



タバコシバンムシにおける後胚子発育の温度と光周期による制御

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Temperature and Photoperiodic Regulation of the Postembryonic Development of the Cigarette Beetle, *Lasioderma serricorne* (Coleoptera: Anobiidae)

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ABSTRACT

The life cycle characteristics of a stored product-household pest, the cigarette beetle, *Lasioderma serricorne* (F.) was investigated by individually rearing under various photoperiod and temperature conditions. Two stocks (E and S) were used for comparison. The insect responded to a short-day rearing by extending the period of ultimate larval instar, undergoing supernumerary molts. The period of last larval instars under LD 12:12 varied between 30 and 205 days at 23°C in the S stock and between 24 and 208 days at 25°C in the E stock. The frequency of supernumerary molts under LD 12:12 was the highest at 23°C of the 4 temperatures investigated, 20, 23, 25 and 30°C in the S stock and at 25°C in the E stock. The E stock extended the second instar period of larval development also which occurred under LD 16:8. The short day effect was more prominent at 23°C and 25°C. 30°C overrode photoperiodic effect producing all fast developing individuals. The extension of larval period did not result in the larger body size. This indicates that the extension of larval period is due to stationary molts in diapause, not to the extension of feeding period. The two stocks had different threshold temperatures that were very high to compare with outdoor insects, 15.3 and 14.9°C for the S and E stocks, respectively. The number of eggs found in the ovary of newly emerged females that were reared at 20°C was less than half that of females reared at higher temperatures, 23, 25 and 30°C in the S stock. Grading of developmental speed seems therefore to be controlled at multiple check points in this species that supplies founders of new colony continuously after population collapses due to occasionally occurring environmental hazards. Artificial selection for slow developing individuals showed a plasticity of this trait, which means the versatility in the life cycle regulation is supported not only by a rich repertoire of physiological adaptations but also a genetic variability.

Key words; *Lasioderma serricorne*, Larval diapause, Photoperiodic response, Stored product pest, Cigarette beetle, Supernumerary molt

Introduction

The tobacco beetle, *Lasioderma serricorne* (F.) is an important stored product pest. It has been found all over the tropical and subtropical as well as in most parts of temperate regions (Howe, 1957). Since its infestation sometimes causes large economic losses, this species occupies a rank of the most important pests especially on stored tobacco leaves (Takaoka and Nakazawa, 1956). The biology and the control methods of this species have, therefore, been studied in many countries.

L. serricorne infests on a wide range of foodstuff. When Howe (1957) reviewed the biology of this beetle, he listed

the products that had records of infestation by this beetle. A typical poly- or omni-phagy has been shown in this list including almost all kinds of stored products such as grains, beans, nuts, flour, dry woods, as well as tobacco. Not only plant materials but also animal materials are listed.

Recently, this beetle has attracted much attention in Japan since its parasitoid, *Cephalonomia gallicola* (Bethyridae) causes a serious medical problem of stinging residents in the ferro-concrete apartments. In such buildings larvae of the host beetle damage tatami mats made of imported rice straws. Therefore, the ultimate solution of this problem is to eradicate the beetle

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stinging residents in the ferro-concrete apartments. In such buildings larvae of the host beetle damage tatami mats made of imported rice straws. Therefore, the ultimate solution of this problem is to eradicate the beetle larvae (Imoto and Momoi, 1992; Momoi and Tanioka, 1994).

The beetle somehow succeeded to adapt themselves from forest dwelling, first to store-house situation and then to residences, changing their original life-cycle parameters to more extensively colonize urban situations that are characterized as more buffered conditions from the fluctuation in environmental factors. Urban environment provides the beetle with not only more stable buffered environment but also with warm and more humid conditions that favor reproduction to produce more generations annually.

The present investigation aims to clarify the life cycle regulation of this beetle not only to solve these sanitary and medical problems but also to characterize urban environment for insect colonization by observing a larva individually reared in a vial.

