Genetic Compatibility and Geographic Profile of Two Closely Related Species of *Allonemobius* (Gryllidae: Orthoptera)

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ABSTRACT   Genetic compatibility between two species of ground crickets, *Allonemobius fasciatus* De Geer and *A. socius* Scudder, was studied by crossing experiments. Reciprocal crosses produced viable offspring. However, the number of eggs produced by *A. fasciatus* (♀) × *A. socius* (♂) was significantly smaller than that by the reciprocal cross or intraspecific crosses; the hatchability was <10%, whereas most eggs produced in the other crosses overwintered and hatched. In the laboratory, development time for the male hybrids produced by *A. socius* (♀) × *A. fasciatus* (♂) was similar to that of their mothers rather than fathers, but the hybrid females were intermediate between the parent species, suggesting that nymphal development is primarily controlled by the X chromosome. The two species and their hybrids showed different ranges of embryonic stages for water absorption and diapause. Crickets collected from different localities in eastern North America were identified to species by their different diapause stages. The results were consistent with others' observations that the two species meet at around 38–39° N where hybrids occur. The geographic profiles and the possible isolating mechanisms between the two species are discussed.

KEY WORDS   Insecta, *Allonemobius* spp., hybridization, diapause

THE GROUND CRICKETS, *Allonemobius fasciatus* De Geer and *A. socius* Scudder, are distributed in the northern and southern parts of North America, respectively. They are morphologically indistinguishable so that they had been regarded as one species until Howard (1982) in his excellent study suggested that they differed genetically enough to be considered two species.

Although *A. fasciatus* and *A. socius* may be so-called cryptic species, they show conspicuous differences in a number of developmental traits. As in other orthopteran species (Hinton 1981), eggs of both species absorb water from the environment after deposition. However, water absorption in *A. socius* occurs at a much earlier embryonic stage than in *A. fasciatus* (Tanaka 1986a). Likewise, the embryonic stage at which diapause is induced is earlier in the former species. Embryonic diapause is photoperiodically controlled in the southern populations of *A. socius* (Tanaka 1986b) and the life cycle is multivoltine in the south and univoltine in the north (Howard & Furth 1986). In *A. fasciatus*, diapause induction is not photoperiodically controlled and the life cycle is thus univoltine throughout the range of its distribution (Howard 1982, 1986; Howard & Furth 1986; Tanaka 1986b).

Reproductive compatibility between *A. fasciatus* and *A. socius* has been studied by Fulton (1937), Howard (1986), and Tanaka (1986b). In all cases, reciprocal crosses produced offspring, indicating that these two species are closely related. Howard (1986) concluded that postmating barriers between the two species are weak and suggested a slight

difference between the male calling songs of the two species as a possible isolating mechanism. However, successful production and maturation of hybrids in the laboratory does not necessarily mean that they also do well in nature. Although Howard (1986) indicated that interspecific crosses produced fewer offspring (hatchlings) than intraspecific crosses, the number of pairs examined was rather small. Furthermore, it is not clear from his study if the observed differences in the number of hatchlings between the crosses were due to premating or postmating barriers. In this study, I crossed the two species to confirm these points and to determine if any premating or postmating barriers occurred between them. Howard (1986) found that in eastern North America the two species meet at 38–40° N where a relatively narrow hybrid zone exists. As mentioned above, the two species differ in developmental traits, which could be used to identify the species and their hybrids. Thus in my study, some effort also was made to confirm the distribution of the two species and existence of their hybrids, using such traits.

Materials and Methods

Crossing Experiments. To examine the reproductive compatibility between *A. fasciatus* and *A. socius*, nymphs were collected in August 1986, from Tuscarawas, Ohio (40.3° N), where only *A. fasciatus* occurs; and from Lexington, Va. (37.5° N), where only *A. socius* occurs (Howard 1986). Last and penultimate instars collected were kept at a 12:12

(L:D) photoperiod and 25°C, according to the method of Tanaka & Brookes (1983). Shortly before adult emergence, the sex was determined and they were separated to ensure that all were virgin. Adults of each species were kept individually in Petri dishes (9 cm) with a ball of moist glass wool and hamster pellets. A week after adult emergence, each female was paired with a male of the same or the other species. Eggs laid in balls of glass wool were washed in water, and the number of eggs produced during the first 7-d oviposition period was determined for each female.

Water Uptake and Embryonic Development. To observe changes in egg size after deposition, eggs obtained in the above experiment were placed on pieces of moist filter paper in Petri dishes (9 cm) and kept at 20°C. The maximal egg width during the first 30 d was measured using an ocular micrometer ($n = 30$ each).

