

Thank you very much,  
Seiji

## Developmental characteristics of two closely related species of *Allonemobius* and their hybrids

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**Summary.** Two species of ground crickets, *Allonemobius fasciatus* (from Corvallis, 44.3 N) and *A. socius* (from Gainesville, 30.3 N), and their hybrids were compared for nymphal development, wing form, and embryonic diapause. *A. fasciatus* matured more rapidly at a short photoperiod than at a long photoperiod and also than *A. socius* which showed no developmental response to photoperiod. The proportion of long-winged forms varied with nymphal photoperiod greatly in *A. fasciatus* but slightly in *A. socius*. *A. fasciatus* laid only diapause eggs, while *A. socius* responded to a long parental photoperiod and a high incubation temperature by averting diapause. *A. fasciatus* showed temperature-dependent shift of the diapause stage but *A. socius* entered diapause only at the early stage. These differences are related to their voltinism and distribution.

Reciprocal crosses between the two species produced viable hybrids. In development rate, female hybrids were intermediate between their parents while male hybrids were closer to their mothers, suggesting that the development rate is controlled primarily by the X chromosome. Overdominance occurred in wing form; reciprocal crosses produced either higher or lower proportions of long-winged forms than their parents. Diapause of F1 hybrid embryos was determined only by the female parent and the paternal effect appeared in F2 embryos.

*Allonemobius* species are widely distributed in North America (Blatchley 1920; Fulton 1931; Alexander and Thomas 1959; Alexander 1968a; Vickery and Johnstone 1973) and *A. fasciatus* is one of the most common. Fulton (1937) noted that in the eastern states this species consisted of several distinct races. Recently, Howard (1983), using electrophoretic techniques, demonstrated that the northern and southern populations of *A. fasciatus* differed genetically from each other enough to be considered as two species which he named *A. fasciatus* and *A. socius*, respectively. The two species are partly sympatric at around 38–40 N where hybrids occur (Howard 1982).

Although most studies with *A. fasciatus* have been done with eastern strains, this cricket also occurs in western parts of North America (Sarai 1967; Tanaka and Brookes 1983; Tanaka 1984). In both East and West it maintains a univoltine life cycle with an embryonic diapause.

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*A. socius* has been known only from eastern states. It is univoltine north of Richmond, Virginia, bivoltine from Richmond through South Carolina, and multivoltine in Florida (Howard 1982). Wherever it undergoes diapause, it does so in the embryonic stage.

In the present paper, I compare several physiological traits between a western strain of *A. fasciatus* and an eastern multivoltine strain of *A. socius* to understand the nature of life cycle differences, and use interspecific crosses to examine the genetic basis for these traits as well as the genetic compatibility between the two species.

### Materials and methods

#### *Experimental animals*

A colony of *A. fasciatus* originated from about 25 female adults collected in Corvallis, Oregon, in September, 1982. Because eggs of this species entered diapause (Tanaka 1984), they were usually chilled at 3°C for at least 3 months. Nymphs were obtained and reared according to the method of Tanaka and Brookes (1983). Groups of about 60 nymphs were reared in a 2-L jar with clean, dry sand covering the bottom to a depth of about 1 cm. They were fed on hamster pellets and slices of carrot with a continuous supply of water in a vial plugged with absorbent cotton. In the present study, nymphs were also provided with clover leaves once a week, which appeared to improve egg production. Because this species oviposited in dry sand, adults were maintained in a jar without sand and allowed to lay eggs into moist glass wool plugged in a vial.

A colony of *A. socius* was established with 12 female adults caught in Gainesville, Florida, in July, 1983, and maintained at LD 16:8 and 27°C. Under such conditions, the colony persisted over 3 generations without diapause.

Reciprocal crosses between the two species produced hybrid eggs. 10–20 females were crossed with 5–10 males of the other species. Eggs produced by *A. socius* females × *A. fasciatus* males hatched in 3 weeks at 27°C without diapause. However, those obtained from the reverse cross entered diapause and were kept at 16°C for 2 months before incubation at 27°C for hatching.

