Threshold weight for starvation-triggered metamorphosis in the yellow-spotted longicorn beetle, *Psacotha hilaris* (Coleoptera: Cerambycidae)

Florence Njeri MUNYIRI, Wataru ASANO, Yoshinori SHINTANI[†] and Yukio ISHIKAWA*

Laboratory of Applied Entomology, Graduate School of Agricultural and Life Sciences, The University of Tokyo; Tokyo 113–8657, Japan

(Received 3 February 2003; Accepted 23 June 2003)

Abstract

The development of 4th stadium *Psacotha hilaris* larvae under various feeding and starving regimens was investigated to determine whether there is a threshold weight for metamorphosis. In larvae fed *ad libitum*, 56% of individuals spent a mean of 13 d in the 4th stadium and 18 d in the 5th stadium before pupation, whereas the rest remained in the 4th stadium for 24 d and pupated. When starved upon ecdysis to the 4th stadium, no larvae molted to the 5th stadium and most eventually died without pupation. In contrast, when larvae were fed for 1 d and then starved, 47% prematurely metamorphosed into small pupae after a mean of 18 d in the 4th stadium. Pupation success from the 4th stadium increased as the feeding period was extended, reaching 97% in the larvae that had fed for four days. All these pupae gave rise to small but morphologically normal adults. The relationships between the weight changes of experimental larvae during starvation and their pupation success suggested the threshold weight for metamorphosis to be 180 mg. The adaptive significance of premature pupation in starved *P. hilaris* is discussed as a life history strategy under unpredictable food conditions for larval growth.

Key words: *Psacotha hilaris*; premature pupation; starvation; threshold weight; survival

INTRODUCTION

Food shortage is a constraint that insects often have to contend with in nature. Starvation in many lepidopteran larvae results in delayed metamorphosis (Beck, 1950; Lower, 1961; Jones et al., 1980; Cymborowski et al., 1982; Morita and Tojo, 1985). In the tobacco hornworm *Manduca sexta*, for example, a body weight of 5 g is a proximate cue for metamorphosis (Nijhout and Williams, 1974). If larvae of this insect do not attain this size at the initial stage of the 5th stadium (normal last larval stadium), they undergo supernumerary larval molts, which in nature probably allow more time for the individuals to search for food and pursue further growth (Nijhout, 1975; for other species see: Blakley and Goodner, 1978; Blakley, 1981; Fischer and Fiedler, 2001). Some species of dermestid beetles such as *Trogoderma glabrum* are known to repeat larval molts into increasingly smaller individuals if deprived of food for extended periods of time, and when given food, resume growth and metamorphosis (Beck, 1971, 1972).

In contrast to the above species, two coleopteran species, a mushroom beetle *Dacne picta* and a dung beetle *Onthophagus taurus*, have been reported to shorten their larval period, instead of prolonging it, and pupate at smaller sizes when food supply is exhausted (Sato and Suzuki, 2001; Shafiei et al., 2001). More recently, we found that the yellow-spotted longicorn beetle *Psacotha hilaris*, also pupated prematurely upon starvation (Shintani et al., 2003). Since the number of species reported to show such a phenomenon is limited, little is known about starvation-induced premature metamorphosis.

P. hilaris is an important pest of mulberry and fig trees in Japan. Female beetles lay their eggs in the subcortical tissues of the trunk and the neonate larvae bore tunnels within the trunks. At 25°C and under a long day photoperiod (15 h light : 9 h dark), about half of normally fed *P. hilaris* larvae pupate from the 4th stadium and the remainder pupate after an additional larval molt to the 5th stadium (Shintani et al., 1996a, b). The mechanism that dictates whether the larvae pupate from the 4th or the

* To whom correspondence should be addressed at: E-mail: ayucky@mail.ecc.u-tokyo.ac.jp

[†] Present address: Hokuriku Research Center, National Agricultural Research Center, Joetsu, Niigata 943–0193, Japan

5th larval stadium remains unknown.

P. hilaris larvae that have fed for the first few days of the 4th stadium appear to acquire competence for metamorphosis; upon starvation, they terminate larval life and pupate prematurely (Shintani et al., 2003). Moreover, when 4th stadium larvae are provided with a low nutritive diet after having fed on a normal diet for a few days, they tend to avert molting to the next larval stadium and pupate earlier than those continuously given a normal diet (Shintani et al., 2003). These results suggest that only the first few days of feeding during the 4th stadium are sufficient for larvae to acquire the competence for metamorphosis. However, the physiological process determining the acquisition of the competence has remained unknown.