Materials and Methods

Stock colonies of *Lasioderma serricorne* (F.) used in this experiment have been cultured in our laboratory for more than 8 years. The experiments were conducted in our laboratory between 1987 and 1991. One stock (E) is derived from the Health Research Institute of Nagoya City, and the other (S) from the Central Research Institute of Japan Tobacco and Salt Public Corporation (Now JT Industry Co., Ltd). The insects were reared in mass at 25°C under LD 16:8. Three walk-in constant temperature rooms (3 m² floor area and 1.8 m high each) set at 20, 25 and 30°C, 70% R.H. and two incubators (NK model, capacity more than 400 liters) set at 23°C, ca.50% R.H. were used for rearing. Two photoperiods, LD 16:8 and 12:12 were used as representative long-day and short-day conditions, respectively. In each walk-in room, set at LD 16:8, a wooden cabinet of 45×70×50 cm with electric timer controlling a fan and a 10 W fluorescent light was placed to make LD 12:12.

The experiments were started with eggs collected on corrugated sheets of filter papers of 10 cm² on which a tea-spoonful of dry yeast powder ("Ebiosu", Asahi Beer Co., Ltd.) was placed. The sheets were kept with ca. 200 adults in a cylindrical plastic container of 13 cm across and 5 cm deep with a lid. The adults were allowed to oviposit on the sheet for 24 hours. The next day, the sheet was cut to provide an equal number of eggs.

A 5 ml glass tube of 1.5 cm across and 4 cm length was used for each individual. Sixty individuals were used for each experimental replica. Development was individually

recorded subsequently in various environmental conditions and food (dry yeast) consumed was compensated at each observation. Dates of egg hatching, larval molts, pupation, pupal eclosion, and adult emergence from the cocoons, as well as the width of adult prothorax and the number of eggs carried by a newly emerged female were observed under a binocular microscope with a scored eye piece. Newly emerged adults stay inside the cocoon until cuticular hardening and sexual maturation (Howe, 1957; Niiho, 1982).

Forty earliest emerging adults of the S stock were selected every generation that were kept in mass under LD12:12 at 25°C to examine the plasticity in the rate of development. Offspring was reared individually for developmental test at the third and sixth generation.

Results

Figure 1 depicts developmental events that mark stages of development. Each bar represents records of an individual for hatching, each of three larval molts, supernumerary molts, pupation, pupal eclosion and adult emergence. The individual recordings for each event are connected vertically. Two such events designate a specific stage (a-g). **Figures 2–5** show the developmental profiles of individuals at different temperatures under LD 12:12 and 16:8. Photoperiodic effect appeared clearly in the period of fourth instar larva except at 30°C. **Table 1** summarizes the developmental characteristics at a mature larval stage, while **Table 2** for total post-embryonic period.

Under LD 16:8 at 20°C, mature larvae, fourth and supernumerary instars, of the S stock developed uniformly fast but under LD 12:12 development was retarded significantly, i.e., 20-29 vs. 24-184 days respectively (**Fig. 2** a vs. b). In the E stock, photoperiodic effect was not so apparent as in the S stock (**Fig. 2** cd). When development was retarded, they very often underwent supernumerary molts under both photoperiods. The period of the 4th instar larva was longer under LD 12:12 than under LD 16:8, while the period of the 2nd instar was longer under LD 16:8 than under LD 12:12, though the retardation in the 2nd instar is much smaller than in the 4th instar. **Figure 6** illustrates this condition. Under LD 12:12 the distribution of 2nd larval period is uniformly short and independent of the total larval period but under LD 16:8 distribution of relative length of second instar differed from the pattern obtained under LD 12:12 where some individuals had longer second instar period than others. Individuals having short 2nd instar had short 4th instar and the other having long 2nd instar had long 4th instar. The two periods were dependent. The figures were plotted against total period of larval development.