To determine the embryonic stage at which water was absorbed, a group of eggs obtained from each type of cross was incubated at 20°C and those attaining a maximal width between 0.59 and 0.69 mm were removed daily, fixed at 75°C in water for 8 min, and dissected under a binocular microscope (Tanaka 1986a). The criteria for the embryonic stages were as described in Tanaka (1984). The first half of embryonic development is divided into seven stages: stages I and IIa, embryos dumbbell-shaped; stages IIb and IIc, embryos elongating; stages IIIa–VII, embryos developing appendages. Eggs before stage I were categorized as stage 0.

Diapause and Embryonic Development. To determine the embryonic stage at which diapause occurred, eggs produced by reciprocal or conspecific crosses (10 females and 10 males each) were incubated at 20°C for 20–30 d to allow the embryo to attain the diapause stage (Tanaka 1986a,b) and were dissected as described above.

To examine if hybrid eggs can overwinter and hatch in the same way as eggs of the parent species, they were kept at room temperature for 2 mo and exposed to the outdoor conditions on the campus of Ohio State University, Columbus, on 1 November 1986. All eggs were kept on moist filter paper and covered with pieces of moist tissue paper in Petri dishes. Those dishes were held in plastic bags and placed on the ground on the north side of a building. On 15 April 1987, they were transferred to 25 ± 0.5°C in the laboratory for hatching.

Nymphal Development. Nymphs obtained in the above experiment were reared at 12:12 (L:D) and 25°C, using the rearing method of Tanaka & Brookes (1983).

Geographic Variation and Distribution of the Two Species. To examine the distribution of the two species and confirm the existence of their hybridization in nature, adult crickets were collected in mid-August 1986, at Solon (41.2° N), Tuscarawas (40.3° N), and Marietta (39.3° N), Ohio; Kenna (38.4° N) and London (38.1° N), W. Va.; Lexington (37.5° N) and Wytheville (36.8° N), Va. The sex

Table 1. Egg production during the first 7 d of the oviposition period at 25°C in different types of crosses between *A. fasciatus* (f) and *A. socius* (s)

Cross	Collection site	Fraction of crosses producing eggs	$\bar{x}$ no. eggs per cross ± SD
f × f	TU × TU	9/9	111.3 ± 41.0
s × s	LE × LE	10/10	112.4 ± 50.1
s × f	LE × TU	10/10	96.6 ± 42.6
f × s	TU × LE	8/10	50.9 ± 43.7

In each cross, the female parent is listed first. TU, Tuscarawas; LE, Lexington.

was determined at each collection site and they were brought to the laboratory in separate plastic containers. Females were then individually kept in Petri dishes with food and a ball of glass wool into which eggs were laid. About 10 eggs laid by each female within 5 d at 12:12 (L:D) and 25°C were incubated at 20°C for 30 d and dissected to determine their embryonic stage. If eggs contained an embryo at stage II or III, their parents were identified as *A. socius* whereas if the embryos were at stage VII, their parents were *A. fasciatus* (Tanaka 1986b). During the current study, I found that F_1 hybrids of the two species entered diapause at one of the stages ranging from II to VII. Therefore, if eggs laid by a female showed widely different diapause stages, they were regarded as hybrids. F_2 hybrids also showed a similar tendency (Tanaka 1986b). Some eggs developed without diapause and, when dissected 30 d after deposition, contained an embryo that had already passed the stage of anatrepsis (stage VII). The females laying such eggs were regarded as a separate group.

After identification to species, about 20 eggs were collected from each female and their lengths measured the day after deposition. These females then were anesthetized with carbon dioxide and their head widths measured. The females of each population, except for those which laid hybrid eggs, were then pooled to collect more eggs. The eggs obtained were kept at 20°C for a month and chilled at 3°C for 3 mo to ensure their simultaneous hatching upon incubation at 25°C (Tanaka 1987). Newly hatched nymphs were reared at 12:12 (L:D) and 25°C to compare duration of nymphal development among the populations.

Results

Egg Production of Interspecific Crossing. Reciprocal crosses between *A. fasciatus* and *A. socius*, as well as intraspecific crosses, produced eggs (Table 1). An analysis of variance indicated a significant difference in egg production among the different types of crossing ($F = 4.13$; df = 3, 35; $P < 0.05$). This difference was due to the significantly reduced egg production by *A. fasciatus* females paired with *A. socius* males (t test, $P < 0.05$ each).

