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## Seasonal adaptations of the fall webworm *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) following its invasion of Japan

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**Abstract** The fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), invaded Japan from North America about 60 years ago. Immediately after its invasion – and for the first three decades – its life cycle was bivoltine, two generations per year throughout its entire distribution in Japan. Thereafter, its life cycle shifted to trivoltine in the southwestern areas of Japan. In the present study we examined the life-history traits proposed to be implicated in this event with the aim of clarifying the mechanism of this life-cycle shift. The critical photoperiod for diapause induction, as defined by the photoperiod at which 50% of individuals enter diapause, was shorter in the trivoltine populations than in their bivoltine counterparts. The temperature sensitivity of the photoperiodic response, as defined by the difference in the critical photoperiod between 20 and 25°C, was greater in the trivoltine populations than in the bivoltine ones. The geographic variation in larval and pupal periods was positively correlated to the latitude of the original localities of the populations. The change in the number of larval instars would be one of the main factors accounting for the regional differences in the developmental period. These results suggest that some life-history traits of *H. cunea* have changed following its invasion of Japan as an adaptive response to local climates.

**Keywords** Developmental traits · Diapause · Life cycle · Photoperiodic response · Voltinism

### Introduction

Alien species show various patterns of adaptations in terms of life-history traits following their invasion of new regions (Cox 2004). Substantial modifications in life-history traits and voltinism have been documented in some species of insects closely following their expansion into new habitats (Riedl and Croft 1978; Takeda and Chippendale 1982; Walker et al. 1983). In some invaded and introduced plants, adaptations along a latitudinal gradient have appeared, such as the age of reproduction in wild carrot (Lacey 1988) and the time of flowering in burr medic (Del Pozo et al. 2002). The response of seed germination in cheatgrass to temperature and flowering phenology varies according to local habitat conditions (Rice and Mack 1991; Meyer and Allen 1999). Some introduced vertebrates have evolved gradients in body size in different climatic conditions (Johnston and Selander 1964; Blem 1974; Yom-Tov et al. 1986; Williams and Moore 1989).

Widely distributed insects frequently develop local adaptations along a climatic gradient with respect to their various life-history traits and, consequently, in voltinism (Tauber et al. 1986; Danks 2006). Geographic variation in the photoperiodic control of diapause induction is one of the most remarkable of such adaptations and has been investigated in many species (Beck 1980; Danks 1987). Danilevsky (1965) found a general pattern that insect populations inhabiting higher latitudes have a longer critical photoperiod than those of the same species inhabiting lower latitudes. Other life-history traits, such as developmental rate, diapause intensity and body size, also frequently exhibit geographic clines (Masaki 1961, 1972, 1978; Bradshaw and Lounibos 1977). While there is no doubt that such a clinal variation is formed in each local population through natural selection (Tauber et al. 1986; Danks 1987; Bradshaw et al. 2004), little information is available on either the length of time or the process required for the establishment of such modifications of life-history traits and

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voltinism. A detailed study of both introduced and invading insects would be useful for obtaining more information on these issues (Tauber et al. 1986).

The distribution of the fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), was limited exclusively to North America before 1940; during the 1940s it invaded central Europe and eastern Asia (Warren and Tadic 1970; Umeya and Itô 1977). The first report of *H. cunea* in Japan was in Tokyo (35°40'N) in 1945 (Masaki 1975); from there, it expanded its distribution southwards to 32°N and northwards to 41°N (Tate 2000; Gomi et al. 2004). Mitochondrial (mt)DNA analyses suggest that the invasion of Japan was a single event and that the invading individuals originated in a single North American population (Gomi et al. 2004). The winter diapause in the pupal stage is primarily induced by the photoperiod, and early larval instars are stage sensitive to the photoperiod (Masaki 1977a). In the early stage of the invasion, the critical photoperiod, which is defined as a photoperiod that induces diapause in 50% of the individuals, was 14 h and 35 min at 25°C (Masaki et al. 1968) and was relatively stable within the range of 17–25°C (Masaki 1977a).

