. Photoperiod did not influence wing morph determination in the Ishigaki population. No significant difference was observed in the frequency of SW adults between 25°C and 30°C in any population. The three populations showed geographic variation in wing morph; the frequency of SW individuals under short-day conditions tended to be higher as the latitude increased. After mass selection over 10 generations the frequency of SW adults in a SW selected line increased substantially, whereas it remained at a low level in a LW selected line. Crossing experiments indicated that wing morph was under polygenetic control. Based on these results, we discuss the evolutionary significance of wing dimorphism in this subtropical insect.

Key words: Wing dimorphism, photoperiod, temperature, genetic control, *Modicogryllus confirmatus*.

Introduction

Many species of crickets show wing dimorphism. Generally, long-winged (LW) crickets with well-developed hind wings can fly, whereas short-winged (SW) crickets can not because their wings and flight muscles are reduced. It is often suggested that different wing morphs of insects show different physiological states associated with reproduction; LW individuals are migrants and SW ones sedentary, rapid reproducers (JOHNSON, 1969; HARRISON, 1980; DINGLE, 1985; ROFF, 1990; FUJISAKI, 1994). Therefore, whether an insect develops to a LW

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morph or a SW morph is an important issue on survivorship and reproduction.

Wing polymorphism is also common in other insects including grasshoppers, beetles, flies, thrips, ants, termites, moths, psocids, earwigs, cockroaches, aphids, bugs and planthoppers (FUJISAKI, 1994). In crickets, the environmental factors influencing wing dimorphism include crowding, photoperiod, temperature and food quality (ALEXANDER, 1968; MASAKI & WALKER, 1987; TANAKA, 1993b). In particular, photoperiod (daylength) that changes with an exact rule throughout the year appears to be important. In several species of crickets, wing morph is influenced by changes in photoperiod (MASAKI & OYAMA, 1963; ISMAIL & FUZEAU-BRAESH, 1976; TANAKA, 1978, 1979; TANAKA *et al.* 1976). In many wing-dimorphic species, the occurrence of LW individuals is usually favored by long days which are associated with warm seasons, although the pattern of response to photoperiod may slightly vary among species (MASAKI, 1972, 1979; MASAKI & WALKER, 1987).

Wing morph may be under the control of one-locus with two-alleles or polygene systems (ROFF, 1986). One-locus with two-alleles is prevalent in beetles but wing morph in other insects is mainly controlled by a polygene system. In crickets, *Gryllus rubens* (ZERA & RANKIN, 1989) and *Dianemobius fascipes* (MASAKI & SENO, 1990; SHIMIZU & MASAKI, 1993a), wing morph is under polygenetic control, but a relatively few species have been studied on the genetic control of wing morph determination.

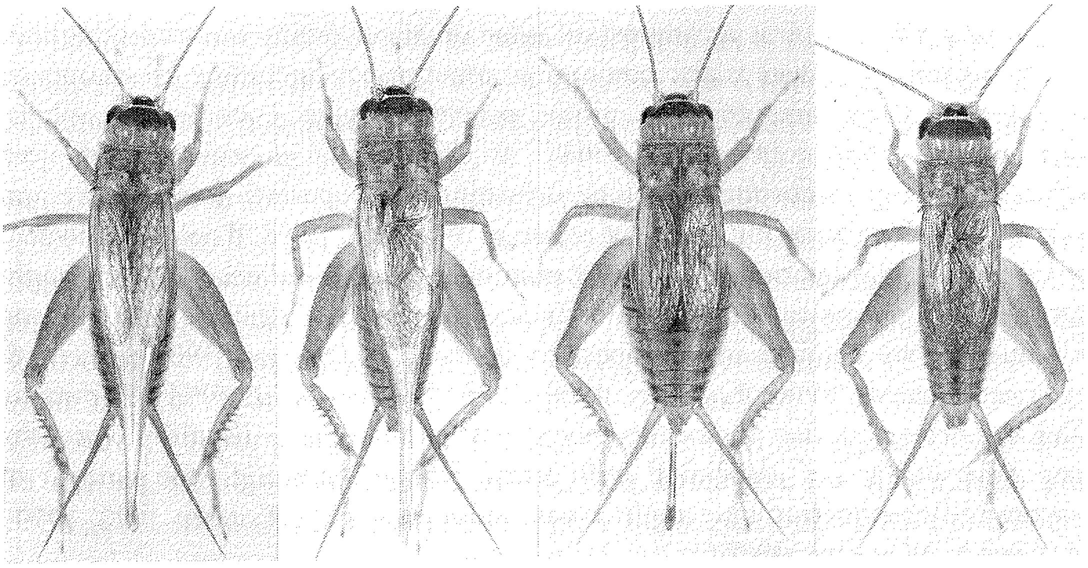
In this study we examined the environmental and genetic factors controlling wing morph determination in a cricket, *Modicogryllus confirmatus* WALKER. Three geographical populations derived from different subtropical islands were exposed to various photoperiods and temperatures, and the proportion of the two wing morphs was compared among the three populations. To understand the genetic basis for wing morph determination, selection was carried out for different wing morphs over successive generations. Crosses were also made between different wing morphs using a recently established laboratory colony as well as nearly true bred lines with respect to wing morph. Based on these results, we discuss the evolutionary significance of wing morph in *M. confirmatus.*