#### *Measurements of nymphal development*

The rates of nymphal development among the two species and their hybrids were compared at 30±1°C and LD

14:10. Because of the limited space available for the experiment, only one or two jars, each containing about 60 nymphs, were allotted to each species or each hybrid strain. Adults were removed from their jars daily, and wing form and nymphal development time were recorded. The photoperiodic responses were tested at  $27 \pm 1^\circ\text{C}$  with 3 different photoperiods, LD 12:12, 14:10, and 16:8, covering the range of daylengths in both Oregon and Florida (Beck 1980).

#### Determination of diapause

To examine the incidence of diapause, eggs obtained from each species and each F1 hybrid were placed on moist paper in petri dishes and incubated at  $30 \pm 1^\circ\text{C}$  or  $21 \pm 1.5^\circ\text{C}$ . Some *A. fasciatus* eggs may develop without diapause when laid by field-collected females in fall and incubated at high temperatures (Tanaka 1984). Such eggs hatched within 20 days at  $30^\circ\text{C}$  while those which entered diapause at the same temperature took much longer. Because a similar pattern of embryonic development was observed in *A. socius* (Tanaka, unpublished observations), eggs which hatched within 20 days at  $30^\circ\text{C}$  were regarded as non-diapause eggs, while those which hatched after this period or remained unhatched during the 90-day experimental period were considered as diapause eggs. Incubation at  $21^\circ\text{C}$  also induced a bimodal pattern of development in *A. socius*. In one group, eggs hatched within 55 days of incubation and, in the other, hatching started about 70 days after oviposition and occurred sporadically over a long period. The former were regarded as non-diapause eggs and the latter as diapause eggs. The same criterion was used for *A. fasciatus* and the hybrids to distinguish the two types of development at this temperature.

#### Determination of diapause stage

To compare the stage at which diapause occurs among embryos produced by the two species and their F1 hybrids, embryonic development was observed at  $30 \pm 1^\circ\text{C}$  and  $21 \pm 1.5^\circ\text{C}$ . Eggs which were laid by crickets reared at  $27^\circ\text{C}$  and LD 12:12 were dissected to determine their embryonic stage after 30 or 40 days of incubation at each temperature. The methods of dissecting eggs and staging embryos were described by Tanaka (1984); Stage I: embryo dumbbell shaped; stage II: embryo elongating; stages III–VII: embryo developing appendages; stage VIII: all embryos after stage VII or after anatrepsis. Once an embryo reaches stage VIII, it rotates inside the egg shell and develops without interruption until hatching. At both  $30^\circ$  and  $21^\circ\text{C}$ , embryos which did not enter diapause hatched or reached stage VIII within 30 days. Only those which remained unhatched and before stage VIII were selected for each dissection to determine the embryonic stage of diapause.

## Results

#### Nymphal development

*A. fasciatus* developed faster than *A. socius* at  $30^\circ\text{C}$  ( $t=9.1$  and  $7.1$  in males and females, respectively;  $P<0.05$ ; Fig. 1). In the male hybrids, development time was similar to that of the female parent while the female hybrids showed a value intermediate between the values of the two parents.

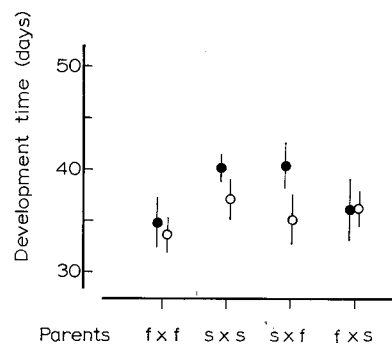


Fig. 1. Nymphal development in *Allonemobius fasciatus* (f), *A. socius* (s), and their reciprocal hybrids at  $30^\circ\text{C}$  and LD 14:10. Mean development time  $\pm$  S.D. is given. o; females, ●; males. In each cross, the female parent is listed first

