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ORIGINAL RESEARCH PAPER

Environmental control of the seasonal life cycle of a zoophytophagous mirid, *Adelphocoris triannulatus* (Hemiptera: Miridae)

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Abstract

Adelphocoris triannulatus (Stål) (Heteroptera: Miridae) is a zoophytophagous bug that inhabits grasslands and crop fields, and is widely distributed in eastern Asia. In this study, the seasonal occurrence and environmental factors controlling the seasonal life cycle of this bug were investigated in a local population in southern Kyushu, Japan. When insects were reared under different photoperiods at 20 and 25 °C, they produced diapause or nondiapause eggs depending on the photoperiod: when reared under short-day photoperiods (≤ 13 h/day), females laid diapause eggs, whereas they laid nondiapause eggs when reared under long-day photoperiods (≥ 14 h/day). Because the developmental duration of the pre-adult stages and maturation (minimum duration of one generation) is estimated to be approximately 30 days at summer temperatures, these results suggest that this bug has a multivoltine seasonal life cycle. In agreement with the laboratory results, only nondiapause eggs were produced until mid-August in the field, and an increasing proportion of diapause eggs were produced from early September. In addition to these findings, field sampling from spring to autumn in 2009 indicated that three or four generations were produced in one year. These results suggest that egg diapause plays a role in preventing nymphs of *A. triannulatus* from developing in winter, and thereby ensures the survival of the population in adverse seasons.

Keywords Egg diapause · Zoophytophagy · Voltinism · Photoperiodism · Seasonal adaptation · *Adelphocoris triannulatus*

Introduction

True bugs (Heteroptera) include more than 38,000 species and comprise the largest suborder of hemipteran insects (Schuh and Slater 1995). Their food habits are diverse and each species plays a specific role in ecosystems: some feed on fungi or various parts of plants, while others are known to be predators of insects or other arthropods. In addition, a few true bug species feed on both plants and insects (Southwood and Leston 1959; Schuh and Slater 1995). Plant bugs (Miridae) include species with various food habits (Wheeler 2001).

Adelphocoris triannulatus (Stål) is a mirid with an adult body length of about 8 mm. This bug is widely distributed in eastern Asia, including Japan. It inhabits grasslands and crop fields, and often sucks leaves and flowers (Tomokuni et al. 1993). During summer, we found that its density is very high in sweet potato fields in southern Kyushu. Although the genus *Adelphocoris* includes many agricultural pests and the life cycles of those pests have been investigated (e.g., Lu et al. 2011), *A. triannulatus* has not been regarded as an agricultural pest and thus has received little attention. Although it was thought that all *Adelphocoris* species are phytophagous, our preliminary rearing study showed that *A. triannulatus* adults stay on newly killed larvae of the sweet potato leaf worm, *Aedia leucomelas* (L.), to suck the larvae. Furthermore, under laboratory conditions, the bugs are often subjected to cannibalism at the nymphal stage (Tajima and Shintani, unpublished data). These facts suggest that *A. triannulatus* is a zoophytophagous mirid, and that sucking insect larvae may make this bug grow and reproduce better.

Insects have species-specific seasonal life cycles, and the mechanisms controlling these life cycles have been examined for many temperate insects, particularly in relation to diapause induction (Danks 1987; Tauber et al. 1986). In true bugs, various effects of the temperature and photoperiod on their development and reproduction have been investigated (Musolin and Saulich 1999; Numata 2004; Saulich

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and Musolin, 2012). In mirids, the seasonal incidence of diapause and the mechanisms underlying diapause induction have been examined for many herbivores, since they are often serious agricultural pests. *Adelphocoris lineolatus* (Goeze) (Ewen 1966), *Pseudatomoscelis seriatus* (Reuter) (Gaylor and Sterling 1977), *Trigonotylus caelestialium* (Kirkaldy) (Higuchi and Takahashi 2005; Kudô and Kurihara 1988, 1989; Okuyama 1982), *T. tenuis* (Reuter) (Shintani and Higuchi 2008), and *Stenotus rubrovittatus* (Matsumura) (Shigehisa 2008) present an egg winter diapause, which is induced by the photoperiodic and temperature conditions experienced by the maternal generation. These insects possibly have multivoltine seasonal life cycles, and autumn-generation adults lay diapause eggs for overwintering in response to a mild temperature and short photoperiod. Other mirids such as *Deraeocoris brevis* (Uhler) (Horton et al. 1998) and *Lygus lineolaris* (Beauvois) (Snodgrass 2003) exhibit short-day-induced reproductive diapause for overwintering.