Materials and Methods

Insects

LW and SW adults of *M. confirmatus* are shown in Fig. 1. Adults and nymphs were collected on 3 islands, Okinawa Is., Yonaguni Is. and Ishigaki Is. in Okinawa Prefecture in November, 1993 (Table 1). These localities will be designated as NAH, YON and ISH, respectively. The offspring of field-collected crickets were used for experiments.

Groups of 50–70 nymphs were reared in plastic containers (diameter 15 cm;



Long-winged Short-winged

Fig. 1. LW (left) and SW (right) pairs of *M. confirmatus*. In each pair, the left specimen is female and the right one male.

Table 1. Locations and mean air temperatures recorded between 1951 and 1980 at the collection sites.

Locality	Latitude (°N)	Longitude (°E)	Mean temperature* (°C)		
			Mean	Minimum	Maximum
Naha (NAH)	26°14′	127°41′	22.4 (16.0–28.1)**	20.1 (13.7–25.6)**	25.1 (18.6–31.0)**
Yonaguni (YON)	24°28′	123°01′	23.4 (17.7–28.5)	21.5 (15.4–26.9)	25.8 (19.8–31.7)
Ishigaki (ISH)	24°20′	124°10′	23.8 (17.7–29.1)	21.5 (15.8–26.3)	26.6 (20.5–32.0)

* Based on monthly average temperatures (Junior Asahi Nenkan, 1989).
** Range.

height 9 cm). Upon reaching the final nymphal instar, they were transferred to bigger containers (20×35×26 cm) in order to remove the newly emerged adults from the containers easily. They were constantly provided with food (Insect pellets, Oriental Yeast Industry Co.) and water supplied in a plastic vial plugged with cotton. Eggs were laid into the cotton plugs. Hatchlings were obtained for experiments by incubating eggs in cotton plugs at 30°C.

Effects of photoperiod and temperature on wing morph

Nymphs of the first laboratory generation were exposed to 12L–12D, 14L–

10D or 16L–8D at 30°C, while at 25°C they were maintained at 12L–12D, 13L–11D, 14L–10D, 15L–9D or 16L–8D. At 30°C, the three populations were examined in two trials. Because the two trials produced similar results, we will present the date for the first trial. At 25°C, two populations from YON and NAH were tested in one trial using nymphs of the first laboratory generation. The number of adults obtained in each experimental regime varied from 50 to 150, and the data were analyzed by χ^2-test.

Selection and crossing

All experiments were carried out at 30°C and 14L–10D. Individuals of the NAH population were selected for SW (S-line) and LW morphs (L-line) up to 10 successive generations. In each generation, about 100 adults were obtained for each line.

Crosses were made between individuals of the same or different wing morphs using the first laboratory unselected colony of the NAH population. In each cross type, 5 pairs of a female and a male adult were separately crossed, and 314–1300 progenies were obtained for each pair.