Under LD 16:8 at 23°C, mature larvae of the S stock

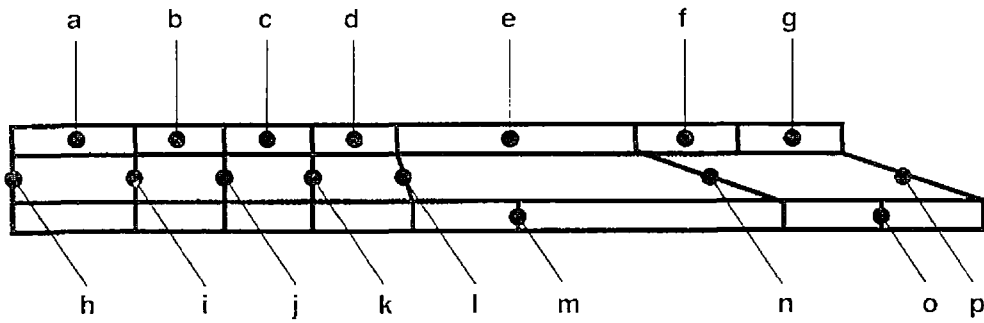


Fig. 1 Developmental events and the stages delineated by them, depicted in Figs. 2-5. a, egg; b-e, 1st-4th larval instars; f, pupa; g, adult inside the cocoon; h, egg-laying; i, hatching; j-l, 1st-3rd larval-larval molt; m, supernumerary molt; n, pupation; o, pupal eclosion; p, adult emergence.

developed fast but under LD 12:12 development was retarded significantly, i.e., ca 17-41 vs. 30-205 days, respectively (**Fig. 3 a b**). When development was retarded, they underwent supernumerary molts. In the E stock, photoperiodic effect was apparent but it was less clear-cut than in the S stock (**Fig. 3 c d**). Not only the rate of development in the E stock was faster than in the S stock under LD 16:8, but also the degree of extension in developmental time under LD 12:12 was much smaller in the E stock than in the S stock. Under LD 12:12, the extension of larval period was greater at 23°C than at 20°C. Also, the number of larvae undergoing multiple supernumerary molts was higher than at 20°C. The incidence of supernumerary molts was very low in the E stock compared to the S stock under LD 16:8.

At 25°C, photoperiodic effect appeared in the same way as at 23°C in both the stocks, though a small proportion of the population took longer time to pupation than at 23°C except under LD 16:8 in the E stock (**Fig. 4 a d**). Photoperiodic effect was most dramatic at this temperature of the three low-intermediate temperatures used. This temperature suppressed the incidence of supernumerary molts under LD 16:8. Adult emergence of the S stock under LD 12:12 occurred at nearly the same time as at 23°C though developmental period to reach the 3rd instar was shortened. In the E stock under LD 12:12, some adults emerged earlier than at 23°C but many emerged later than at 23°C. Under LD 12:12, the extension of larval period was again greater at 25°C than at 20°C.

At 30°C, photoperiodic effect was no longer apparent in the S stock and they developed at nearly the same rates under both photoperiods, while the E stock was not investigated (**Fig. 5**). Supernumerary molts was not observed under both photoperiods except one individual under LD 12:12.

Table 1 shows that mature larval diapause was most intense at 25°C where photoperiodic effect was most clearly expressed. It also shows that high incidence of

supernumerary molts occurred under both photoperiods at intermediate temperatures, 23 and 25 °C, in the S stock. Contrarily, in the E stock the percentage increased when temperature rose under LD 12:12 but decreased when temperature fell under LD 16:8. Developmental thresholds from egg to adult emergence (t_0) were calculated from the data collected under LD 16:8 (**Table 2**) as 15.3°C for the S stock and 14.9°C for the E stock. **Table 3** shows that females are larger than males and that differences between the two stocks and between the two photoperiods are slight. **Table 4** shows that the numbers of eggs found in the ovary of newly emerged females seems not different between the stocks and at temperatures between 23 and 30°C but that the number greatly decreased at 20°C, especially in the S stock. Whether the number will increase to an equivalent level to that at higher temperatures during adult life remains uncertain.