The life cycle of *H. cunea* was mostly bivoltine throughout its distribution for the first three decades following its invasion of Japan (Masaki 1975). In the bivoltine life cycle, adults of the overwintering generation appear in late spring, while adults of the first generation occur in mid-summer and produce a second generation. Pupae of the second generation enter diapause for overwintering. However, in the mid-1970s partially trivoltine life cycles were reported in two populations occurring about 500 km apart (Arai and Akiyama 1976; Uezumi 1976). Much later, a population in Kobe (34°41'N) was found to be trivoltine (Gomi and Takeda 1990). In this population, both the critical photoperiod for diapause induction and the developmental period were shorter than those found in the population of *H. cunea* that first invaded Japan (Itô et al. 1968, 1970; Gomi and Takeda 1990, 1991, 1996). Thus, the life-history traits had been modified in the Kobe population in terms of a shift in the life cycle from bivoltine to trivoltine.

photoperiods of the trivoltine populations were similar, and they were shorter than those of the bivoltine populations. A similar result was obtained at 20°C, although the difference in the critical photoperiod between the bivoltine and trivoltine populations was small. The critical photoperiod of the Tsukuba population, originating from the transition zone (Gomi 1996a), was relatively short at 20°C and intermediate at 25°C between the bivoltine and trivoltine populations.

In some native insect and mite species, the critical photoperiod for diapause induction shows a high correlation with the latitude of origin (e.g.,  $r = 0.96$  for *Chilo suppressalis*,  $r = 0.98$  for *Wyeomyia smithii* and  $r = 0.99$  for *Tetranychus urticae*) (Kishino 1970; Bradshaw and Lounibos 1977; Vaz Nunes et al. 1990). The codling moth, *Cydia pomonella*, formed a linear cline ( $r = 0.87$ ) in the geographic variation of this life-history trait about 200 years after its invasion of North America from Europe (Riedl and Croft 1978; Riedl 1983). In *H. cunea*, the correlation was relatively low at both 20 or 25°C, and the geographic pattern was step-wise rather than linear. These results suggest that this species has not spent enough time in Japan to form a linear cline in this trait and that the formation of the linear cline can be mediated by a step-wise pattern.

#### Temperature sensitivity in the photoperiodic response

The temperature sensitivity of the photoperiodic response is one of the more important life-history traits. In the linden bug, *Pyrrhocoris apterus*, the temperature sensitivity of the photoperiodic response controlling diapause induction was suggested to contribute to stabilization of the life cycle in the transition region between the univoltine and bivoltine areas (Numata et al. 1993; Saulich et al. 1994). A number of insects and mites have been investigated in terms of geographic variations of this trait in order to gain a better understanding of their respective life cycles (e.g. Sauer et al. 1986; Pittendrigh and Takamura 1987; Takafuji et al. 1991; Tanaka 1994).

### Geographic variation of photoperiodic responses

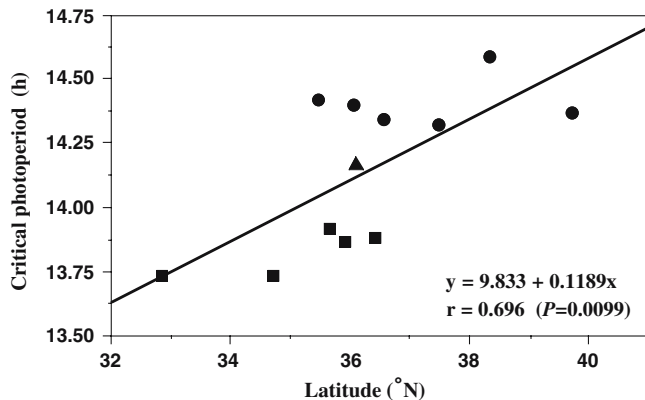
#### Critical photoperiod for diapause induction

The list of localities where *H. cunea* was collected for this study is given in Table 1 (Gomi and Takeda 1996; Gomi 1997). The photoperiodic response controlling diapause induction was investigated at 20 and 25°C (Fig. 1), and the critical photoperiod was found to be shorter at 25°C than at 20°C in all but the Sendai population. The correlation between the critical photoperiod and the latitude of origin was significant at each temperature ( $r = 0.526$  for 20°C,  $df = 10$ ,  $P = 0.0792$ ;  $r = 0.696$  for 25°C,  $df = 10$ ,  $P = 0.0099$ ). At 25°C, the critical

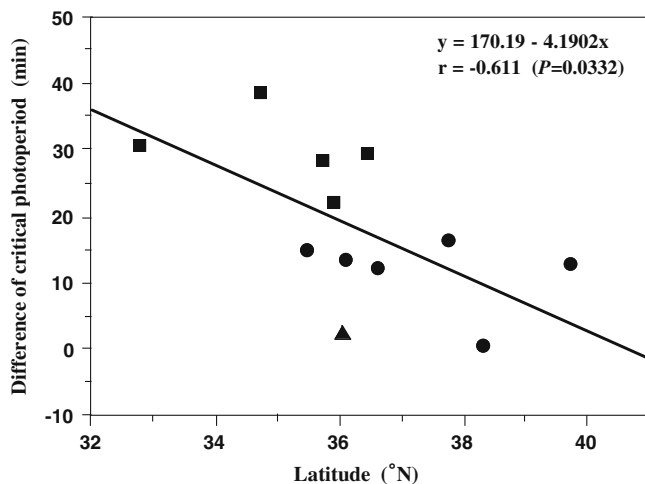
**Table 1** The list of localities from which *Hyphantria cunea* was collected