Laboratory cultures originally derived from Iriomote Island (24°20′) were selected for each wing morph over 30 generations. The frequency of SW morphs was more than 98% in the SW selected line (S-line) and less than 5% in the LW selected line (L-line). We conducted reciprocal crosses between different wing morphs. To express crossing combinations, we list the female parent first and use L and S to designate LW and SW morphs, respectively. Backcrosses were also made between progenies of L×S and those of the S-line or L-line, i.e. L×L(LS), L(LS)×L, L×S(LS), S(LS)×L, S×S(LS) and S(LS)×S. Usually 5 pairs were used in each cross type, but in the case of backcross to S-line crickets, mass breeding of about 20 pairs was adopted. The number of progenies used ranged from 800 to 1300 in the former, and from 100 to 200 in the latter. The data obtained were arc-sine transformed and tested by Tukey multiple comparisons (Systat).

Results

Effects of photoperiod and temperature

Figure 2 compares the frequencies of SW adults of *M. confirmatus* obtained at different photoperiods and 30°C in three populations. In the ISH population, only a few SW adults occurred and photoperiod did not influence the frequency significantly ($\chi^2=2.20$; df=2; $P>0.05$). In the YON and NAH populations, on the other hand, the frequency of SW adults varied among the three photoperiods (YON, $\chi^2=33.27$; df=2; $P<0.01$; NAH, $\chi^2=29.38$; df=2; $P<0.01$). In these two populations, it was relatively high at 12L–12D and low at 14L–10D and

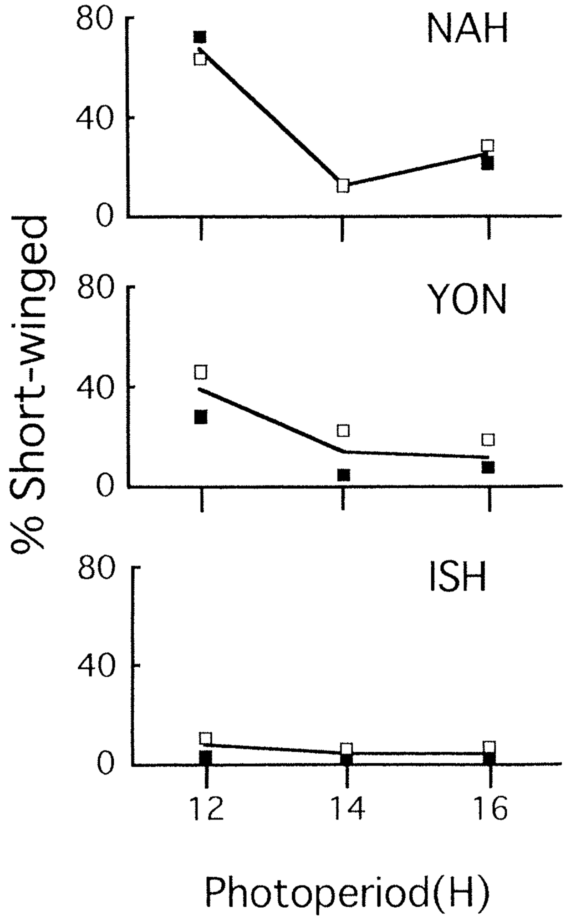


Fig. 2. Effect of photoperiods on wing morph in the Naha (NAH), Yonaguni (YON) and Ishigaki (ISH) populations of *M. confirmatus* at 30°C. Closed squares indicate females and opened ones males.

16L–8D. A highly significant inter-population difference was observed in the frequency of SW morphs at 12L–12D ($\chi^2=60.14$; df=2; $P<0.01$) and 16L–8D ($\chi^2=17.64$; df=2; $P<0.01$), and a less significant difference at 14L–10D ($\chi^2=8.99$; df=2; $0.05>P>0.01$). These results indicated that both photoperiod and locality influenced wing morph in this species.