Clear effects of photoperiod on development have not been detected in zoophytophagous mirids [e.g., Hughes et al. 2009; Pazyuk et al. 2014 for *Nesidiocoris tenuis* (Reuter)]. This may be because the diversity of food sources makes food availability for zoophytophagous mirids during an adverse season (i.e., in winter) a relatively minor issue. Therefore, the timing of diapause induction may not be precisely regulated by the photoperiod. However, this may not hold true for every zoophytophagous mirid species. Thus, the purpose of the present study was to examine the effects of photoperiod on development and the mechanisms that regulate the seasonal life cycle of *A. triannulatus*. First, developmental parameters were determined by rearing insects at different temperatures. Second, the photoperiodic response was examined at two temperatures. Third, since it became clear that *A. triannulatus* presents a maternally induced egg diapause, the seasonal change in the proportion of diapause eggs produced in the field was investigated. Finally, the seasonal change in developmental stage composition in the field was examined, and the number of generations produced in a year was predicted from field temperatures, estimated developmental thresholds, and thermal constants. The adaptive significance of the egg winter diapause in *A. triannulatus* was also considered.

Materials and methods

Insects

Adults of *A. triannulatus* were collected by sweeping the grassland on the campus of Minami Kyushu University, Takanabe (32°06′N, 131°31′E, ca. 50 m altitude), Miyazaki Prefecture, Japan with an insect net (36 cm diameter, 150 cm rod length) in early summer 2009. The insects were collected with an insect aspirator, brought to the laboratory, and placed in acrylic insect cages (34 × 25 × 34 cm) with nylon mesh on three sides. The cages were kept under a photoperiod of 16L–8D (16 h photophase and 8 h scotophase) at 25 °C. Paper towel was placed at the bottom of each cage and wheat seedlings (8–12 cm tall) nursed in a glass Petri dish (9 cm in diameter) were placed on the paper towel. The bugs were supplied with leaves and flowers of the white clover, *Trifolium repens* L., as food, along with some pieces of killed 4th- to 6th-instar larvae (unfrozen) of the common armyworm, *Spodoptera litura* (Fabricius), which are easily reared in the laboratory. The armyworm larvae were put on filter paper placed on the lids of small plastic Petri dishes (4 cm in diameter). Although females lay eggs inside various parts of plants, we found that the petiole of sweet potato, *Ipomoea batatas* L., is one of their preferred substrates for oviposition. Therefore, sweet potato petioles were added for egg collection purposes. Eggs laid inside the petioles were collected by dissecting the petioles with forceps. They were then placed on slightly moistened filter paper in plastic Petri dishes (6 cm in diameter) and kept under a 16L–8D photoperiod at 25 °C, unless otherwise stated.

Hatched nymphs were individually placed in plastic Petri dishes (6 cm in diameter) within 24 h after hatching, and were supplied with white clover flowers and leaves and pieces of killed armyworm larvae as food. The food was changed or replenished every day. Adults that emerged were paired in Petri dishes (6 cm in diameter) within 24 h and supplied with clover flowers and leaves, killed armyworm larvae, and sweet potato petioles. For laboratory culture, the insects were mass-reared in acrylic cages under a 16L–8D photoperiod at 25 °C for successive generations.

Determination of developmental thresholds and thermal constants

To determine the developmental threshold (T_0) and thermal constant (K) for each of the egg, nymphal, and adult preoviposition periods, the insects were incubated or reared from egg to adult stages at 15, 20, 22.5, 25, 27.5, and 30 °C under a 16L–8D photoperiod. Approximately 50 eggs laid within 24 h from the mass-rearing culture were placed in each Petri dish (6 cm in diameter) and kept at one of these temperatures. Hatched nymphs were reared at the same temperature. Adults that emerged were paired within 24 h and oviposition was checked daily. T_0 and K were determined using a formula proposed by Ikemoto and Takai (2000).