Locality	Latitude	Longitude	Voltinism
Akita	39.7°N	140.1°E	Bivoltine
Sendai	38.3°N	140.9°E	Bivoltine
Fukushima	37.8°N	140.5°E	Bivoltine
Utsunomiya	36.6°N	139.9°E	Bivoltine
Maebashi	36.4°N	139.1°E	Trivoltine
Tsukuba	36.1°N	140.1°E	Bi- and trivoltine
Fukui	36.1°N	136.2°E	Bivoltine
Saitama	35.9°N	139.6°E	Trivoltine
Kofu	35.7°N	138.6°E	Trivoltine
Tottori	35.5°N	134.2°E	Bivoltine
Kobe	34.7°N	135.2°E	Trivoltine
Kumamoto	32.8°N	130.7°E	Trivoltine

Temperature sensitivity, which is defined as the difference in the critical photoperiod for diapause induction between 20 and 25°C (Gomi 1995, 1997), was significantly larger in the trivoltine population than in the bivoltine populations ( $t$  test:  $df = 9$ ,  $t = 4.85$ ,  $P < 0.001$ ) and was negatively correlated to the latitude of origin ( $r = -0.611$ ,  $df = 10$ ,  $P = 0.0332$ ) (Fig. 1, 2). These results suggest that rearing temperature influenced the photoperiodic induction of diapause less in the bivoltine and transition populations. Thus, changes in the temperature sensitivity are closely implicated in the shift of the life cycle in *H. cunea*.



**Fig. 1** Geographic variation of the critical photoperiod for diapause induction at 25°C in *Hyphantria cunea* in Japan. The critical photoperiod is defined as the photoperiod at which 50% of individuals enter diapause when the incidence of diapause is investigated in photoperiods at 15-min intervals. Circles bivoltine populations, triangle transition population, squares trivoltine populations



**Fig. 2** Geographic variation of the temperature sensitivity for the photoperiodic response controlling diapause induction in *H. cunea* in Japan. Temperature sensitivity is defined as the difference in the critical photoperiod between 20 and 25°C. Circles bivoltine populations, triangle transition population, squares trivoltine populations

Sauer et al. (1986) found that in *Pieris brassicae* the difference in the critical photoperiod between 15 and 20°C decreased as the latitude of origin increased. In *H. cunea*, this same geographic trend was observed, with the southern trivoltine populations showing a greater temperature sensitivity in their photoperiodic response than the northern bivoltine populations. A similar result was obtained in the rice stem maggot, *Chlorops oryzae*, with once again a southern trivoltine population showing greater temperature sensitivity between 20 and 23°C than a bivoltine population (Takeda 1996). These results suggest that the temperature sensitivity of the photoperiodic response is implicated in the life cycle of insects and, consequently, is correlated to the latitudes of inhabited localities.

## Geographic variation of developmental traits

### Developmental period

Insects are ectothermic and their developmental rates are primarily regulated by ambient temperature. However, in many species of insects, the developmental rate is controlled not only by temperature but also by biological and other physical factors (Danks 1994). Photoperiod is a major factor regulating developmental rates in insects (Masaki 1967, 1972, 1978; Obrycki and Tauber 1981). In some insects, there is very little inter-population difference in the developmental period between different life cycles (Ritland and Scriber 1985; Pullin 1986; Bradford and Roff 1995). Bradford and Roff (1995) suggested that selection pressure is weaker in the developmental period than in the photoperiodic response controlling diapause induction in a cricket, *Allonemobius socius*. In the rice stem borer, *C. suppressalis*, however, the developmental period is shorter in the univoltine population than in the bivoltine population occurring at similar latitudes (Kishino 1970). In this moth, the developmental period is shorter in the northern populations than in the southern populations in each voltinism area (Kisino 1974). This type of geographic variation in life-history traits, called a “saw-toothed cline”, is observed in some insects (e.g. Kidokoro and Masaki 1978; Masaki and Walker 1987; Mousseau and Roff 1989; Scot and Dingle 1990; Nylin and Svård 1991; Ishihara 1998), and has been theoretically analyzed (Roff 2002).