Artificial selection for fast development induced a significant reduction in developmental period before pupation in 3 generations (**Fig. 7**). Cumulative percentage of pupation 60 days after egg-laying was 14, 43 and 69 % in generations 0, 3 and 6, respectively. Medians of larval period were 164, 70 and 51 days for generations 0, 3 and 6. This demonstrates the plasticity of this trait.

Discussion

The two laboratory stocks of *L. serricorne* responded to short photoperiods and intermediate temperature by extending the period of mature larval stages. Both stocks showed a long-day type response at mature larval stage where short-days retard development. Although temperatures higher than 30°C suppressed the incidence of diapause, photoperiodic response is clearly expressed at other temperatures, particularly 23°C and 25°C in this species. Development took longer time at higher temperature below 30°C under LD 12:12 more typically in

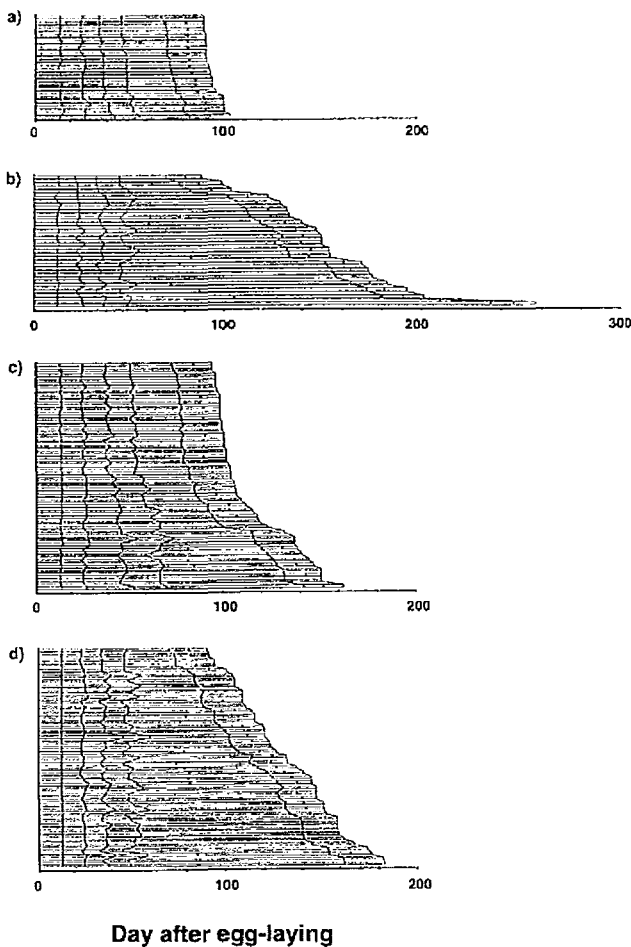


Fig. 2 Developmental profile of *L. serricornis* at 20°C. a) LD 16:8; b) LD 12:12 of the S stock; c) LD 16:8; d) LD 12:12 of the E stock.

the S stock (Table 1) which is unusual among long-day species. Developmental check-points occur not only at larval stages but also at adult stage in this species. The number of eggs in the ovary of newly emerged females raised at 20°C was less than half that of the numbers found in females reared at high temperatures (Table 4). This could be an incipient adult diapause induced by low temperature signals.

Each stock was clearly characterized based on its response to photoperiod and temperature conditions. The S stock shows more straight-forward responses than does the E stock. The E stock, however, showed a developmental retardation also at the 2nd instar under LD 16:8 at 20°C (Fig. 6) that was not observed in the S stock. The response is a short-day type that is frequently observed as an adaptation for dormancy for estivation. This type of photoperiodic response is usually intensified at higher temperatures but not in this species. Therefore, adaptive significance of this response remains uncertain. The effect of temperature on the response to short-days in the E stock is also difficult to understand. More individuals