Based on previous findings, we hypothesized that there is a threshold weight that *P. hiliaris* larvae must attain in order to gain the competence for metamorphosis. In the present study, we tested this hypothesis by examining growth, molting and metamorphosis of *P. hiliaris* under various feeding and starvation regimens.

MATERIALS AND METHODS

Insect rearing. A colony of *P. hilaris* was established from more than 20 adults collected from a mulberry field at Ino (33.5°N, 133.4°E) in 1996. Insects were reared on commercial artificial diets for the silkworm (Silkmate 2S®) until the 3rd stadium and thereafter changed to Insecta LF®, Nihon

Nosan, Co., Yokohama) following the method of Shintani et al. (1996a). Neonate larvae placed individually in Petri dishes containing fresh diet were reared at 60% relative humidity, 25°C and under a long day photoperiod (15 h light and 9 h dark, 15L:9D).

Effect of starvation after some feeding in the 4th stadium. Larvae were reared under the long day photoperiod at 25°C until the end of the 3rd stadium. On the day of ecdysis to the 4th stadium (day 0), they were randomly assigned to either the experimental or control group. Control larvae were provided with food *ad libitum* during the entire larval development. Experimental larvae were weighed and transferred to clean Petri dishes with no food or moisture source on days 0, 1, 2, 3, or 4 of the 4th stadium (Fig. 1, Experiment A, S, 1F-S, 2F-S, 3F-S, 4F-S). All experimental and control larvae were checked daily for molting and/or pupation, and their body weights were recorded after each molt. To trace the daily body weight changes of larvae, S, 1F-S and 4F-S experiments were repeated once more. The general state of health of the larvae was estimated by their response to probing with a forceps. For those individuals that died, the date and their developmental stage were also recorded.

Effect of re-feeding after starvation on the development of larvae. To examine if acquisition of the competence for metamorphosis is limited to the initial stage of the 4th stadium, newly ecdysed 4th stadium larvae were starved for 6 or 20 days, and

Fig. 1. Schematic representation showing the development of 4th stadium *P. hilaris* larvae under various feeding and starvation regimens at 25°C and 15 h light : 9 h dark. Between 20 and 33 *P. hilaris* larvae were subjected to each feeding regimen within 12 h of ecdysis to the 4th stadium. Feeding and starvation are designated by F and S, respectively. For example, 4F-4S-F indicates that newly ecdysed 4th stadium larvae were fed for four days, starved for four days and then fed *ad libitum*. Only typical patterns of pupation are shown in each feeding regimen.

Table 1. Developmental success of the 4th stadium *P. hilaris* larvae under different feeding and starvation regimes^a

Feeding regime ^b	N	Weight after ecdysis to 4th stadium (mg)	Weight at initiation of starvation (mg)	% larvae molted to 5th stadium	% 5th stadium larvae pupated	Larval period (day)		Overall pupation rate (%)	Pupal weight ^d (mg)	Pupal period (day)
						4th	4th+5th ^c			
S	30	189±54 a	189±54 a	0 (0)	—	19.5±2.1 b (2)	— (0)	7	135±7 a	11.5±0.7 a
1F-S	30	186±49 a	257±66 b	0 (0)	—	17.9±1.7 a (14)	— (0)	47	136±44 a	10.9±0.6 a
2F-S	26	185±39 a	306±75 c	4 (1)	0	18.0±2.4 a (20)	— (0)	77	171±45 b	11.0±0.8 a
3F-S	29	183±44 a	311±93 c	17 (5)	17 (1)	18.2±1.6 a (24)	32 (1)	86	188±55 b	11.2±0.7 a
4F-S	32	196±46 a	351±81 d	3 (1)	0	19.0±1.9 a (31)	— (0)	97	219±54 c	11.4±1.4 a
F	27	205±63 a	—	56 (15)	100 (15)	23.8±2.1 b (12)	30.5±3.0 ^e (15)	100	392±65 d	11.5±1.3 a

^a Values are means±S.D. Means followed by the same letter in the same column are not significantly different at 5% level by Tukey-Kramer's multiple range test. Numbers of insects that pupated are shown in parentheses.

^b See Fig. 1 for the feeding and starvation regimes.

^c Total duration of the 4th and 5th stadia of larvae that pupated in the 5th stadium.

^d Values for those individuals that pupated in the 4th stadium.

^e Duration of the 4th and 5th stadia: 12.6±1.9 d and 17.9±3.5 d, respectively.

thereafter provided with food *ad libitum* (Fig. 1, Experiment B, 6S-F, 20S-F). Next, to examine whether starvation-triggered metamorphosis can be suppressed if the larvae are fed again, a group of 4th stadium larvae were given food for four days, then deprived of food for four days and again allowed access to food (Fig. 1, Experiment C, 4F-4S-F). In this experiment, ingestion of food was checked by observing the midgut through the integument of larvae.