Table 2. The proportion of eggs absorbing water after 30 d of incubation at 20°C

Cross	n	$\bar{x}\%$ Eggs absorbing water ± SD
f × f	50 × 10	98.6 ± 1.64a
s × s	50 × 10	99.6 ± 0.80a
s × f	50 × 10	98.6 ± 1.60a
f × s	50 × 10	14.4 ± 3.80b

Eggs were laid by intraspecific or interspecific crosses between *A. fasciatus* (f) from Tuscarawas and *A. socius* (s) from Lexington. Percentages between different crosses followed by different letter are significant at 5% (*t* test).

In each cross mentioned below, the female parent will be listed first.

Water Absorption and Embryonic Development of Hybrids. Eggs produced by intraspecific crosses and *A. socius* × *A. fasciatus* started increasing in size 2 wk after incubation at 20°C (Fig. 1). This increase was due to water absorption by the eggs from the environment. The pattern of changes in egg size was similar for those groups, but eggs obtained from *A. fasciatus* × *A. socius* remained small throughout the observation period and the majority failed to absorb water. To confirm this observation, 10 groups of 50 eggs produced by each of the interspecific or intraspecific crosses were incubated at 20°C for 30 d, and the number of eggs that had absorbed water was counted. The results showed that only 14.4% of eggs obtained from *A. fasciatus* × *A. socius* absorbed water, but almost all eggs (>98%) produced by the other crosses did so (Table 2); this result is consistent with the result in Fig. 1.