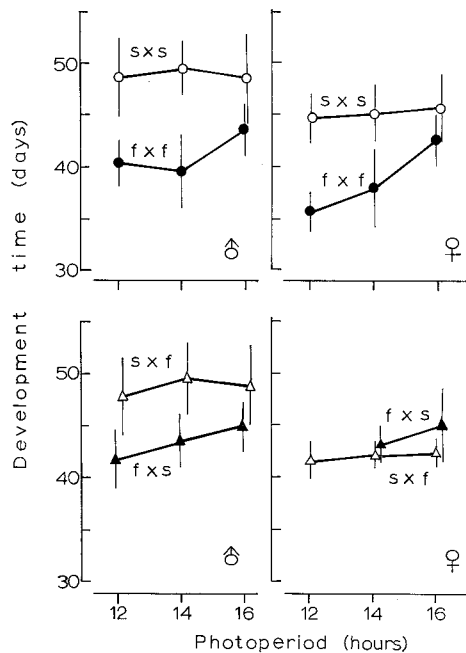
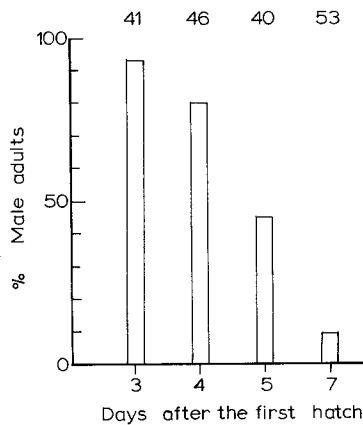


Fig. 2. Effect of photoperiod on nymphal development in *Allonemobius fasciatus* (f), *A. socius* (s), and their reciprocal hybrids at  $27^\circ\text{C}$ . Mean development time  $\pm$  S.D. is given

In all except the hybrids with *A. fasciatus* mothers, females matured more rapidly than did males. A similar result was obtained from crickets reared at  $27^\circ\text{C}$  and different photoperiods (Fig. 2). At all photoperiods used, *A. fasciatus* developed more rapidly than *A. socius*. In the former, nymphs tended to mature faster at a short photoperiod than at a long photoperiod, showing a short-day type of response. In *A. socius*, on the other hand, no significant difference was obtained in development time among the photoperiods ( $P>0.05$ ).

The mean development time for the F1 hybrids was intermediate between their parents at all photoperiods. However, as found at  $30^\circ\text{C}$ , male hybrids showed a development time more similar to that in their female parent than that in their male parent. Namely, a short-day type of response was maintained when their mother was *A. fasciatus* but not when she was *A. socius*. In the former, a significant difference was obtained in development time be-



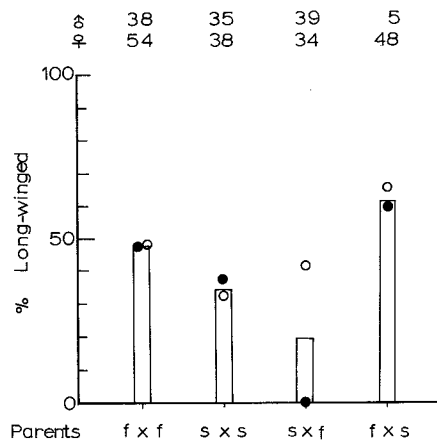
**Fig. 3.** Proportion of males in the hybrids between *Allonemobius fasciatus* females and *A. socius* males that hatched over several days at 27° C. The eggs were chilled at 16° C for 2 months before transferring to 27° C for hatching. Nymphs were reared at different photoperiods and 27° or 30° C. Numbers on the top indicate sample sizes

tween LD 12:12 and 16:8 ( $t=4.78$ ;  $P<0.05$ ). In female hybrids, however, no significant difference was detected between the two reciprocal crosses either at LD 14:10 or 16:8 ( $P>0.05$ ). The data for  $f \times s$  female hybrids at LD 12:12 were omitted because only 3 adults were obtained. Two of these took 44 days to mature and the other 46 days. The reason for this small number of females will be explained below.