Adult longevity and fecundity

Adults reared as female–male pairs at 20, 22.5, 25, and 27.5 °C in the experiments for determining the developmental threshold and the thermal constant of the adult pre-oviposition period were allowed to lay eggs until they died. Eggs were collected daily. When the male died earlier, another male of the same age was placed in the Petri dish. The number of eggs laid and the date of death were recorded.

Diapause induction

Eggs were collected from the mass-rearing culture and kept under a 16L–8D photoperiod at 25 °C. Hatched nymphs were reared under photoperiods of 10L–14D, 12L–12D, 13L–11D, 14L–10D, and 16L–8D at 20 and 25 °C. Adults were paired within 24 h after eclosion and allowed to lay eggs, and the eggs were collected for 7 and 5 days from the start of oviposition at 20 and 25 °C, respectively. The eggs were transferred to a 16L–8D photoperiod at 25 °C within 24 h after being laid and their diapause status was determined. A high percentage of the eggs laid by each female were unfertilized or collapsed (see "Results"). Although unfertilized eggs had a similar appearance to normal eggs immediately after collection, they could be distinguished from normal eggs because they did not become a pale flesh color (see "Results"). The diapause status of the eggs (diapause or nondiapause) was determined by the duration of the egg period (see "Results"). The proportion of diapause eggs under each condition was calculated as the number of diapause eggs relative to the total number of eggs from all pairs, excluding unfertilized or collapsed eggs.

Effect of changing the photoperiod on diapause induction

Adults reared under long-day conditions (16L–8D, 25 °C) in the nymphal stage were transferred to short-day conditions (12L–12D, 25 °C) on the day of adult eclosion, and simultaneously paired ($n = 10$) in Petri dishes. When the male died earlier, another male of the same age that had experienced the same conditions was put in the Petri dish. Eggs were collected daily until the female died, and the diapause status of each egg was determined.

Seasonal incidence of diapause

Adults of *A. triannulatus* were collected nine times from late May to late October 2009 by sweeping the grassland and sweet potato field on the campus with an insect net. They were reared as female–male pairs in Petri dishes (6 cm in diameter) and allowed to lay eggs under a 16L–8D photoperiod at 25 °C for 3 days. The diapause status of the eggs was determined.

Seasonal changes in stage composition in the field population

Adults and nymphs of *A. triannulatus* were collected 49 times every 4–7 days from early March to late November 2009 by sweeping the vegetation with an insect net 100 times. The collection site was only the grassland on the campus until June and the grassland and sweet potato field on the campus from July onward. Collected insects were evaluated to determine the developmental stage (nymph or adult) and the instar for nymphs.

Meteorological data

Temperature data were obtained from the records of meteorological data on the campus. The temperatures for Takanabe during summer to autumn 2009 were typical of an average year (Japan Meteorological Agency 2015). The natural day length for Takanabe was obtained by adding 1 h of civil twilight to the duration from sunrise to sunset calculated using the Keisan Online Calculator (Casio Computer Co., Ltd. 2017).

Statistical analysis

Data for durations and fecundity were compared using the Tukey–Kramer multiple comparison test or the Steel–Dwass test, depending on the normality of data. Proportions were compared using a Tukey-type multiple comparisons test for proportions (Zar 2009).

Results

Developmental thresholds, thermal constants, and effects of the photoperiod and temperature on nymphal periods

Egg, nymphal, and pre-oviposition periods of *A. triannulatus* at different temperatures under a 16L–8D photoperiod are shown in Table 1. From these data, T_0 and K were estimated as 10.0 °C and 186.3 degree-days for the egg period, 12.7 °C and 184.8 degree-days for the nymphal period, and 13.5 °C and 67.5 degree-days for the adult pre-oviposition period. There was no significant difference in the duration of the nymphal period between photoperiods at 20 or 25 °C (ANOVA, $p > 0.05$); thus, nymphal period data for photoperiods other than 16L–8D are not shown. Photoperiods other than 16L–8D were not tested for the