Fig. 2 illustrates the embryonic stages at which water uptake took place. As already demonstrated for the Oregon strain of *A. fasciatus* and the Florida strain of *A. socius* (Tanaka 1986a), the two species showed a difference in embryonic stage at
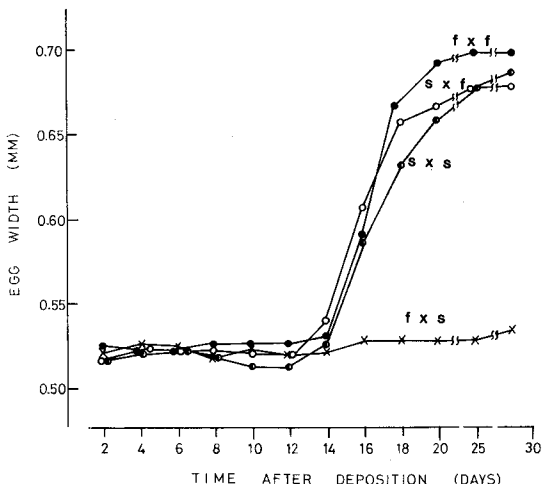
Fig. 1. Changes in egg width of *A. fasciatus*, *A. socius*, and their hybrids at 20°C. $n = 30$ each. In each cross, the female parent is listed first.
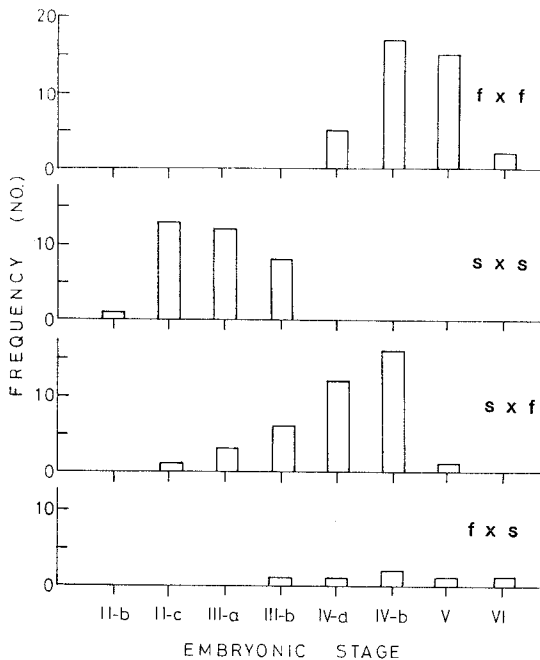
Fig. 2. The embryonic stages of *A. fasciatus*, *A. socius*, and their hybrids during the period of water absorption at 20°C. For the embryonic stages, see Tanaka (1984).
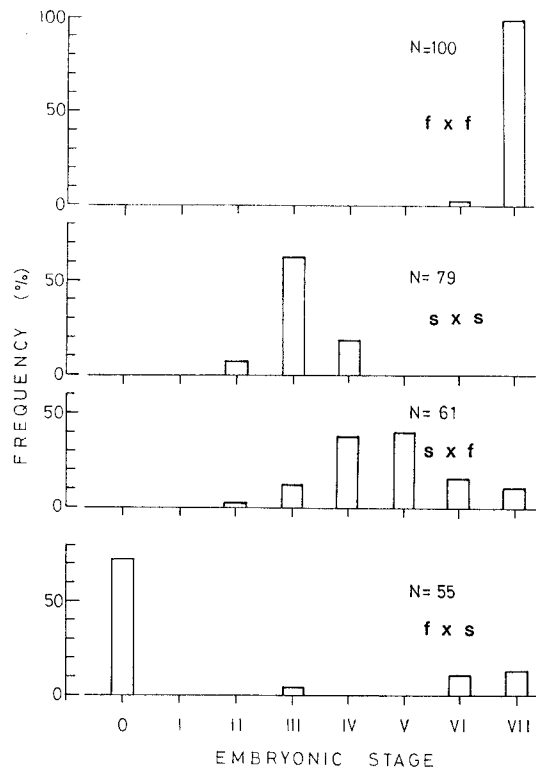
Fig. 3. The embryonic stages of diapausing *A. fasciatus*, *A. socius* and their hybrids at 20°C. For the embryonic stages, see Tanaka (1984).
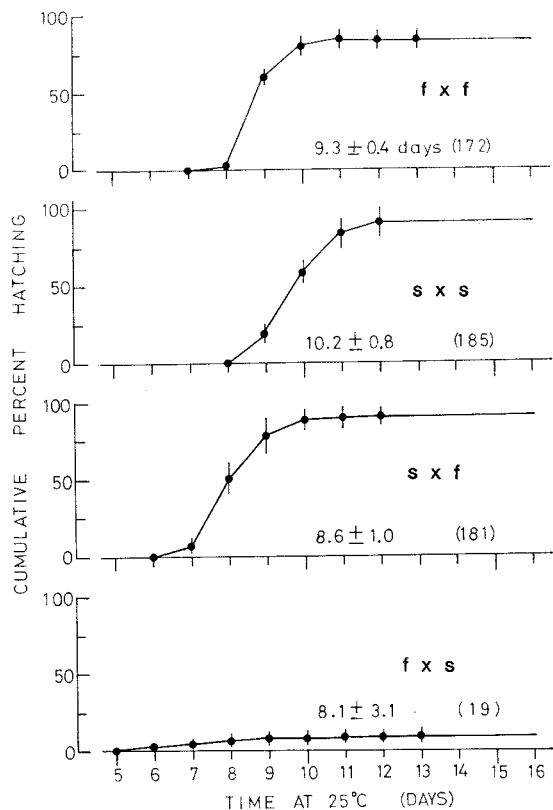
Fig. 4. Cumulative percentage hatching at 25°C after overwintering in eggs produced by *A. fasciatus* (Tuscarawas, Ohio), *A. socius* (Lexington, Va.), and their reciprocal crosses. Vertical lines indicate SD. Numbers in each panel show mean ± SD. Numbers in parentheses indicate sample sizes.
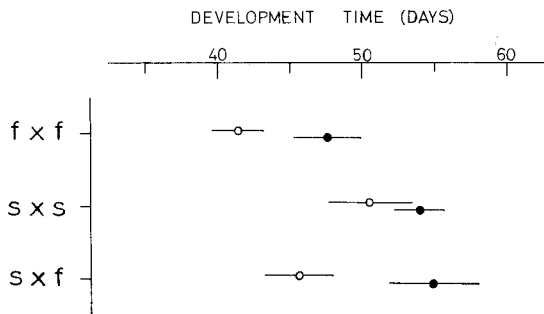

Fig. 5. Nymphal development of *A. fasciatus*, *A. socius*, and their hybrids at 25°C and 12:12 (L:D). Open and closed circles indicate females and males, respectively. Vertical lines indicate SD. $n = 17$–35.

which water was absorbed, although both took almost the same time to absorb water (Fig. 1). This was because embryonic development started decelerating earlier in *A. socius* than in *A. fasciatus*. In hybrid eggs, water uptake was observed in a wide range of embryonic stages, which overlapped the ranges for the two species.

Diapause Stage of Hybrids. Embryonic diapause was induced at earlier stages in *A. socius* than in *A. fasciatus* (Fig. 3), conforming to the previous observation (Tanaka 1986b). Hybrid embryos entered diapause at the stage overlapping the ranges of diapause stages for the two parental species. Most eggs produced by *A. fasciatus* × *A. socius* were found at stage 0 (i.e., the stages before the formation of a dumbbell-shaped embryo). In this work, none of them contained an embryo.