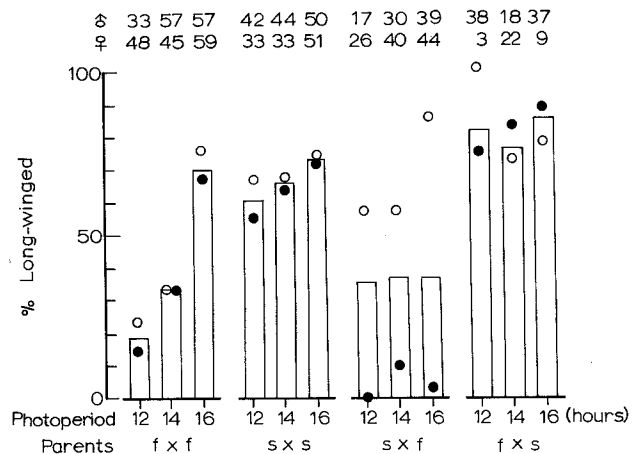
The proportion of male adults obtained from the cross between *A. fasciatus* females and *A. socius* males is given in Fig. 3. As will be shown later, this particular cross produced diapause eggs so that they were chilled at 16° C for 2 months before transferred to 27° C for hatching. Hatching did not occur simultaneously but in a rather sporadic fashion. Therefore, to obtain enough crickets for the experiment shown in Fig. 1, nymphs that hatched over several days were used. Figure 3 indicates that the proportion of male adults decreased from more than 90% to less than 10% as their hatching was delayed, suggesting that embryonic development was more rapid in males than in females. The first group of nymphs, which hatched 3 days after the first egg hatching, were the sample kept at LD 12:12 with the result that most nymphs were males and only 3 females emerged as adults. This phenomenon of more rapid development in males was confirmed by another set of experiments but never observed in eggs obtained from the *A. socius* female  $\times$  *A. fasciatus* male cross (Tanaka, unpublished observations).

#### Wing form

The total proportion of long-winged forms was significantly larger in *A. fasciatus* than in *A. socius* at 30° C and LD 14:10 ( $\chi^2=5.68$ ;  $P<0.05$ ) (Fig. 4). The F1 hybrid with *A. fasciatus* mothers showed a higher proportion of long-winged forms than either *A. fasciatus* ( $\chi^2=4.46$ ;  $P<0.05$ ) or *A. socius* ( $\chi^2=16.90$ ;  $P<0.05$ ), indicating overdominance. In the hybrid obtained from the other cross, on the other hand, the proportion of long-winged forms was smaller than in either parent. In this case, however, males were all short-winged while females showed an intermediate value between the parental species.



**Fig. 4.** Proportion of long-winged adults in *Allonemobius fasciatus* (f), *A. socius* (s), and their reciprocal hybrids at 30° C and LD 14:10. o; females, ●; males. Histograms show the proportion of long-winged adults with sexes combined. Numbers on the top indicate sample sizes

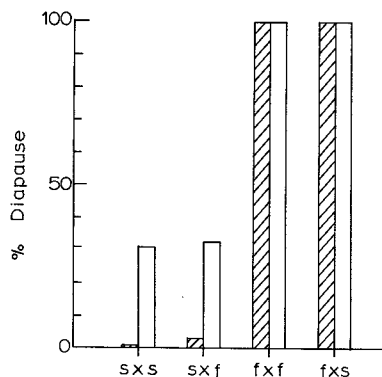


**Fig. 5.** Effect of photoperiod on the proportion of long-winged adults in *Allonemobius fasciatus* (f), *A. socius* (s), and their reciprocal hybrids at 27° C. o; females, ●; males. Histograms show the total proportion of long-winged adults. Numbers on the top indicate sample sizes

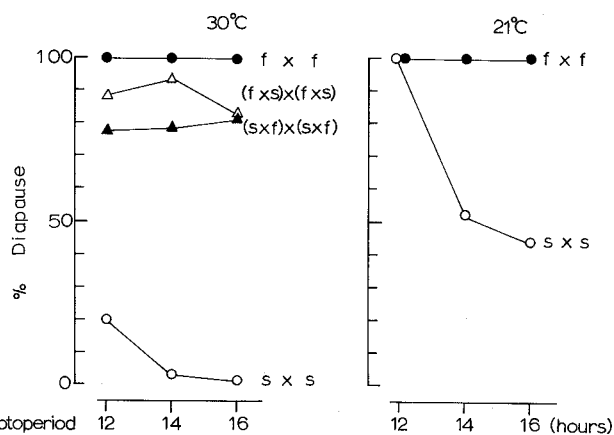
Similar results were obtained at 27° C except that at this temperature the proportion of long-winged forms was generally higher in *A. socius* than in *A. fasciatus* (Fig. 5), the reverse of the situation at 30° C. The two species tended to produce a greater proportion of long-winged forms at a longer photoperiod. Between the two sexes no statistically significant difference was observed at any photoperiod in either species ( $P>0.05$ ).