The larval and pupal periods of *H. cunea*, which were not destined for diapause, positively correlated with their latitudes of origin (Fig. 3), indicating that the developmental period of the bivoltine population occurring in the northern area is longer than that in the trivoltine population occurring in the southern area. However, no conspicuous difference in the developmental period was found among populations occurring around 36°N, which represents the transition zone between the voltinisms. Thus, the developmental period of

*H. cunea* corresponds less clearly to the life cycle than the critical photoperiod for diapause induction.

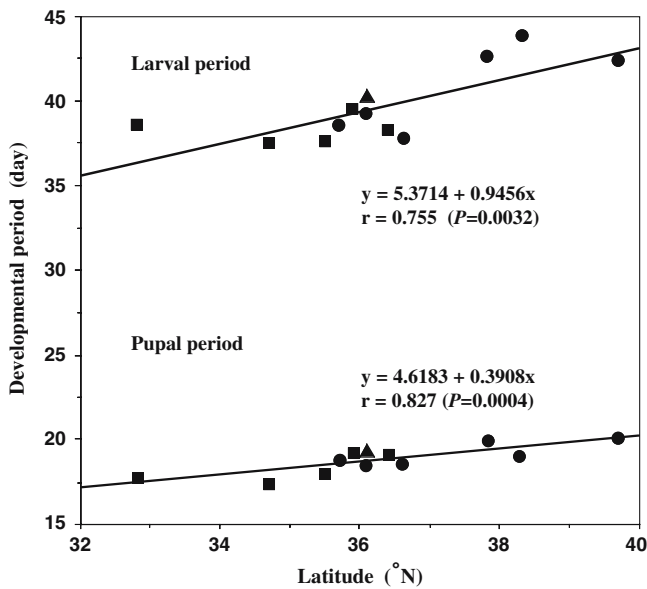
### Regional differences in the number of larval instars

The larvae of *H. cunea* aggregate and construct nest webs in the field until the fourth instar; thereafter, they disperse and live individually. Two types of *H. cunea* larvae, the six-instar and seven-instar, have been reported in North America (Morris and Fulton 1970) and Japan (Itô and Miyashita 1968). In Japan, the seven-instar type was predominant during the early stage of the invasion (Itô and Miyashita 1968). Gomi (1996b) and Gomi et al. (2003) investigated the larval developmental period and the incidence of the seven-instar larvae in four populations of *H. cunea* (Table 2). In the group-rearing experiment, where larvae were reared

under crowded conditions throughout the larval stage, the larval period differed significantly among the populations (Tukey-Kramer test:  $P < 0.05$ ). In the individual-rearing experiments, in which the larvae were reared individually from the fifth instar onwards, the larval period of the six-instar type was not different between the Akita and Saitama populations and between the Kobe and Kumamoto populations ( $P > 0.05$ ). The larval period of the seven-instar types was significantly longer than that of the six-instar type in the Akita and Kumamoto populations ( $t$  test:  $P < 0.0001$ ), while the incidence of the seven-instar type was significantly higher in the Kumamoto population than in the other populations (Tukey-type multiple comparisons for proportions:  $P < 0.05$ ). These results suggest that the high incidence of the seven-instar type is one of the underlying factors for the longer larval period.

The incidence of the instar type is affected by sex and environmental factors in *H. cunea* (Gomi 1996b, 2006; Gomi et al. 2005). Gomi et al. (2005) found that the quality of the host leaves affect the larval period of the Kobe population and that the incidence of the seven-instar type increased when the larvae were reared on hosts in which the larval period was extended. A similar tendency was observed in *Helicoverpa armigera* (Casimero et al. 2000). The incidence of the seven-instar type has been found to increase at higher temperatures in females (Gomi 2006). In addition, the pupal weight of the seven-instar type is heavier than that of the six-instar type (Gomi 1996b; Gomi et al. 2003, 2005). There is a positive correlation between female body size and fecundity in *H. cunea* (Morris and Fulton 1970; Gomi 2000), as is the case in many other insects (Honek 1993). Therefore, while females of the seven-instar type have the advantage of a larger body size for fecundity, they suffer the disadvantage of a longer larval period for survival, as in a number of other insects (Fitzgerald et al. 1988; Loader and Damman 1991; Slansky 1993; Atkinson 1994).