Figure 3 illustrates the results at 25°C in the YON and NAH populations. The pattern of response to photoperiod was basically the same between 30°C (Fig. 2) and this temperature in either population. Temperature had no significant influence on the frequency of SW adults at any photoperiod in either population except at 14L–10D in the YON population ($\chi^2=15.39$; df=1; $P<0.01$). The photoperiod at which 50% of the adults became SW fell between 12L–12D and 13L–11D in the NAH population but close to 12L–12D in the YON population.

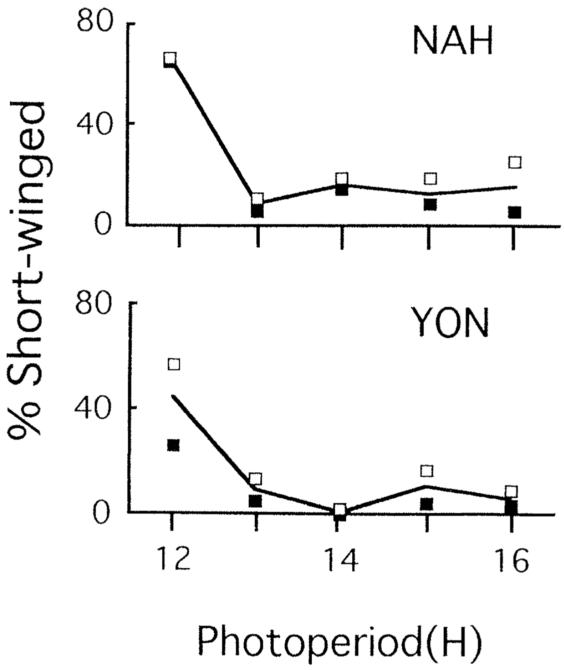


Fig. 3. Effect of photoperiods on wing morph in the Yonaguni (YON) and Naha (NAH) populations of *M. confirmatus* at 25°C. Closed squares indicate females and opened ones males.

Selection and crossing

After selecting over 10 generations for SW morphs, the relative frequency of SW morphs was greatly changed (Fig. 4). It was about 23% in the first generation, increased gradually over the following 5 generations and levelled off. In the LW selected line (L-line), on the other hand, the frequency of SW morphs was very low even in the first generation, and remained at low levels in the following generations.

To understand the genetic basis for wing morph determination, reciprocal crosses were made between SW and LW adults of the first NAH laboratory unselected generation, and the results were compared with those of crossing between the same wing morphs. As expected from the results of the mass selection experiment (Fig. 4), the frequency of SW morphs was greatly influenced by the wing morph of their parents (Fig. 5). It was significantly higher in the offspring of S×S than in those of L×L in both females and males (Tukey multiple comparison; $P<0.05$). In reciprocal crosses, the frequencies were intermediate between L×L and S×S. The mean frequency of SW morphs was higher in S×L than in L×S, though the variance was so large that the difference was not statistically significant at 5% level in either sex (Tukey multiple comparison; $P=0.063$ in female; $P=0.247$ in male).

To determine if there is a maternal effect on wing morph determination in

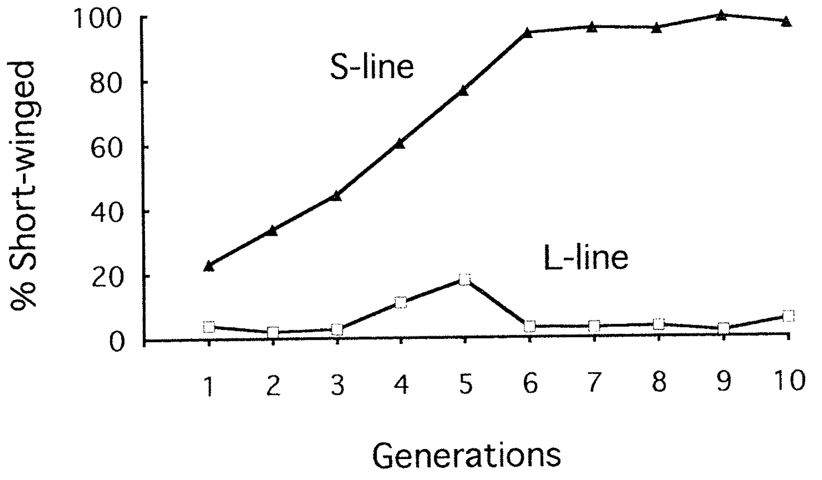


Fig. 4. Changes in frequencies of SW phenotypes in progenies of mass selected Naha lines of *M. confirmatus*. Selection was made in each generation for SW morphs (S-line) and LW morphs (L-line).