#### Diapause incidence

Whether embryos entered diapause depended upon the female parent as shown in Fig. 6. All eggs produced by an *A. fasciatus* female entered diapause even when she was crossed with an *A. socius* male. Unexpectedly, some of the eggs produced by *A. socius* entered diapause. The incidence of diapause was influenced not only by the temperature of incubation but also by the photoperiod to which the parents were exposed (Fig. 7). However, it was not affected



**Fig. 6.** Embryonic diapause incidence in *Allonemobius fasciatus* (f), *A. socius* (s), and their reciprocal hybrids. Eggs were obtained from crickets reared at 27° C and LD 16:8, and incubated at 30° C (hatched histograms) or at 21° C (open histograms). Each  $n=90$



**Fig. 7.** Effect of parental photoperiod on diapause incidence in *A. fasciatus* (f), *A. socius* (s), and their F2 hybrid embryos. Eggs were obtained from adults reared at 27° C and different photoperiods, and incubated at 30° or 21° C.  $N=580$ , on the average, ranging from 255 to 932

by the male parent (Fig. 6). The male influence appeared in F2 embryos, most (80–90%) of which entered diapause irrespective of the parental photoperiod.

#### Diapause stage

Embryonic development was suppressed at stage II or III in all diapausing eggs at 30° C (Table 1). At 21° C, *A. fasciatus* embryos continued to develop until stage VII at which diapause was induced, conforming to the previous results obtained by Tanaka (1984). In *A. socius*, on the other hand, the diapause stage did not vary with the temperature of incubation; most embryos entered diapause at stage II. In the F2 embryos at 21° C, development appeared to be suppressed at stage II and VII. Embryos in between these stages might be on their way to stage VII after termination of the diapause at stage II. It was not certain whether or not development was suppressed at intermediate stages between II and VII in F2 embryos.

#### Discussion

##### Seasonal life cycles

*A. fasciatus* shows a univoltine life cycle with an embryonic diapause while *A. socius* is suggested to be a continuous breeder in the southern parts of its range (Alexander and Thomas 1959; Alexander 1968a). In Oregon, nymphs of *A. fasciatus* hatch from overwintered eggs in early summer and mature in about two months (Tanaka and Brookes 1983). The nymphal development is accelerated as day-lengths become shorter (Tanaka and Brookes 1983; Fig. 2). A photoperiodic response of this type is common in other species of cricket which mature in late summer or fall (Masaki 1967, 1972a, 1978; Kidokoro and Masaki 1978), indicating that it functions as a mechanism synchronizing development with the season. *A. socius*, on the other hand, developed at similar rates under different photoperiodic condi-

**Table 1.** Stages of diapausing *Allonemobius fasciatus* (f), *A. socius* (s), and their F2 hybrid embryos after 30 and 40 days of incubation at 30° and 21° C. In each cross, the female parent is listed first

Temperature °C	Parents	Days after deposition	Embryonic stage <sup>a</sup>							No. eggs dissected
			I	II	III	IV	V	VI	VII	
30	s x s	30		5						5
		40		9						9
30	(s x f) x (s x f)	30		14	1					15
		40		16						16
30	(f x s) x (f x s)	30		15						15
		40		17						17
30	f x f	30		14	1					15
		40		11	4					15
21	s x s	30		10						10
		40		9	1					10
21	(s x f) x (s x f)	30		6	7	1				14
		40		2	3	1		2	2	10
21	(f x s) x (f x s)	30		2	6	4			3	15
		40		1	1	6		2	3	13
21	f x f	30					1	3	11	15
		40							10	10

<sup>a</sup> For stages, see Tanaka (1984)

tions (Fig. 2). This may indicate that selection for synchrony of adult emergence is less intense than it is in *A. fasciatus*. In fact, Alexander and Thomas (1959) reported that adults of "*A. fasciatus*" in Florida (= *A. socius*) can be found throughout the year.