Table 1 Developmental periods of *Adelphocoris triannulatus* at different temperatures under a 16L–8D photoperiod, and estimated developmental threshold (T_0) and thermal constant (K) in each of the egg, nymphal, and adult pre-oviposition periods

Temperature (°C)	Egg period (days)[a]	Nymphal period (days)[a]	Pre-oviposition period (days)[a]
15	37.3 ± 2.1 (125)	–	–
20	19.7 ± 1.3 (111)	26.1 ± 1.0 (34)	10.3 ± 2.1 (12)
22.5	14.4 ± 0.9 (110)	18.0 ± 0.7 (35)	7.8 ± 1.8 (12)
25	11.9 ± 0.7 (115)	14.2 ± 0.5 (37)	5.7 ± 1.1 (14)
27.5	10.7 ± 0.9 (109)	12.5 ± 0.6 (34)	4.9 ± 1.1 (7)
30	9.7 ± 0.9 (117)	11.4 ± 0.6 (35)	–
T_0 (°C)	10.0	12.7	13.5
K (degree-days)	186.3	184.8	67.5
r^2	0.996	0.983	0.997

[a] Mean ± SD. *Numbers in parentheses* represent sample size

– Not tested

pre-oviposition period, so it is unclear if pre-oviposition period is affected by photoperiod.

Effects of temperature on female adult longevity, oviposition period, and fecundity

Female adult longevity, oviposition period, and total fecundity at different temperatures are shown in Table 2. Female adult longevity differed significantly among temperatures (Steel–Dwass test, $p < 0.05$) and tended to be prolonged at lower temperatures. Oviposition period and total fecundity did not differ significantly at different temperatures (Steel–Dwass test and Tukey–Kramer multiple comparison test, respectively, $p > 0.05$). At the temperatures tested, as many as 46–72% of the eggs were collapsed or unfertilized.

Diapause and nondiapause eggs

Two distinct patterns of embryonic development were observed (Fig. 1). Most eggs laid by females reared under long-day conditions (16L–8D at 25 °C) hatched mostly on days 11–13 after oviposition (early-hatching eggs, Fig. 1a). In contrast, the eggs laid by females reared from hatching under short-day conditions (12L–12D at 25 °C) hatched sporadically and later than those laid by females reared from hatching under long-day conditions (late-hatching eggs, Fig. 1b). More than half of the eggs hatched by day 80, but 10% of all the eggs did not hatch until day 180. Both types of eggs had a banana shape and an opaque white color within 24 h after oviposition (day 0) and were impossible to distinguish up to day 8, when both types became a pale flesh color. However, their appearances differed from day 9 on: late-hatching eggs remained a pale flesh color, whereas early-hatching eggs showed red-pigmented eyes. The appearance of the late-hatching eggs remained unchanged for a long period (usually ≥ 30 days). Thus, the late-hatching and early-hatching eggs were designated diapause and nondiapause eggs, respectively. Since the eggs were kept under the same conditions (16L–8D at 25 °C), this egg (embryonic) diapause was considered to be induced maternally.

Table 2 Effects of temperature on female adult longevity, oviposition period, and fecundity in *Adelphocoris triannulatus* under a 16L–8D photoperiod

Temperature (°C)	N	Longevity (median and range, days)[a]	Females that laid eggs (%)[b]	Oviposition period (median and range, days)[c,d]	Total fecundity (mean ± SD)[c,e]	Developed eggs (%)[f]
20	18	22a (5–37)	16 (88.9)	12 (1–29)	88.3 ± 82.9	28.0a
22.5	16	19a (5–37)	13 (81.3)	13 (2–31)	150.2 ± 85.0	38.8b
25	15	13ab (5–32)	14 (93.3)	9.5 (2–25)	171.8 ± 111.1	53.8c
27.5	16	11b (1–20)	11 (68.8)	8 (3–15)	92.6 ± 65.2	36.5b

[a] Medians with the same letters do not differ significantly at $p = 0.05$ by Steel–Dwass test

[b] Proportions did not differ significantly at $p = 0.05$ by Tukey-type multiple comparisons for proportions

[c] Data for females that laid no eggs were excluded

[d] Medians did not differ significantly at $p = 0.05$ by Steel–Dwass test

[e] Means did not differ significantly at $p = 0.05$ by Tukey–Kramer multiple comparison test