Data analysis. Statistical analyses were conducted using a software package, Statview® (SAS Institute Inc., NC, USA). Data were analyzed by ANOVA, and the significance of differences among means was determined by Tukey-Kramer's multiple range test. In the text and figures, values are presented as means±standard deviation.

RESULTS

Effect of total starvation after different periods of feeding in the 4th stadium (Experiment A)

When food was supplied to 4th stadium *P. hilaris* larvae *ad libitum*, all pupated successfully after showing one of these two patterns; 56% of larvae molted to the 5th stadium after a mean of

12.6 d and subsequently pupated 17.9 d later, whereas the remainder pupated after a mean of 23.8 d without molting to the 5th larval stadium (Table 1).

The timing of starvation significantly affected the survival of larvae (Table 1). Most of the larvae that never had access to food in the 4th stadium eventually succumbed to death without undergoing metamorphosis (Table 1, S; mean survival time=28.7±3.2 days, $n=28$). In contrast, 47% of the larvae that fed for one day in the 4th stadium pupated successfully (Table 1, 1F-S). Pupation success increased to 77% after feeding for two days (2F-S), and four days of continuous feeding in the 4th stadium was sufficient to support metamorphosis in 97% of the larvae (4F-S). This value was similar to that of the larvae fed *ad libitum* (100%, F).

The pupae obtained from the 4F-S regimen were significantly heavier than those obtained from the 1F-S, 2F-S and 3F-S regimens, but they were still significantly smaller than the fed controls (Table 1). All controls and experimental pupae produced morphologically normal adults except for the difference in size. Adult weights were strictly dependent on pupal weights (data not shown; $r^2=0.98$, $p<0.001$).

The relationships between the weight of a respective larva at the start of starvation and its pupation success suggested the presence of a threshold weight for metamorphosis (Fig. 2). None of the larvae weighing <180 mg survived to pupation, while all the larvae weighing >360 mg successfully pupated. The pupation success of larvae weighing in between was apparently dependent on the timing of food deprivation. When larvae of a similar weight were compared, those that were starved later in the 4th stadium had a higher chance of pupation (Fig. 2). This result suggests that the destiny of the starved larvae was not determined simply by the weight after a specific period of starvation, other-

Fig. 2. Pupation success of all experimental *P. hiliaris* larvae in Experiment A as a function of larval weight at the start of starvation and the day of starvation. Each symbol represents an individual. Symbols are shifted horizontally to avoid overlapping.

wise, larvae of a similar weight should have displayed similar pupation success regardless of the timing of food deprivation.

Starvation greatly reduced the proportion of individuals that molted to the 5th larval stadium (Table 1). While 56% of larvae molted to the 5th stadium when given food *ad libitum*, only a few molted to the 5th stadium when starved. Furthermore, the few that molted to the 5th stadium rarely survived to pupation (Table 1).

In those individuals that successfully pupated from the 4th larval stadium, starvation significantly decreased the duration of the 4th stadium ($F=17.6$, $p<0.001$, Table 1). Whereas the duration of the 4th stadium for control individuals was 24 days, the larvae in the 1F-S, 2F-S, 3F-S and 4F-S regimens pupated in 18–19 days (see Fig. 1). On the other hand, no significant difference was found in the duration of the pupal stage between experimental and control animals ($F=0.8$, $p>0.05$, Table 1).

Effect of re-feeding after starvation on the development of larvae (Experiment B)

All larvae that were starved for six days in the 4th stadium pupated successfully after re-feeding (Table 2, 6S-F). Interestingly, all but one individual pupated from the 4th stadium. All the larvae, except two, withstood starvation for 20 days and pupated after re-feeding (20S-F). However, their developmental process was apparently different from that of the controls or larvae in the 6S-F regimen. The larvae in the 20S-F regimen gained weight very slowly (Table 2): they gained only 16 mg

Table 2. Effect of starvation with subsequent furnishing of food on growth and development of *P. hiliaris* larvae^a

Feeding regime ^b	N	Weight after ecdysis to 4th stadium (mg)	Weight after starvation (mg)	Weight 1 d after re-feeding (mg)	Weight 4 d after re-feeding (mg)	% molted to 5th stadium	Larval period (day)		Pupal weight (mg)	
							4th	4th+5th ^c	4th	5th
6S-F	22	169±39 a	121±28 a	208±71 a	337±73 a	5 (1)	23.5±4.7 a (21)	36.0 (1)	290±48 b (21)	420 (1)
20S-F*	20	166±43 a	93±26 b	109±39 b	246±86 b	65 (13)	39.8±16.5 b (5)	56.7±6.3 ^d (13)	175±65 c (5)	426±76 a (13)
F	25	183±31 a	—	—	—	52 (13)	24.3±2.1 a (12)	32.3±2.7 (13)	367±86 a (12)	410±36 a (13)

^a See the footnote to Table 1. * Two individuals died during starvation on days 18 and 19.