Oviposition starts in late summer in *A. fasciatus* in Oregon (Tanaka and Brookes 1983). While all enter diapause at a low temperature, e.g. 20°C, some eggs laid in fall hatch without diapause when incubated at a high temperature, e.g. 30°C (Tanaka 1984). Such eggs are rare in late summer and, in the laboratory, all embryos entered diapause even at 30°C when their parents were reared at 24°C (Tanaka 1984) or 27°C (Fig. 7) irrespective of the photoperiod. This, together with my unpublished observations, suggests that parental temperature is the main factor responsible for the seasonal variation in the response of embryos to temperature. No information is available for the timing of oviposition in *A. socius* in Florida. However, the fact that adults occur throughout the year (Alexander and Thomas 1959) suggests that oviposition may take place all year around.

The present study demonstrated that *A. socius* produced diapause eggs and the proportion of these eggs was higher at a shorter photoperiod (Fig. 7). It is likely that this species is similar to *Gryllus firmus* in its adaptation to the climatic conditions of Florida. In *G. firmus*, adults also occur at all seasons, but a majority of the population overwinters in the egg stage (Walker 1980). Female adults lay both diapause and non-diapause ("fast-developing") eggs. The proportion of diapause eggs is very low in spring and summer but increases towards the end of the year. Physiological mechanisms causing this seasonal variation are unknown. However, as observed in *A. socius* as well as in *A. fasciatus*, the induction of diapause apparently involves two steps; (1) maternal determination of diapause and (2) embryonic response to temperature. Walker (1980) explained the significance of the facultative diapause of fall-laid *G. firmus* eggs in relation in the wide range of temperatures in October–December in Florida. That is, in years having cool falls, eggs that enter diapause may be more likely to survive the winter than the hatchlings they would otherwise produce (Walker 1980), although a cool fall may not always be followed by a severe winter.

*A. socius* and *A. fasciatus* showed an interesting difference in the diapause stage (Table 1). The former entered diapause at an early embryonic stage (stage II) both at 30° and 21°C. The latter also did so at the same stage at 30°C but at a later stage (stage VII) at 21°C. This temperature-dependent shift in the stage of diapause was also observed in an eastern population of *A. fasciatus* collected in Niagara Falls, New York (Tanaka, unpublished observation). Among several species of crickets examined, *A. fasciatus* is the only species in which diapause occurs as late as the end of anatrepsis (Sarai 1967; Tanaka 1984).

In eastern North America, most individuals of *A. fasciatus* are short-winged and the proportion of long-winged crickets has been reported to be as low as 10% (Alexander 1968a). However, this figure was probably based on mixed specimens of *A. socius* and *A. fasciatus*, because these had been regarded as the same species (Howard 1983). No information is available about the proportion of long-winged forms in western North America. However, I observed that long-winged forms of *A. fasciatus* make up only 3.4% ( $n=380$ ) in Corvallis and the proportions of long-winged forms

tend to be higher in more southern areas. For example, the proportion of long-winged females was 4.3% ( $n=23$ ), 2.6% ( $n=234$ ), 6.8% ( $n=44$ ), 16.9% ( $n=71$ ), and 57.5% ( $n=26$ ) in Shelton (47.2 N), Corvallis (44.3 N), Roseburg (43.1 N), Medford (42.2 N), and Ashland (42.1 N), respectively. In the laboratory, *A. fasciatus* from Corvallis produced more long-winged forms when reared at a higher temperature and a longer photoperiod (Figs. 4 and 5). Photoperiodic control of wing dimorphism is known in other species of crickets (Saeki 1966; Masaki 1972b, 1979; Ismail and Fuzeau-Braesch 1976; Tanaka et al. 1976; Tanaka 1978; Arai 1978).

Comparable data for *A. socius* are lacking. In the laboratory, the proportion of long-winged forms was generally higher in this species than in *A. fasciatus* at 27°C but lower at 30°C (Figs. 4 and 5). As in *A. fasciatus*, a higher proportion of long-winged forms was observed at a longer photoperiod, although this species does not usually encounter a photoperiod of as long as 16 h in Florida.

#### Hybrid responses

Ground crickets lack a Y chromosome, and have XX, XO sex determination so that males receive their X chromosomes from their mothers (Alexander 1968b). Bentley and Hoy (1972) made use of this in analyzing the genetics of cricket song in *Teleogryllus*. In reciprocal crosses between two species, the hybrid male offspring have similar genotypes except that they differ in the X chromosomes received from their mothers. Genetic differences can thus be localized to the X chromosome.