[f] Proportion of the eggs that became a pale flesh color. Proportions with the same letters do not differ significantly at $p = 0.05$ by Tukey-type multiple comparisons for proportions

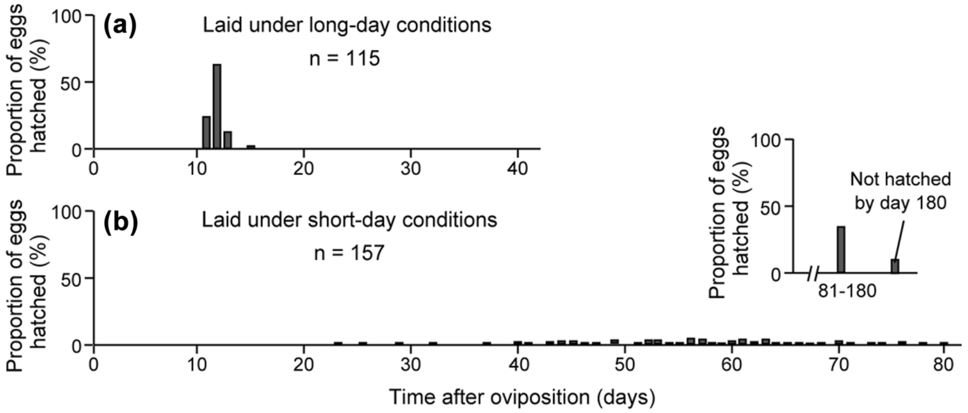


Fig. 1a–b Effects of maternal conditions on the embryonic development in *Adelphocoris triannulatus*. Plots showing the proportions of the eggs that hatched when the eggs were laid by **a** females reared from hatching under a long-day photoperiod (16L–8D) at 25 °C and **b** females reared from hatching under a short-day photoperiod (12L–12D) at 25 °C. The eggs were kept under long-day conditions. In **b**, the eggs that hatched on days 81–180 and those that survived until day 180 but did not hatch were pooled

Effects of photoperiod on the induction of egg diapause

Based on the above results, we defined the eggs that were pale flesh colored 20 days after oviposition when kept under a 16L–8D photoperiod at 25 °C as diapause eggs. Clear long-day photoperiodic responses were observed with critical photophases of 13.4 and 13.7 h/day at 20 and 25 °C, respectively (Fig. 2). At both temperatures, females reared under long-day photoperiods laid nondiapause eggs, whereas those reared under short-day photoperiods laid diapause eggs. When comparing the results obtained when the egg-laying individuals were reared at 20 and 25 °C, the proportion of diapause eggs did not differ significantly for any photoperiod except 13L–11D (Fisher exact test, $p < 0.001$). Some females laid both diapause and nondiapause eggs.

Effects of changing the photoperiod on diapause induction

Five of the 10 females that were transferred from long-day to short-day conditions on the day of adult eclosion initially laid only nondiapause eggs, but then started to lay diapause eggs 15.6 ± 2.4 (mean ± SD) days after transfer (Fig. 3). One laid both types of eggs for 4 days before starting to lay only diapause eggs. The other five females laid only nondiapause eggs and died within 15 days.