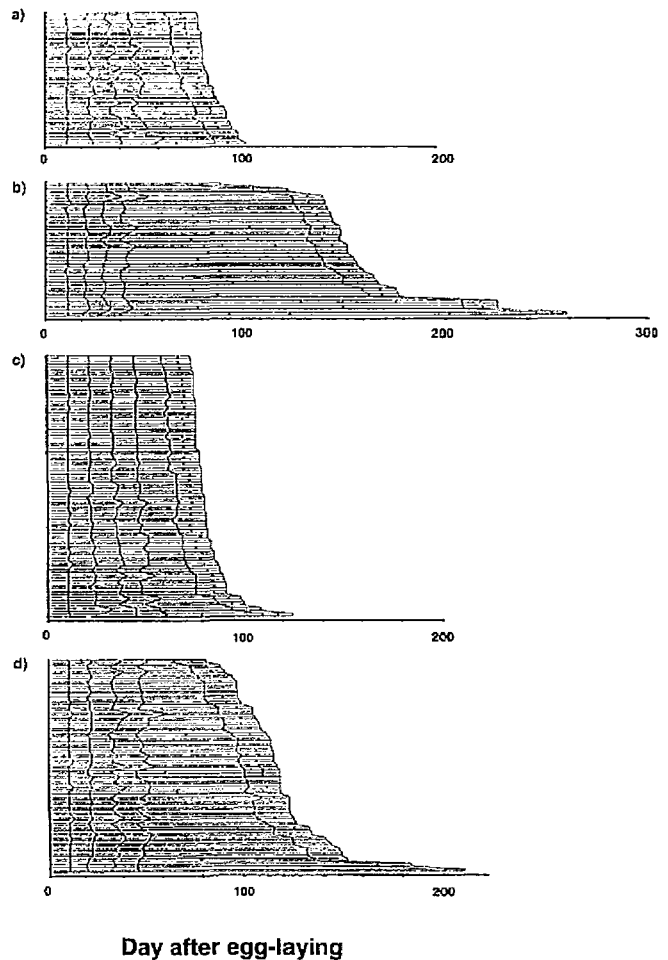


Fig. 3 Developmental profile of *L. serricornis* at 23°C. a) LD 16:8; b) LD 12:12 of the S stock; c) LD 16:8; d) LD 12:12 of the E stock.

extended larval period responding to a short-day at 25°C than at 23°C (Figs. 3, 4). Response to short-day in the long-day type photoperiodic response is usually intensified at lower temperatures but that is not the case in this species.

These unusual features may represent the intermediate steps of adaptations in the process of colonization of urban habitat or storehouse environment. One of the most complex modes of diapause regulation and the variability is found in the Indian meal-moth, *Plodia interpunctella* which is also a stored product pest (Tsuji, 1963). This species responds to three distinct cues to arrest larval development, short-days, temperature-fall and crowding. The types of diapause induced by different cues were different, and required different cues to resume development. The complicated responses found in this species may be due to artificial indoor lighting and heating, or even cooling unlike more regular change in seasonal stresses prevailing outdoors.

The extension of the mature larval stage is accompanied with supernumerary molts typically observed in larval