Postdiapause Development of Hybrids. After overwintering under natural conditions in Columbus, Ohio, eggs obtained from different crosses were brought into the laboratory on 15 April 1987, and postdiapause development was observed at 25°C. The first hatchlings appeared from eggs produced by *A. fasciatus* × *A. socius* (Fig. 4). In this group, only 9.5% of eggs hatched during the 30-d obser-

vation period. They were among those that had absorbed water before overwintering, and the rest had rotted before they were transferred back to the laboratory. Most eggs from the other crosses (≥86%) hatched within 2 wk at 25°C. Mean time spent at 25°C before hatching was slightly but significantly shorter in either type of hybrid eggs than in eggs of either species (*t* test; $P < 0.05$).

Nymphal Development of Hybrids. Newly hatched hybrid nymphs were reared at 12:12 (L:D) and 25°C to compare the duration of nymphal development with that in each species. In the hybrids produced by *A. socius* × *A. fasciatus*, males were similar to their female parent, whereas females were intermediate between the parents (Fig. 5). Those hybrids produced viable F_2 offspring (data not shown). Unfortunately, the number of nymphs obtained from the reversed cross was not large enough to produce meaningful data, though a few individuals matured and laid viable F_2 offspring.

Geographic Variation and Distribution. Because the two species and their hybrids enter diapause at different embryonic stages, this could be used to identify the species. To examine the geographic distribution of the two species and to confirm the existence of hybrids in nature (Howard 1986), crickets were collected from different localities in Ohio, West Virginia, and Virginia in August 1986. Female adults collected in Lexington, Va., and Kenna, W. Va., laid eggs that entered diapause at a stage characteristic of *A. socius* (i.e., stage II or III) while those collected in Tuscarawas and Solon, Ohio, produced eggs entering diapause at stage VII (Fig. 6A), the diapause stage for *A. fasciatus*. A few individuals collected in Kenna, W. Va., and Marietta, Ohio, produced eggs behaving like hybrid eggs (see Fig. 3). In the London, W. Va., population, hybrids of the two species had been known (Howard 1986) and diapause occurred at mixed stages of the two species (Fig. 6A), which suggests interspecific crossing. In the southern three populations from London, W. Va., Lexington, and Wytheville, Va., some females laid nondiapause eggs or a mixture of diapause and nondiapause
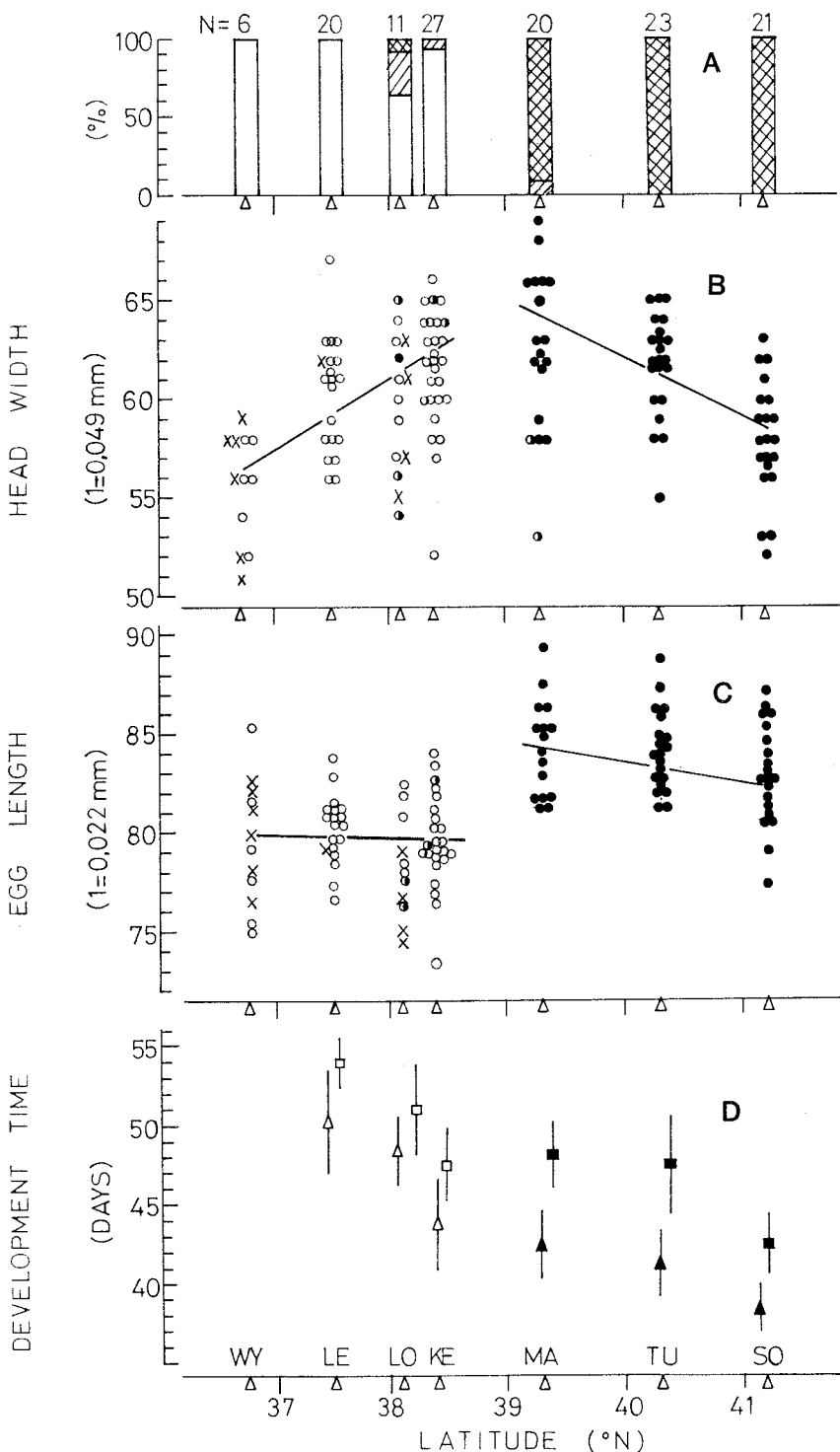
Fig. 6. Geographic profiles of *A. fasciatus* and *A. socius*. (A) Compositions of *A. fasciatus* (hatched bars), *A. socius* (open bars), and their hybrids (striped bars), as identified by the diapause stage of deposited eggs, collected at different localities in August 1986. (B) Head widths of female adults. (C) Mean lengths of 20 eggs laid by each field-collected female adult. (D) Nymphal development at 25°C and 12:12 (L:D). Open and closed symbols indicate *A. socius* and *A. fasciatus*, respectively. Half-closed symbols indicate hybrids, and crosses indicate females producing nondiapause eggs in B and diapause eggs in C. The names of collecting sites were abbreviated using the first two letters.