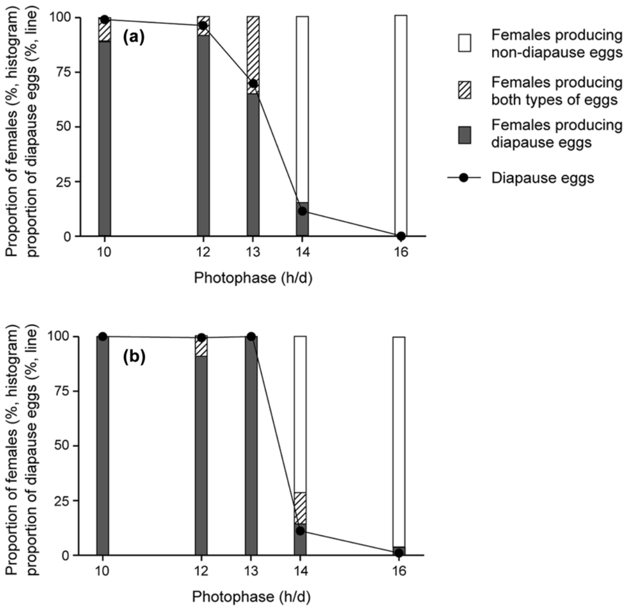


Fig. 2a–b The proportions of diapause *Adelphocoris triannulatus* eggs produced by insects reared from hatching under different photoperiods at 20 °C (**a**) or 25 °C (**b**). Proportions of females producing nondiapause eggs, diapause eggs, and both types of eggs as well as the proportion of diapause eggs relative to the total number of eggs per photoperiodic condition are shown. At 20 °C: number of females, 9–13; total number of eggs, 167–292. At 25 °C: number of females, 11–14; total number of eggs, 327–451

Seasonal change in diapause incidence

The proportion of diapause eggs laid changed seasonally (Fig. 4). From May to mid-August, almost exclusively nondiapause eggs were laid. However, the diapause incidence markedly increased in early September and was almost 100% from mid-September onward.

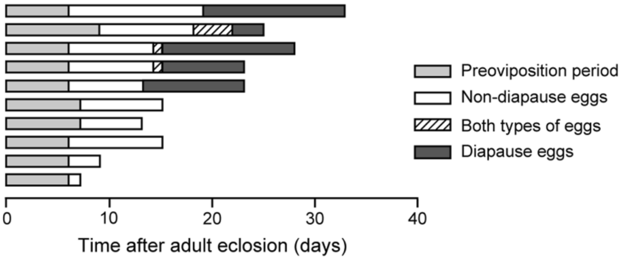


Fig. 3 Effects of the transfer of *Adelphocoris triannulatus* females from long-day to short-day conditions on the diapause status of their eggs. Insects were transferred from a 16L–8D to a 12L–12D photoperiod at 25 °C on the day of adult eclosion. Each *bar* indicates the oviposition history of an individual female and the diapause status of her eggs. The end of each bar indicates the day on which the female died

Seasonal changes in stage composition in the field population

Seasonal changes in the stage composition are shown in Fig. 5. First-instar nymphs were found from early March, and only nymphs were found until late April. After this time, adults occurred continuously, with their frequency peaking in July to September. Only adults were found from October to early November, and no insects were found later in the year.

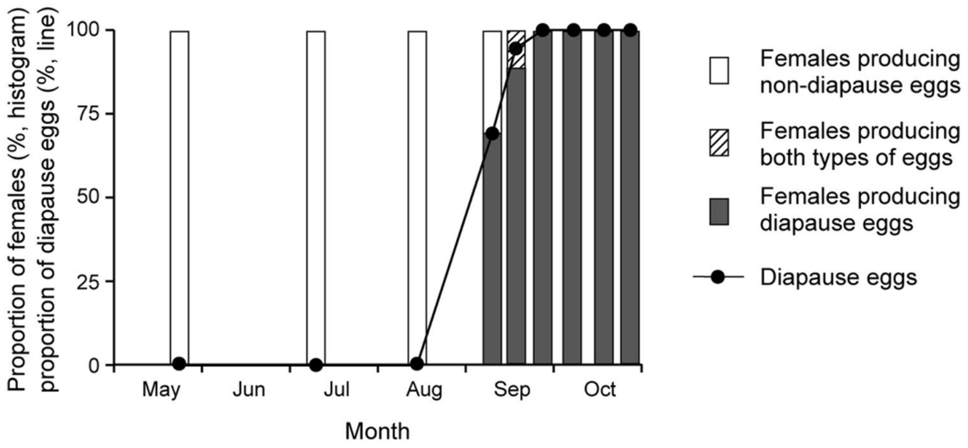
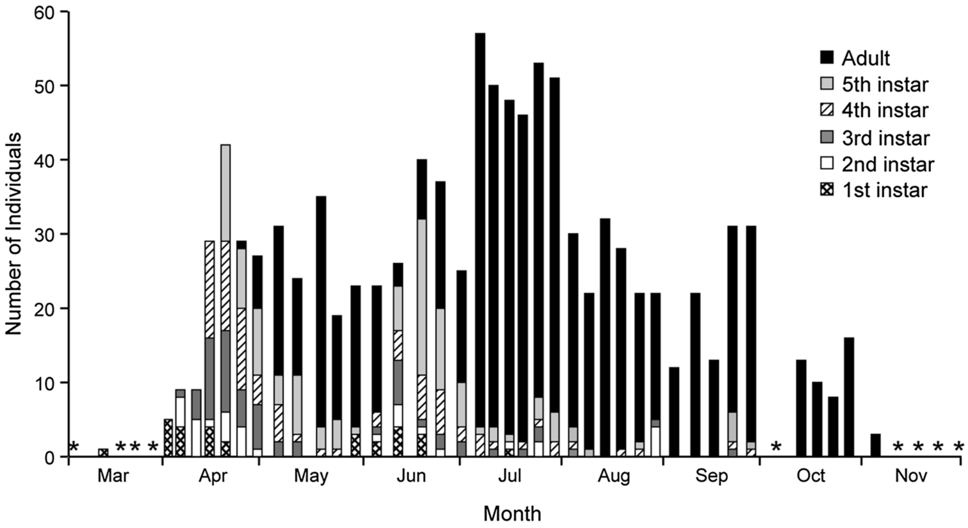