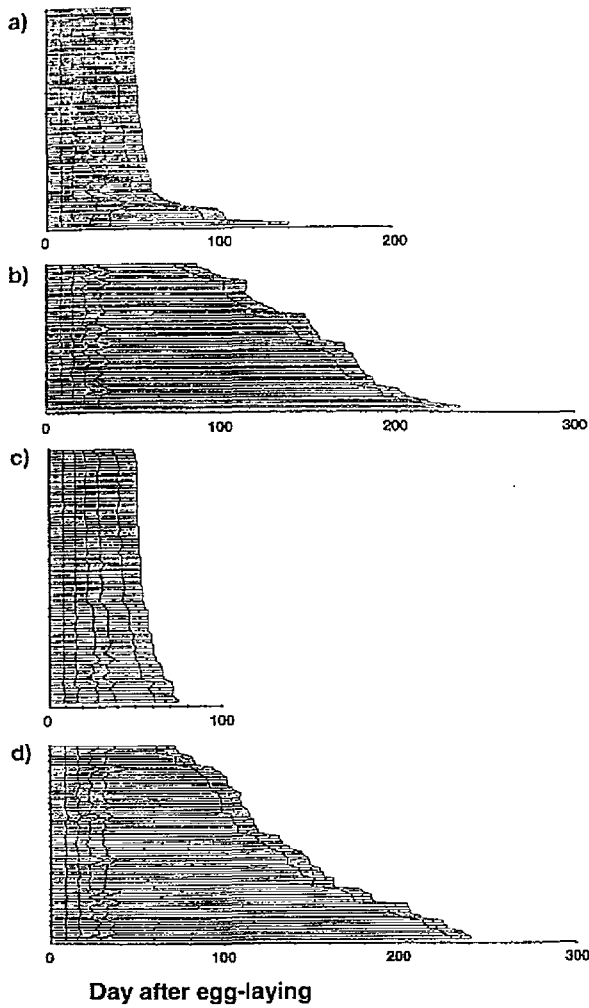


Fig. 4 Developmental profile of *L.serricorne* at 25°C. a) LD 16:8; b) LD 12:12 of the S stock; c) LD 16:8; d) LD 12:12 of the E stock.

diapause regulated by the titer of juvenile hormone (Yin and Chippendale, 1973). Whether larval diapause of this species is also regulated by JH remains as a subject of future study. The supernumerary molts usually occur once but in some conditions it occurs in multiple times such as under LD 12:12, 23°C (Table 1). Some of the S stock larvae underwent stationary molts four times at mature larval stage. This species can therefore change various developmental properties such as the fate of larval development at second and fourth larval instars, the rate of development, the rate of egg maturation and the number of stationary molts to fine-tune their life cycle, responding to various photoperiodic and temperature conditions. The present results also showed an extensive degree of variability between the stocks and within the stock in these properties. Such a multiplicity of check points for developmental determination may be general characteristics to stored product pests. Plasticity of the rate of larval development seems to be characteristics shared with other stored product insects such as *P.*

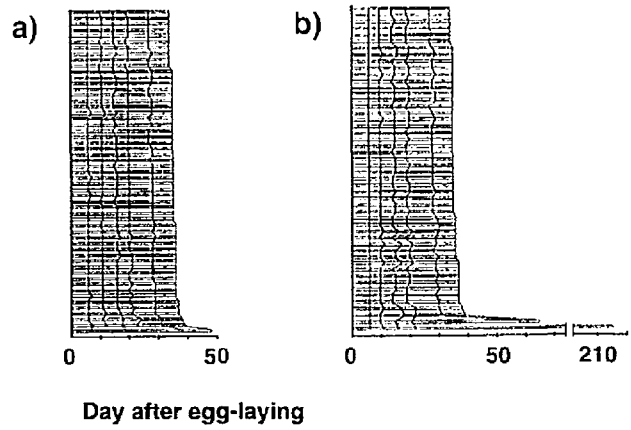


Fig. 5 Developmental profile of the S stock of *L.serricorne* at 30°C. a) LD 16:8; b) LD 12:12 of the S stock.

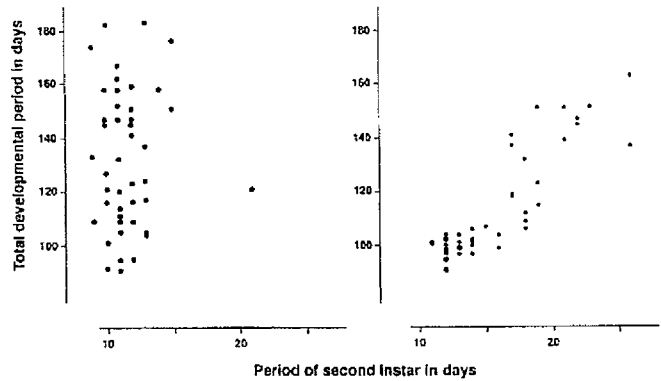


Fig. 6 The duration of 2nd larval instar relative to the duration of total postembryonic development of the E stock of *L.serricorne* at 20°C. Left, LD 12:12; right, LD 16:8.