eggs. Without diapause, embryos developed beyond stage VII within 30 d.

Fig. 6B and C show head widths of the females used in the above observation and mean lengths of eggs produced by those females. In *A. fasciatus*, both head width ($Y = -2.95X + 179.93$; $r = -0.62$, df = 55, $P < 0.01$) and egg size ($Y = -0.98X + 122.87$; $r = -0.31$, df = 55, $P < 0.05$) tended to increase toward the south, and the two traits were positively correlated with each other ($r = 0.29$, df = 55, $P < 0.05$). This means that larger females tend to produce larger eggs. In *A. socius*, on the other hand, the head width decreased toward the south ($Y = 3.73X - 80.80$; $r = 0.60$, df = 52, $P < 0.01$), and egg length remained constant over the range of latitude covered. Between the two traits no significant correlation was found ($r = 0.10$, df = 52; $P > 0.05$). All individuals from Wytheville that laid nondiapause eggs were included in *A. socius*.

When reared under the same laboratory conditions (i.e., 12:12 [L:D] and 25°C), *A. socius* took longer to mature than did *A. fasciatus*, and in both species development was shorter in the northern populations than in the southern ones (Fig. 6D).

Discussion

Genetic Compatibility and Isolating Mechanisms. *A. fasciatus* and *A. socius* had been regarded as one species occurring widely in North America (Fulton 1931, Alexander & Thomas 1959, Vickery & Johnstone 1973). The two can be easily distinguished from the other members of *Allonemobius* not only by morphological characters (including head banding intensity, ovipositor length, stridulatory vein size, and file teeth number) but also by male calling songs (Alexander & Thomas 1959, Howard & Furth 1986). However, none of these characters, except for male calling songs, is enough to distinguish between *A. fasciatus* and *A. socius*. Howard & Furth (1986), who separated the two species using electrophoretic techniques, found a slight difference in male calling songs between the two species, but, as pointed out by Howard (1986), this finding is based on small sample sizes and needs to be confirmed by further observations. The current study has demonstrated that the two species can be separated easily by the difference in embryonic stage at which diapause occurs. In the family Gryllidae, *A. fasciatus* is the only known species in which diapause occurs as late as the end of anatrepsis (Tanaka 1984, 1986b; unpublished data). Another trait which separates *A. fasciatus* from *A. socius* is the timing of water absorption by the diapause eggs.