Univoltine grasshoppers in Europe were observed to have similar patterns of nymphal instar variation as *H. cunea*, in which the proportions of individuals with the larger number of instars increase with increases in



**Fig. 3** Geographic variation of the larval and pupal periods in *H. cunea* in Japan. Circles bivoltine populations, triangles transition population, squares trivoltine populations

**Table 2** The larval period and the incidence of the seven-instar type in *H. cunea* at 20°C under long-day conditions (16 h light/8 h dark)

Population	Larval developmental period (day) (mean ± SD)		Incidence of the seven-instar type (%)	
	Group rearing( $n$ ) <sup>a,c</sup>	Individual rearing <sup>b,c</sup>		
		Six-instar type ( $n$ )		Seven-instar type ( $n$ )
Akita	42.54 ± 3.04 (193) a	41.08 ± 2.18 (59) A	47.70 ± 1.90* (10)	14.49 b
Saitama	39.43 ± 2.14 (146) b	40.71 ± 1.88 (56) A	45.50 ± 0.71 (2)	3.45 b
Kobe	37.41 ± 2.35 (207) d	37.90 ± 1.42 (71) B	44 (2)	2.74 b
Kumamoto	38.59 ± 1.76 (231) c	38.06 ± 1.44 (47) B	43.19 ± 1.18* (27)	36.49 a

\*Significant difference ( $P < 0.001$ ) between the instar types according to the  $t$  test

<sup>a</sup>In the group rearing, larvae were reared crowdedly throughout the larval stage

<sup>b</sup>In the individual rearing, larvae were reared individually from the fifth instar

<sup>c</sup>The number of individuals is given in parenthesis. Means followed by the same letters are significantly different in the larval period by the Tukey-Kramer test at the 5% level and Tukey-type multiple comparisons for proportions in the incidence of the seven-instar type

temperature (Willott and Hassall 1998), at low latitudes (Telfer and Hassall 1999) and in females (Cherrill 2005). The temperature-size rule in grasshoppers was theoretically analyzed by Walters and Hassall (2006). In *H. cunea*, the incidence of the seven-instar type was not significantly different among the Akita, Saitama and Kobe populations. This result appears to be different from that in the grasshoppers, although only a small number of *H. cunea* populations have been analyzed to date. One reason for this difference may be that *H. cunea* has not spent enough time in Japan to adapt its developmental traits to the climate. Another explanation may be a difference in voltinism. The developmental traits of univoltine insects would respond more directly to local climate variables than those of multivoltine insects.

### Conclusions and perspectives

If insects enter diapause too early in the season, their reproductive potential may be reduced (Taylor 1980, 1981). In the Tsukuba population of *H. cunea* occurring in the transition zone, the females that entered diapause in the third generation produced a larger egg mass than those that did so in the second generation (Gomi 2000). This result can be applied to the situation in the southwestern areas of Japan, in which the life cycle of *H. cunea* has shifted from bivoltine to trivoltine, most likely because the weather is warm enough to complete three generations. As such, individuals producing a third generation in the southwestern areas would be favored by natural selection.

In the southwestern areas of Japan, *H. cunea* had a bivoltine life cycle for the first three decades immediately following its invasion due to their photoperiodic control of diapause (Masaki 1975, 1977b). At present, the populations occurring in the trivoltine areas show shorter critical photoperiods and greater temperature sensitivity than the northern bivoltine populations. These traits of photoperiodic response contribute to the production of a third generation by reducing the incidence of diapause in the second generation. Therefore, individuals showing a short critical photoperiod and a high temperature sensitivity would have been selected for and, consequently, the present trivoltine populations have established themselves in the southwestern areas of Japan. Additional important factors in the life cycle of insects – other than the photoperiodic response controlling diapause induction – are the developmental traits (Zaslavsky 1988). The developmental traits of *H. cunea* showed local divergence in the present study. The progression of local divergence in developmental traits would modify the timing of photoperiodic induction of diapause and may lead to the formation of a linear geographic cline in the critical photoperiod in the future.

The climate of the Earth has warmed over the past 100 years, and there is ample evidence that climate changes have already affected a wide spectrum of

organisms (Walther et al. 2002). In the pitcher-plant mosquito, *Wyeomyia smithii*, the critical photoperiod for diapause induction has become shorter in the northern area of the USA as a result of adaptation to recent global warming (Bradshaw and Holzapfel 2001). Preliminary evidence suggests that the life cycle of *H. cunea* is being influenced by the effect of global warming (unpublished data). Global warming may therefore be a strong modifying factor for the seasonal adaptation of *H. cunea*.

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