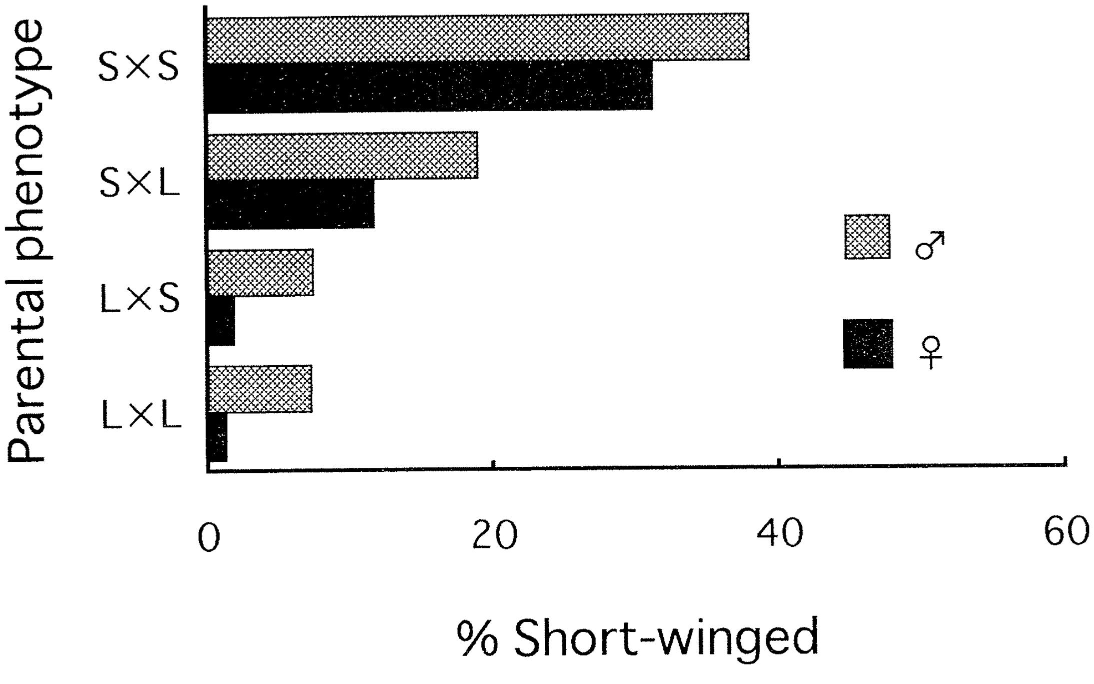


Fig. 5. Mean frequency of SW phenotypes in progenies of various crosses in *M. confirmatus*. SW (S) and LW adults (L) of the first laboratory unselected generation of the Naha population were crossed at 14L–10D and 30°C. In each cross, the female parent is listed first.

this species, reciprocal crosses as well as backcrosses were carried out between SW and LW adults of two genetic lines (S- and L-line) in which selection had been made for SW and LW individuals, respectively, over 30 generations after their founders were collected on Iriomote Island. As shown in Fig. 6, the results were more or less proportional to the relative amounts of genetic material derived from the L- and S-lines. Thus, no significant maternal effect was detected in any combination of crosses including L×L vs L×S, S(LS)×L vs. L×S(LS), and L(LS)×L vs L×L(LS) (Tukey multiple comparisons; $P > 0.05$). This