Fig. 4 Seasonal change in the proportion of diapause eggs laid by *Adelphocoris triannulatus* females. Female adults collected by sweeping vegetation from late spring to autumn 2009 were allowed to lay eggs in the laboratory for 3 days under a 16L–8D photoperiod at 25 °C, and the diapause status of the eggs was determined. The proportions of the females that produced nondiapause eggs, diapause eggs, and both types of eggs as well as the proportion of diapause eggs relative to the total number of eggs per collection date are shown. Number of females per collection date, 5–22; total number of eggs, 32–1054

Fig. 5 Seasonal changes in the stage composition of *Adelphocoris triannulatus* in the field. Insects were sampled every 4–7 days from early March to late November 2009. *Asterisks* indicate that no insects were collected



Discussion

The results of this study show that *A. triannulatus* presents a maternally induced egg diapause, and that photoperiod may be a primary cue for diapause induction. Since this diapause is induced under short-day conditions, it is most likely to be related to overwintering. The critical photophase was found to be almost the same at 20 and 25 °C. In many insects, a lower temperature results in a higher incidence of diapause and/or a longer critical photophase (Danks 1987; Tauber et al. 1986). However, the incidence of diapause in *A. triannulatus* under a 13L–11D photoperiod is higher at 25 °C (100%) than at 20 °C (69.3%), and the reason for this is unclear. In agreement with the laboratory results, *A. triannulatus* adults in the field produce an increasing proportion of diapause eggs from early September (Fig. 4), when the temperature is about 25 °C and the day length approaches the critical photophase of 13.7 h/day (Fig. 6). Thus, this photoperiodic response plays a critical role in inducing the transition from the laying of nondiapause eggs to the laying of diapause eggs in a population in the late summer to early autumn season. It is unclear why the survival rate of *A. triannulatus* eggs is low under our experimental conditions (Table 2), but manipulation during collection or humidity in the laboratory may have had a negative effect on the eggs. Therefore, there is a need to investigate the hatchability of the eggs under natural conditions.