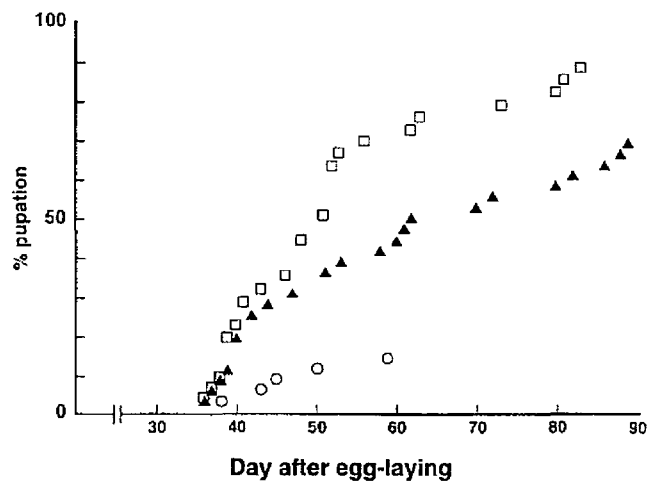


Fig. 7 Effect of artificial selection for fast development from the S stock of *L.serricorne* reared in mass under LD 12:12 at 25°C. Circles, unselected. Triangles, third generation of selection. Squares, sixth generation of selection.

Table 1 Period of mature larvae, i.e., fourth and supernumerary instars, from two stocks of *L.serricorne* reared under LD 16:8 and 12:12 at 20, 23, 25 and 30°C

Temperature	LD	Min	Max	Mean	SD	N	%Spn.molts ^a	%Msn ^b
<i>S stock</i>								
20	16:8	20	29	23.8	2.11	17	0	0
	12:12	24	184	81.9	38.9	20	50	0
23	16:8	17	41	23.7	5.72	28	32.1	0
	12:12	30	205	102	36.2	23	82.6	26.1
25	16:8	10	91	16.7	15.1	45	6.7	0
	12:12	43	192	110	37.4	28	71.4	0
30	16:8	7	19	7.9	1.62	55	0	0
	12:12	7	186	13.2	25.6	49	2.0	0
<i>E stock</i>								
20	16:8	22	71	34.5	15.2	42	14.3	0
	12:12	22	112	61.6	26.0	47	40.7	0
23	16:8	14	48	19.2	6.7	47	6.4	0
	12:12	14	140	52.2	24.4	41	51.2	9.5
25	16:8	10	33	13.9	4.75	45	0	0
	12:12	24	208	100	50.8	38	57.9	0

^a %Spn.molts refers to % larvae that underwent supernumerary.^b %Msn refers to the percent larvae that underwent multiple supernumerary molts.**Table 3** The width of prothorax of newly emerged adults of *L. serricorne*

Temperature	LD	M/F	Mean(mm)	SD	N
<i>S stock</i>					
20	16:8	F	1.48	0.085	9
		M	1.30	0.074	9
	12:12	F	1.52	0.130	12
23	16:8	M	1.36	0.059	8
		F	1.49	0.072	12
	12:12	M	1.33	0.058	15
25	16:8	F	1.57	0.119	11
		M	1.37	0.059	11
	12:12	F	1.44	0.081	26
30	16:8	M	1.34	0.087	19
		F	1.48	0.112	8
	12:12	M	1.30	0.096	19
	16:8	F	1.41	0.058	28
		M	1.31	0.029	27
	12:12	F	1.46	0.059	25
<i>E stock</i>					
20	16:8	F	1.33	0.056	25
		M	1.41	0.087	22
	12:12	M	1.30	0.056	20
23	16:8	F	1.50	0.066	24
		M	1.33	0.065	20
	12:12	F	1.41	0.053	23
25	16:8	M	1.30	0.057	24
		F	1.55	0.77	21
	12:12	M	1.35	0.095	20
	16:8	F	1.46	0.048	14
		M	1.34	0.054	29
	12:12	F	1.54	0.083	16
		M	1.38	0.059	21