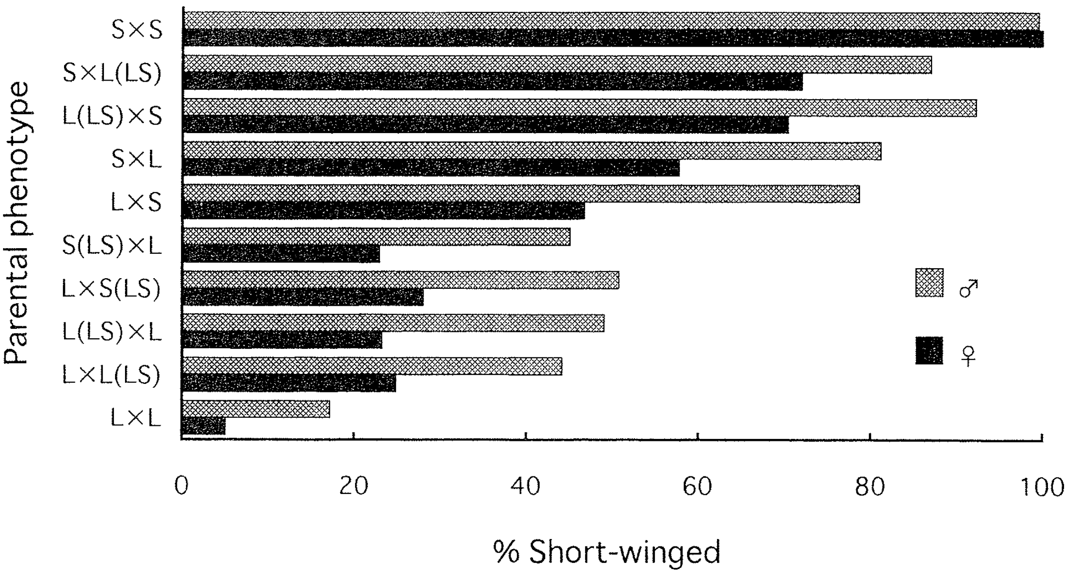


Fig. 6. Mean frequency of SW phenotypes in progenies of various crosses in *M. confirmatus*. SW (S) and LW (L) adults were obtained from laboratory lines of the Iriomote population in which wing morph had been continuously mass-selected over 30 generations, and crossed at 14L–10D and 30°C. In each cross, the female parent is listed first. For backcrosses, L(LS) means LW F_1 individuals obtained from L×S, and S(LS) SW F_1 individuals obtained from L×S.

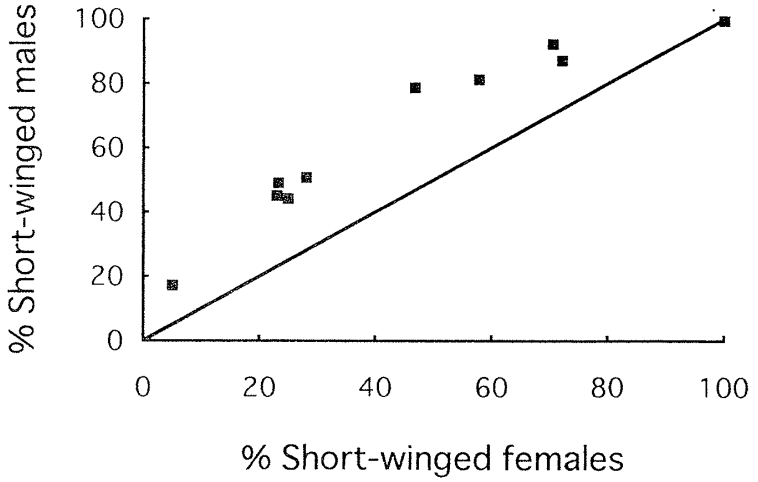


Fig. 7. Relationship between the frequencies of wing morphs of the two sexes in *M. confirmatus*. The line shows $Y=X$. Data are derived from Fig. 6.

result indicates that no significant maternal effect exists in wing morph determination of this species. In almost all crosses, the SW morph was more common in males than in females, and a significant correlation was obtained in the frequency of SW morphs between the two sexes (Fig. 7; $r=0.954$; $df=9$; $P<0.01$). This indicated that some sex-linked factor is involved in wing morph determination.