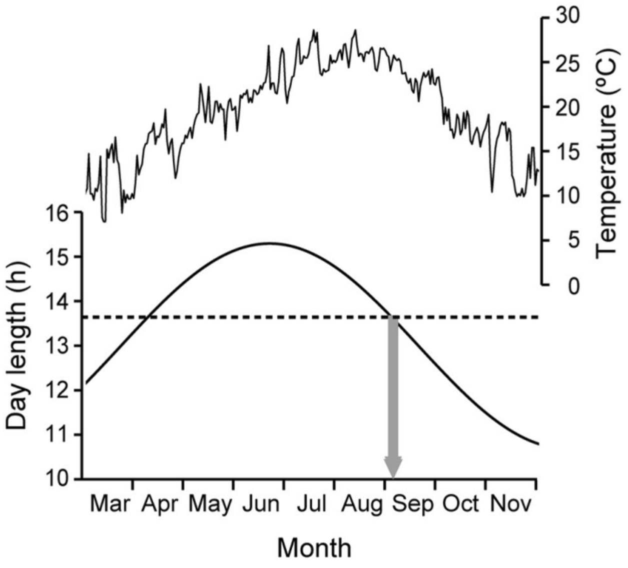


Fig. 6 Seasonal changes in temperature and day length in Takanabe (32°06′N, 131°31′E, ca. 50 m altitude), Miyazaki, Japan. Temperature is shown as a daily average of air temperature in 2009. Day length includes 1 h of twilight. The *broken line* indicates the critical photophase at 25 °C based on Fig. 2

In insects with a facultative egg diapause, induction of the diapause is often affected by the environmental conditions experienced by the mother (Danks 1987; Mousseau and Dingle 1991; Mousseau and Fox 1998; Tauber et al. 1986), and maternally induced egg diapause has been observed in species such as the silkworm, *Bombyx mori* L. (Kogure 1933) and the band-legged ground cricket, *Dianemobius nigrofasciatus* (Matsumura) (Shiga and Numata 1997), in addition to the mirids mentioned above. However, changes in the diapause status of eggs as a response of the females to photoperiod changes, as observed here for *A. triannulatus* (Fig. 3), have been described in only a few species (e.g., Bradford and Roff 1993 for *Allonemobius fasciatus* (De Geer); Kudô and Kurihara 1989; Shintani 2009 for *Trigonotylus caelestialium*). In the field, such a transition in response to a change in environmental conditions probably enhances the fitness of insects with facultative egg diapause.

Based on field collection and laboratory experiments, the seasonal life cycle of *A. triannulatus* is thought to be as follows. Adults occurring from late April to early June are considered to be overwintered-generation individuals, whereas those occurring in late June to July are individuals belonging to the first generation of the year. Since the duration of the pre-adult stages and maturation (minimum duration of one generation) at summer temperatures is 28 days (27.5 °C) to 32 days (25 °C) (Table 1), adults occurring in August and September are considered to be second-generation individuals. In this generation, earlier adults may lay nondiapause eggs and later adults may lay diapause eggs. As shown in the current study, a transition from laying nondiapause to diapause eggs may occur in some females. However, this transition may be costly because it occurred only in long-lived adults (Fig. 3). Thus, only a small proportion of the individuals may respond to a change in photoperiod in the field, and it is important to examine the proportion of adults that undergo this transition. Some of the adults occurring in September to November may be third-generation individuals. Thus, *A. triannulatus* has three or four generations each year in southern Kyushu.

If *A. triannulatus* adults produced nondiapause eggs in later seasons, the progeny would not reach adulthood or reproduce before winter, since the developmental period is prolonged due to the decreased temperature: if nondiapause eggs were laid in late September or later, the nymphs would hatch in mid-October and reach adulthood in mid- to late November at the earliest (average temperature is 19.4 °C in October and 15.0 °C in November). In this case, the adults would not mature due to the low temperatures in early winter. Furthermore, prey insects may be scarce in late autumn. Although *A. triannulatus* nymphs can develop to adulthood without prey, they may fail to grow well because they perform well on limited herbaceous plants that are preferred (Tajima and Shintani, unpublished data). This host-plant preference has been examined in another zoophytophagous mirid, *Macrolophus pygmaeus* (Rambur) (Ingegno et al. 2011). Furthermore, the quality of host plants may decline in autumn, as generally acknowledged for herbivorous insects (Awmack and Leather 2002; Schoonhoven et al. 1998). In this situation, individuals derived from late-season hatched nymphs would die before reaching the diapause (late embryonic) stage by winter. This time constraint may be the most important selection pressure that determines the critical photophase of the photoperiodic response in *A. triannulatus*. Indeed, no nymphs were observed in October and November in the current study (Fig. 5). Egg diapause is also often affected by the environmental conditions after oviposition (e.g., Tanaka 1994 for *Locusta migratoria*), so the sporadic hatching from diapause eggs (Fig. 1b) may have occurred because the incubation temperature (25 °C) was consistently higher than the autumnal temperature (Fig. 6). Such hatching leading to untimely development may not occur in the field.

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