Using the embryonic diapause stage as a diagnostic trait, crickets collected from different localities in eastern North America were identified to species. The result shows that *A. fasciatus* occupies the northern part and *A. socius* the southern part,

conforming to the results obtained with an electrophoretic method by Howard (1986).

As first reported by Howard (1986), hybrids of the two species occur in nature, but the zone of overlap and hybridization between them is relatively narrow. Because adults of both species can be found in similar habitats in summer and fall, there must be some isolating mechanism(s) other than seasonal or geographic ones. One might be a slight difference in male calling songs (Howard 1986). However, population density of these crickets is fairly high, so such a mechanism alone would not explain the observed pattern of distribution. My unpublished observations show that the proportion of pairs that mated successfully in Petri dishes within an hour after pairing was much lower in *A. fasciatus* × *A. socius* (33%; $n = 9$) than in *A. fasciatus* × *A. fasciatus* (89%; $n = 9$), although all males in both groups attempted to mate at least once. Interestingly, a similar result was also obtained from the same types of pairing groups even after the stridulating organs on tegmina were removed from the males. That is, the proportion of mated pairs was 20% and 100% in the heterospecific and conspecific crosses, respectively ($n = 10$ each). It is thus possible that, without hearing courtship songs, females can distinguish conspecific males from those of the different species. In the experiment shown in Table 1, the proportion of females that started laying eggs within 2 d after pairing was 56 and 40% for intraspecific crosses of *A. fasciatus* and *A. socius*, respectively, whereas it was only 20% for *A. fasciatus* × *A. socius* and 10% for *A. socius* × *A. fasciatus*.

Postmating barriers also appear to exist. As in other crickets, both *A. fasciatus* and *A. socius* develop eggs but lay very few or no eggs without mating. In *Acheta domesticus* (L.), prostaglandins transferred from males to females by spermatophores stimulate ovipositing activity (Destephano & Brady 1977, Destephano et al. 1982). In *Teleogryllus commodus* (Walker), mated females synthesize prostaglandins in the spermatheca after they receive the synthetase complex from males (Loher 1979, Loher et al. 1981). How ovipositing activity is regulated in *Allonemobius* is not known, but the significantly reduced egg production by *A. fasciatus* × *A. socius*, as compared with egg production by the other crosses (Table 1), may suggest a possible difference in such a mechanism between the two species.

Another conspicuous difference between the different crossing groups was observed in the proportion of eggs that hatched successfully. Only a few hatchlings (<10%) were obtained from eggs produced by *A. fasciatus* × *A. socius*, whereas the majority of eggs obtained from the reciprocal cross, as well as intraspecific crosses, hatched (Fig. 4). Those hybrid eggs that failed to hatch did not develop any visible embryo. This type of abnormality has not been noticed in the hybrids between *A. fasciatus* females from Oregon and *A. socius* males

from Florida, although they showed some abnormality in embryonic development (Tanaka 1986b). These results apparently indicate differences in the degree of genetic compatibility between the two species from different localities. A similar phenomenon has been reported in other organisms (Dobzhansky & Koller 1938, Patterson & Stone 1952).

Laboratory experiments may produce hybrids between different species, and various types of behavioral and developmental abnormalities could be observed from such experiments. However, it is not always easy to identify the exact mechanism of reproductive isolation in nature. Furthermore, there is a possibility that isolation involves more than one mechanism. In the pair of species studied here, isolating barriers are not complete. When A. socius females are paired with A. fasciatus males, viable eggs are produced. These hybrids can survive the winter at least of Columbus (39.6° N), Ohio, and hatch in the spring. Their hatching time was slightly earlier than that of eggs produced in intraspecific crosses. When they were reared in the laboratory, males were similar in development time to their female parent, whereas females were intermediate between the parents. This conforms to the results obtained between the Florida strain of A. socius and the Oregon strain of A. fasciatus, and confirms that nymphal development is regulated by the X chromosome (Tanaka 1986b). In the field, hybrid nymphs may be able to mature in summer, but their fitness would be reduced if their offspring fail to have proper seasonal regulation of diapause. F_1 hybrids of these species produce some nondiapause (F_2) offspring even under those conditions where only diapause eggs are produced by each parental species (Tanaka 1986b). F_1 hybrid males may be able to pass their genes on to the next generation successfully by mating with females of either species, because the diapause character is determined by the female parent in those species (Tanaka 1986b). However, these crickets mate frequently after adult emergence. Therefore, as demonstrated for a pair of ladybird beetles (Nakano 1985, Katakura 1986), such a probability also would depend upon how frequently they mate with a conspecific or heterospecific individual and how hybrid sperm can compete with sperm from conspecific males. Unfortunately, no information is available on sperm competition in the two species of Allonemobius and their hybrids.