^b See Fig. 1 for the feeding and starvation regimes.

^c Total duration of the 4th and 5th stadia of larvae that pupated in the 5th stadium.

^d Duration of the 4th and 5th stadia: 33.3±4.0 d and 23.4±3.6 d, respectively.

(17% of the pre-feeding body weight) after re-feeding for one day, whereas those in the 6S-F regimen gained 87 mg (72%). A marked difference between the two experimental groups was also found in the percentage of larvae that molted to the 5th larval stadium. As much as 65% of larvae in the 20S-F regimen entered the 5th stadium compared with only 5% in the 6S-F regimen. The weights of pupae formed from the 5th stadium larvae in the 20S-F regimen were, although very variable, comparable with their counterparts in the control (Table 2).

The duration of the 4th stadium was similar for controls and larvae in the 6S-F regimen; however, pupae formed from the latter were significantly smaller than control pupae (Table 2). It is clear from this result that commitment for metamorphosis did not occur during the six days of starvation; otherwise pupation should have occurred much earlier.

The very low growth rate observed after re-feeding in the 20S-F regimen suggests that the physiological state of larvae changed when they were starved for a long period. They appeared to have entered quiescence, a state of non-programmed developmental arrest. When the weight at the time of re-feeding was compared, those that pupated from the 4th stadium were heavier (119 ± 11 mg, $n=5$) than those that molted to the 5th stadium (88 ± 25 mg, $n=13$; $F=12.2$, $p<0.001$). This suggests that upon re-feeding, lighter larvae tended to undergo an additional larval molt rather than pupation.

Effect of alternate feeding and starvation on larval development (Experiment C)

When 4th stadium larvae were given a second opportunity to feed after four days of feeding and four days of starvation (4F-4S-F), only 50% fed again, whereas the rest, instead, purged their guts to prepare for pupation. Those larvae that fed again also discontinued feeding in a few days, purged their guts and consequently pupated. The percentage of larvae that pupated from the 4th stadium was similar for the 4F-4S-F and 4F-4S regimens ($>95\%$, Table 3). Both groups of larvae completed the 4th stadium much earlier than the control ($F=31.2$, $p<0.001$, Table 3). The pupae obtained from the 4F-4S-F regimen were significantly heavier than those from the 4F-S regimen ($F=22.6$, $p<0.001$, Table 3). In the 4F-4S-F regimen, interestingly, whether or not larvae fed again did not cause a significant difference in the pupal weight ($F=0.9$, $p>0.05$). This is because at the 2nd opportunity for feeding, only lighter larvae (130–280 mg, mean 213 mg, $n=13$) re-fed for a few days but heavier ones (280–380 mg, mean 316 mg, $n=13$) did not.

DISCUSSION

It was noted that the occurrence of pupation in the 4th stadium was concentrated in two discrete periods irrespective of the feeding regimens (Fig. 1). The control and larvae in the 6S-F regimen pupated with a mean period of 24 days, while all others except for larvae in the 20S-F regimen pupated with a mean period of 18–20 days. These results strongly suggest that commitment for premature

Table 3. Effect of alternate feeding and starvation on larval development of *P. hilaris*^a

Feeding regime ^b	N	Weight after 4 days feeding (mg)	% entered 5th stadium	% pupated from 4th stadium	Larval period (day)		Pupal weight (mg)	
							Final stadium	
					4th	4th+5th ^c	4th	5th
4F-S	29	369±73 a	3 (1)	97 (28)	18.8±2.8 a (28)	26 (1)	220±56 a (28)	280 (1)
4F-4S-F	25	343±79 a	4 (1)	96 (24)	19.7±3.7 a (24)	31 (1)	277±53 b (24)	300 (1)
F	26	374±37 a	50 (13)	50 (13)	24.4±3.2 b (13)	31.2±4.7 (13)	384±60 c (13)	455±81 (13)

^a See the footnote to Table 1.

^b See Fig. 1 for the feeding and starvation regimes.