Reciprocal crosses between *A. fasciatus* and *A. socius* produced viable F1 hybrids. When reared under different environmental conditions, the two kinds of hybrids showed a difference in the rate of nymphal development. In the male hybrids, development time was similar to that of their mothers rather than to that of their fathers. The hybrid males with *A. fasciatus* mothers thus retained a short-day type of photoperiodic response. On the other hand, the female hybrids were intermediate in development time between the two species, and did not show a clear response to photoperiod. These results suggest that the rate of nymphal development is controlled primarily by the X chromosome.

Masaki (1978, 1983) crossed two closely related Japanese crickets, *Pteronemobius mikado* and *P. taprobanensis*, and obtained quite different results. In contrast to the results obtained in the present study, the F1 females produced by the reciprocal crosses were highly sensitive to photoperiod and developed in similar ways. The males, on the other hand, were quite abnormal. When the mother was *P. mikado*, they lost their photoperiodic response and matured in a relatively short period, i.e. less than 50 days on the average at 26°C. When the mother was *A. taprobanensis*, the F1 males died off without maturing after 200 days of rearing. A similar phenomenon was also observed in the F1 hybrids between *P. nigrofasciatus* and *P. fascipes* (Masaki 1983). These results can not be explained simply by X chromosomal genes but suggest some interaction between autosomal and X chromosomal genes.

Wing form displayed overdominance in the F1 hybrids between *A. fasciatus* and *A. socius*. At 30°C, the total proportion of long-winged forms was greater in the hybrids with *A. fasciatus* mothers and smaller in the hybrids with

*A. socius* mothers than that of either parent (Fig. 4). However, the small value in the latter hybrids was mainly due to the absence of the long-winged males; the females were intermediate between the parent species. A similar situation was encountered at 27° C where the proportion of long-winged forms in the hybrids with *A. socius* mothers was extremely low in males while it was high in females (Fig. 5). The hybrids obtained from the reverse cross showed a relatively high production of long-winged forms in both sexes. These results indicate that genes located on both autosomes and X chromosomes are responsible for the determination of wing form, and that their expression is greatly influenced by environmental factors such as temperature and photoperiod. Nymphs of *A. fasciatus* destined to develop long wings emerged as short-winged adults if one of their hind wing pads was removed before the 3rd day of the last nymphal instar (Tanaka 1985). This indicates that the expression of such genes is also influenced by internal factor(s).

Previous hybridization experiments suggest that the diapause character of interspecific hybrids is determined by both parent genes in *Gryllus* (Bigelow 1960), *Teleogryllus* (Bigelow and Cochaux 1962; Hogan 1965, 1966, 1971; Ohmachi and Masaki 1964; McFarlane and Drummond 1969; Masaki and Ohmachi 1967) and *Pteronemobius* (Masaki 1984). In the hybrids between *A. fasciatus* and *A. socius*, diapause was determined by the female parent (Fig. 6), suggesting that the chorion or yolk may contain a factor(s) responsible for diapause in this case while such a factor(s) may be produced as a result of interaction of both parent genes in the other crickets mentioned above. This mode of inheritance of embryonic diapause is not known in other species of cricket but has been found in the beetle, *Atrachya menetriesi* (Ando and Miya 1968). The influence of *A. fasciatus* male genes appeared in the F2 embryos showing a high incidence of diapause (Fig. 7). At 30° C, the F2's entered diapause at stage II as did purebred embryos. At 21° C, however, embryonic development appeared to be suppressed at stage II or VII or in between (Table 1).

McFarlane and Drummond (1969) reported a sex difference in intensity of embryonic diapause in the hybrids between *T. oceanicus* and *T. commodus*. They found that, in eggs with a short diapause of 2 days, the sex ratio was 1:1, but of the eggs delayed for 10 days, 70% were male. A sex difference in the rate of embryonic development was also observed in the F1 hybrid between *A. fasciatus* females and *A. socius* males (Fig. 3). In this case, however, it was males that developed faster, although whether this sex difference was due to a difference in the intensity of diapause or not is unknown.

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