Table 2 Total period of postembryonic development of *L. serricorne*

Temperature	LD	Min	Max	Mean	SD	N
<i>S stock</i>						
20	16:8	90	104	94.4	4.50	18
	12:12	89	258	158	38.8	20
23	16:8	79	104	87.5	7.83	27
	12:12	89	260	162	36.4	22
25	16:8	50	140	60.8	17.6	45
	12:12	87	324	157	39.1	27
30	16:8	34	48	35.5	1.99	55
	12:12	34	215	39.9	25.7	50
<i>E stock</i>						
20	16:8	95	163	114	19.3	41
	12:12	91	183	133	25.9	44
23	16:8	74	115	82.9	8.75	47
	12:12	82	210	120	24.4	41
25	16:8	50	70	57.0	6.53	43
	12:12	73	251	147	50.6	38

Table 4 The number of mature eggs in the ovary of newly emerged females of *L.serricorne*

Temperature	LD	Mean	SD	N
<i>S stock</i>				
20	16:8	14.1	8.8	9
	12:12	14.7	10.2	12
23	16:8	33.2	4.9	12
	12:12	30.3	9.9	11
25	16:8	31.2	9.3	26
	12:12	29.0	10.3	8
30	16:8	32.1	11.5	28
	12:12	31.7	12.3	25
<i>E stock</i>				
20	16:8	13.0	9.0	22
	12:12	15.0	7.9	24
23	16:8	20.5	8.6	23
	12:12	29.1	11.2	21
25	16:8	33.4	11.3	14
	12:12	36.9	8.0	16

interpunctella (Naeemullah and Takeda, 1998).

The developmental thresholds were very high, 15.3 and 14.9°C for the S and E stocks, respectively, which also characterizes stored product pests especially coleopteran species (Kiritani, 2002). Artificial selection for slow developing individuals showed a plasticity of this trait (Fig. 7), which means the versatility in the life cycle regulation is supported not only by a rich repertoire of physiological adaptations but also a genetic variability. Easiness to change developmental traits has been shown in *P. interpunctella* (Naeemullah and Takeda, 1998). This may be also a shared property by stored product pests that may contribute to a restoration of founders upon population catastrophe or sudden changes in environmental conditions.

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タバコシバンムシにおける後胚子発育の温度と光周期による制御

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家屋・貯蔵害虫であるタバコシバンムシの生活史形質を2つの光周期 (LD 12:12と16:8) 及び4つの温度条件 (20, 23, 25, 30°C) で個体飼育することによって調べた。比較のために2つのストック (SおよびE) を用いたが、LD12:12で飼育すると、両系統とも老齢期で過剰脱皮を繰り返して、幼虫休眠に入った。LD12:12での老齢幼虫期間は、S系統で30~205日、E系統では24~208日であった。LD12:12での過剰脱皮の頻度は、S系統では23°C、E系統では25°Cで高かった。E系統ではこの他にLD16:8で2齢を延長して幼虫休眠する傾向も見られた。短日の効果は、23-25°Cの中間温度でより顕著に見られ、30°C高温では、ほとんどの個体が短期に発育を完了した。過剰脱皮は、成虫のサイズの増加を伴わなかった。両系統の発育零点はS系統が15.3°C、E系統が14.9°Cと屋外の害虫に比べ両方とも高かった。20°CでのS系統の産卵数は、23, 25, 30°Cに比べ、半分以下であった。以上の結果から、この害虫の発育は、いくつかのチェックポイントで調節されており、この特性は絶滅にさらされたときに、新たなコロニーの創設者を確保することができるという貯蔵害虫の生活史に適応的なものと考えられる。人為淘汰の実験もこの形質の可塑性を示しており、生理的な特性とともに、遺伝的な多様性に富んでいることが示唆された。