Discussion

The present results suggested that photoperiod plays an important role in wing morph determination of *M. confirmatus*, as reported for other species including crickets, bugs, aphids and moths (JOHNSON, 1969; HARRISON, 1980; BECK, 1980; SAUNDERS, 1982; TAUBER *et al*., 1986; DANKS, 1987). Because nymphs of this cricket enter diapause under short day conditions, i.e. 12L–12D (Y. SUZUKI & S. TANAKA, unpubl.), we thought that there would be a close relationship between nymphal development and wing morph. For example, most individuals of *G. campestris* become SW adults if they experience nymphal diapause, whereas most of them emerge as LW adults if grown under diapause-averting conditions (ISMAIL & FUZEAU-BRAESH, 1976). A similar relationship has been reported in *Pteronemobius nitidus* (TANAKA, 1978) and was obtained in the NAH and YON populations of *M. confirmatus*. In the ISH population of the latter species, however, the frequency of SW morphs was relatively low at any photoperiod, although nymphal diapause was induced by a short photoperiod. Therefore, wing morph and nymphal diapause are not correlated perfectly in this cricket.

Temperature does not appear to be important in the control of wing morph in *M. confirmatus*. However, as the range of temperature used in the present study was relatively high, there is a possibility that lower temperatures may affect wing morph. Crowding decreases the frequency of SW individuals in other crickets including *Gryllodes supplicans* (MCFARLANE, 1966; ARAI, 1978a, b), *Velarifictorus micado* (SAEKI, 1966) and *P. nitidus* (TANAKA, 1979) and increases it in *G. rubens* (ZERA & TIEBEL, 1988). In *M. confirmatus*, crowding does not play a role in wing morph determination (TANAKA, 1994b). Nothing is known about the importance of food in wing morph determination of this species except that starvation during the last nymphal instar has no influence on the wing morph (S. TANAKA, unpubl.).

In addition to these environmental factors, injury to appendages or wingpads is known to change the development pathway from the LW to the SW morph in *Allonemobius fasciatus* (TANAKA, 1985) and *D. fascipes* (SHIMIZU & MASAKI, 1993b). The significance of such a phenomenon is not clear, but it is possible that crickets turning into SW adults may leave more offspring by initiating reproductive life early (TANAKA, 1976, 1986a, 1993a, 1994a, b). If injured individuals had developed to LW adults, they would be unable to use their flight ability, and thus waste their energy and time. Removal of a wing-pad during the penultimate or last nymphal instar was found also effective in inhibiting the formation of LW morph in *M. confirmatus*, but the details of the experimental results will be published elsewhere.

Wing morph determination of *M. confirmatus* is partly under genetic control. Several generations of mass selection for wing morphs produced lines in which most individuals were the selected morphs. In the L-line, the frequency of SW individuals was very low even in the first generations and remained at low levels in the following generations. In the S-line, on the other hand, the frequency of SW individuals increased during the first 6 generations and levelled off thereafter. As observed in other species of crickets (ZERA & RANKIN, 1989; MASAKI & SENO, 1990), no pure-bred lines were obtained through selection even after 10 generations in the NAH population and 30 generations in the Iriomote population of *M. confirmatus.* This fact may suggest that wing morph is controlled by a polygene system.

The above suggestion is supported by the results of reciprocal crosses and backcrosses. Reciprocal crosses between the two wing morphs produced intermediate frequencies of SW individuals between the values of the two homomorphic crosses. The frequency of SW phenotypes was nearly proportional to the amount of genetic material derived from the two selection lines. No significant maternal effect was observed in the present study, but the results of the reciprocal crosses showed a statistically insignificant, but consistent tendency that more SW individuals occurred when their mother was SW (Figs. 5 and 6). Because we used a small number of families for each type of crossing, we might have failed to detect a minor role played by the genes on the sex chromosomes. Nevertheless, there is no doubt that at least the majority of the genes regulating wing morph in this species are located on autosomes.

It is often argued that insects on small islands would tend to be flightless because flying individuals can be blown away easily, although available evidence appears to indicate no such a tendency (ROFF, 1990). In *M. confirmatus*, such a risk may not be important judging from the fact that the LW morph is predominant.