^c Total duration of the 4th and 5th stadia of larvae that pupated in the 5th stadium.

pupation occurred at a specific timing, which is different from that of the fed control. A marked effect of temporary food deprivation in the 4F-4S-F regimen suggests that being in a starved state between day 5 and day 8 is crucial for the induction of premature pupation. Since the destiny of most larvae in the 4F-4S-F regimen was already irreversible when they were given a second opportunity for feeding on day 8, commitment for starvation-triggered pupation should have occurred between day 5 and day 8. Considering that it takes some time for the larvae to fall into 'a starved state' after food deprivation, and that feeding on and after day 7 appears to suppress starvation-triggered premature pupation (see 6S-F in Fig. 1), commitment for premature pupation is likely to have occurred on day 7 or day 8.

Analysis of the body weight changes of starved larvae suggested that the development of starved larvae can be explained by the following hypotheses (Fig. 3): (1) When a starved larva weighs more than 180 mg on the day of commitment (day 7 or 8), it is destined for pupation. (2) In contrast, commitment is suspended in a larva weighing less than 180 mg, and development is eventually arrested if starvation persists. The mean weight of larvae in the S, 1F-S and 4F-S regimens on day 8 was 120, 180 and 260 mg, respectively (Fig. 3). Few larvae in the S regimen weighed >180 mg, while almost

Fig. 3. Body weight as a determinant of larval destiny on the day of commitment—a hypothetical explanation. The threshold weight and the day of commitment are assumed to be 180 mg and day 8, respectively. The lines show the changes of mean body weights of the larvae. Vertical bars indicate standard deviation.

all larvae in the 4F-S regimen weighed >180 mg. In the 1F-S regimen, about 50% of larvae weighed >180 mg on day 8. These findings are concordant with the results that 7%, 47% and 96% of larvae in the S, 1F-S and 4F-S regimens, respectively, achieved metamorphosis. The pupation success of the larvae weighing between 180 and 360 mg was dependent on the timing of food deprivation (Experiment A, Fig. 2). This phenomenon may be explained as follows: When larvae are deprived of food earlier, they would have to wait a longer period of time for the day of commitment. Hence, a larger portion of larvae could not maintain a body weight of >180 mg while waiting, and consequently failed to pupate.

P. hilaris larvae shorten their larval life and pupate at a smaller body size if the food supply is limited. In nature, *P. hilaris* larvae do not move from one host plant to another and have to complete their development in the trunks into which they have been deposited as eggs. Under such circumstances, it seems highly adaptive to shorten larval development time and form a small pupa, rather than to remain as a larva, in the event of exhaustion or deterioration of its food resources.

In a coleopteran, *Onthophagus taurus* (Scarabaeidae), final (3rd) stadium larvae exceeding 80 mg shorten their larval life and pupate upon starvation (Shafiei et al., 2001). Similarly, in *Dacne picta* (Coleoptera: Erotylidae), larval development is shortened if final (4th) stadium larvae are starved after feeding for two days (Sato and Suzuki, 2001). In both *O. taurus* and *D. picta*, larvae have to be in their normal final stadium to undergo pupation upon starvation. The final larval stadium of *P. hilaris* is not fixed under normal conditions; they pupate either after the 4th or 5th stadium under long day conditions. In contrast to the 4th stadium *P. hilaris* larvae, which have to feed for the first few days to acquire the competence for pupation, newly ecdysed 5th stadium larvae can pupate without any feeding (Shintani et al., 2003). This finding can be explained if we assume that there is no stadium-dependent change in threshold weight for metamorphosis; the 5th stadium larvae have far exceeded the threshold weight right from the day of ecdysis.

As already noted, starvation-triggered early metamorphosis has been reported in coleopteran species of Erotylidae (*D. picta*; Sato and Suzuki, 2001) and Scarabaeidae (*O. taurus*; Shafiei et al.,

2001). The present finding in *P. hilaris* is the first example in a third coleopteran family, Cerambycidae. In *O. taurus*, the larvae must complete their larval life by consuming the dung into which their mothers have deposited them as eggs (Sowig, 1996; Moczek, 1998). The larvae of *D. picta* complete their life in a short-lasting food resource, mushrooms (Sato et al., 1999). Thus, in nature, the larvae of these species are similarly faced with substantial variation in food resource availability. Therefore, premature pupation under limited food supply may be a common strategy among coleopteran insects that face restrictive food resource, and is worth further investigation in other species.

ACKNOWLEDGEMENTS

We thank Dr. M. Harris of North Dakota University for critical comments on the manuscript. We thank Dr. S. Tatsuki of our laboratory for his encouragement throughout this study.

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