Geographic Profiles. The pattern of variation in adult body size suggests that the two species of crickets have adapted latitudinally in unique manners. A. fasciatus shows a northward decrease in adult body size and this is probably a consequence of the shorter duration of its nymphal development at a higher latitude (Fig. 6D). Because this species is univoltine and the duration of the growing season becomes shorter as latitude increases, such a developmental response would be highly adaptive and has been well documented in several other univoltine species from North America (Alexander

& Bigelow 1960) and from Japan (Masaki 1967, 1978a).

In A. socius, on the other hand, the size trend is completely reversed, and a maximal mean head width was obtained in the northernmost population covered by the current study. Unlike the other species, A. socius shows variable life cycles. Thus, around the transitional zone between the univoltine and bivoltine areas, a large difference would be expected to occur in the duration of the growing season per generation, thus affecting geographic clines in body size (Masaki 1973, 1978a,b). According to Howard & Furth (1986), such a transitional zone for A. socius lies at around 37.2° N. Therefore, the Wytheville, Va., population is probably bivoltine, as supported by the appearance of nondiapause individuals in the current study, explaining the small adult body sizes at this location as compared with the values for the northern populations. In the northern three populations, no significant difference exists in mean head width, but nymphal development becomes longer as the latitude decreases. This lack of correlation between head width and nymphal development could be due to a strong selection pressure on body size.

The northern populations from Kenna and London, W. Va., and Lexington, Va., are supposedly univoltine (Howard & Furth 1986), but, during the current study, I made a trip to various localities in that area on 1–3 July 1987 and found some adults. The proportion of adults collected was 20% ($n = 25$), 26.9% ($n = 67$), 46.2% ($n = 132$), 9.6% ($n = 188$) and 44.4% ($n = 144$) in Marietta, Ohio (39.3° N), Kenna, W. Va. (38.4° N), London, W. Va. (38.1° N), Lexington (37.5° N), and Richmond (37.2° N), respectively. Because univoltine populations are not likely to mature at least by the end of July and A. fasciatus is strictly univoltine (Alexander & Thomas 1959, Howard & Furth 1986), the adults collected at the beginning of July are probably all A. socius. This suggests that this species has a mixture of univoltine and bivoltine life cycles even at the northern limit of its distribution at least in some years. Some female adults collected from London in mid-August laid nondiapause eggs (Fig. 6B). Those adults were probably bivoltine individuals of A. socius or possibly hybrids between A. socius and A. fasciatus.

Another interesting cline of geographic variation is found in egg size for A. fasciatus. This trait also shows a decreasing trend towards the north and a significant correlation with adult body size ($r = 0.28$, df $= 55$, $P < 0.05$). This correlation could be an adaptive response to the climatic gradient to compensate for the smaller body size which may otherwise decrease the capacity for reproduction at higher latitudes. By producing smaller eggs, females may be able to produce more eggs. This seems to be a reasonable hypothesis. Masaki (1978b, 1987), working with Japanese ground crickets, has also explained in a similar way a positive correlation between adult body size and egg size. In this

case, however, both traits increase northward, instead of southward as in *A. fasciatus*, within the range of the univoltine area. One may thus argue that variation in egg size is a developmental consequence of variation in adult body size which may show a southward or northward increase depending upon the species. In fact, this type of correlation is often found in various groups of organisms (e.g., Lloyd 1987). However, this hypothesis does not explain the lack of correlation between adult body size and egg size in *A. socius* ($r = 0.10$, df $= 52$, $P > 0.05$). In this cricket, egg size remains unchanged over a wide range of the distribution where adult body size varies greatly. Therefore, these results apparently suggest that the two traits are under separate sets of selection pressure, and further investigation is necessary to identify the selection factor(s).

Acknowledgment

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