Although geographically closely located to one another, the three populations examined in this study showed variation in relative frequency of the two wing morphs in the laboratory. Geographic variation in wing morph has been studied for other species of crickets in the laboratory (MASAKI, 1972, 1979; MASAKI *et al.*, 1987; MOUSSEAU & ROFF, 1989). The pattern of geographic variation appears to differ from one species to another. MOUSSEAU & ROFF (1989) found no relationship between the incidence of wing morphs and the geographic origin in '*A. fasciatus*'. In this case, however, the authors apparently used a mixture of at least two cryptic species, *A. fasciatus* and probably *A. socius*, judging from the studies by HOWARD (1986), HOWARD & FURTH (1986), and TANAKA (1991). Unfortunately, few studies examined the geographic profile of wing morph variation in field populations. In *A. fasciatus*, an increasing frequency of SW morphs in more northern populations has been reported based on rather small sample sizes (TANAKA, 1986b). In the present study with *M. confirmatus*, the frequency of SW morphs at 12L–12D tended to increase with latitude. As shown in Table 1, the difference in latitude between the northernmost and southernmost populations is less than 2 degrees, and the thermal environment is similar among these islands, particularly the southernmost two islands. It is thus surprising that the southernmost ISH population did not show a response to photoperiod for wing morph determination while a clear response was manifested in the other populations. There seem to be several explanations for this result. One is an artifact due to sampling error. However, to avoid such a possibility, we collected 30–50 females at each locality to start our laboratory colonies. All experiments testing the photoperiodic effect were carried out within 3 generations after they were brought to the laboratory. Therefore, we believe that the colonies we used represented the field populations well. A second possibility is that patches of habitat host small populations differing from one another with respect to wing morph determination on this island and we happened to collect our sample from a population producing a low incidence of short-winged morphs at any photoperiod. However, this species commonly occurs on this island and LW individuals are common. Therefore, movement of individuals between patches of habitat may not be a rare phenomenon, indicating that the above possibility is less likely. A third possibility is that the absence or obscurity of photoperiodic response for wing morph determination is a trait characteristic of the more southern populations including the ISH population. The pattern of this kind has been reported for *D. fascipes* (MASAKI, *et al*., 1987). Unfortunately, little information is available about the environmental control of wing morph of *M. confirmatus* from the adjacent islands.

From the patterns of response to photoperiod, it is possible that the frequency of wing morphs changes seasonally in the two northern populations. In March, 1991, more than 100 individuals were collected in Naha and most individuals were nymphs at various instars. Unfortunately, wing morph was not recorded for these individuals after adult emergence, but there is no doubt that the majority of this population overwinter as nymphs. Because such individuals experience short daylengths in the winter, the frequency of SW morphs in the spring would be low. The occurrence of SW morphs in the spring may be of selective advantage because flight activity is likely to be suppressed under relatively cool conditions. Furthermore, SW female adults of *M. confirmatus* start ovipositing earlier and produce more eggs during the early stage of adult life than LW female adults (TANAKA, 1993a), as observed in other crickets including *D. mikado* (formerly *P. taprobanensis*) (TANAKA, 1976), *A. fasciatus* (ROFF, 1984; TANAKA, 1986), and *G. rubens* (ZERA & RANKIN, 1989). By allocating the time and energy resources to reproduction rather than to migration (TANAKA, 1993a, 1994a, b), SW morphs would be more successful than LW morphs in the spring. Later in the season this species is exposed to longer daylengths, thus producing more LW morphs. Under warmer conditions, they can probably fly and find a new habitat more efficiently. In more southern areas, the spring would be warmer and more suitable for flight activity than in northern areas. This might be the reason why the Ishigaki population produces a low frequency of SW morph under any photoperiodic conditions. However, this hypothesis would require an explanation for the reason why the Yonaguni population with an almost identical thermal environment to that of the Ishigaki population (Table 1) displayed a relatively high frequency of SW morphs at 12L–12D. Further studies on the frequency of wing morphs on these and other islands will be required to evaluate these possibilities.

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