Variation in Phase Polymorphism in the Common Cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae)\(^1\)

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By changing the rearing conditions of different instars on an artificial diet, it was reconfirmed that larvae of the common cutworm, *Spodoptera litura* were sensitive to density during the fourth and fifth instars and exhibited phase characters in the last (sixth) instar: those from crowded rearing, but isolated during the last instar, had a greater degree of melanization, recovered more quickly from feigned death when dropped, and fed for shorter periods than those reared completely in isolation. There was a great variability in response to density between groups of larvae originating from different batches of eggs collected in the field. Only a few groups showed the typical responses to density for the three phase characters mentioned above, while most groups indicated characters which were slightly altered, and manifested low density-type responses even at high density. One group invariably showed high density-type responses, having a high degree of melanization, quick recovery from feigned death and relatively short feeding periods. Another group exhibited a yellowish brown colour and fed longer in both rearing conditions, but rarely showed feigned death, flipping over to normal position immediately after being dropped, instead. A crossing experiment revealed that the density response patterns of phase characters in *S. litura* are under genetic control.

**Key words:** phase polymorphism, density effect, behaviour, *Spodoptera litura*

**INTRODUCTION**

Some species of Lepidoptera are known to exhibit phase characters in the final larval instar: larvae reared under crowded conditions show a greater degree of melanization, more active behaviour and shorter feeding periods than those reared in isolation (Iwao, 1962). The common cutworm, *Spodoptera litura* is one such species, showing phase polymorphism in which endocrinological studies on phase characters have been carried out (Yagi and Kuramochi, 1976; Tojo et al., 1985 a, b; Morita et al., 1988). On the other hand, Yamanaka et al. (1975) reported that some of the phase characters in this species did not change in a density-dependent manner. Further, in this report, I demonstrate the occurrence of intrapopulation variation with regard to responses to density in *S. litura*.

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MATERIALS AND METHODS

About 30 egg masses of Spodoptera litura were collected at several different areas in Saga Prefecture from August to November. Larvae from a given egg mass were initially reared in crowded conditions on an artificial diet (Oyama and Kamano, 1976) under a 16 hr light and 8 hr dark photo-regime at 25°C. Isolated larvae were prepared by individual rearing from the fourth (antepenultimate) instar on. Crowded larvae were obtained by rearing 100 and 20 individuals for fourth and fifth instars, respectively, in a large cup (i.d. 8.5 cm × 4.5 cm height), and then isolating them individually during the sixth (final) larval instar in a small cup (i.d. 7 cm × 4 cm height). Some crowded larvae were further reared in crowded conditions (8 larvae in the large cup).

Body colour of the final instar larvae was scored eight hours after ecdysis, into one of five grades as follows: 5, totally blackened, 4, grayish black, 3, rust brown, 2, brown and 1, yellowish brown, similar to the methods described previously (Tojo et al., 1985 a). Behaviour of final instar larvae was checked by dropping the larvae 32 hr after the ecdysis from a height of 30 cm and measuring the time to recover from feigned death, which has been accepted to be a typical response of the larvae of this species when attacked by predators. As gut purge of final instar larvae occurred on day 2 (gate I), 3 (gate II), or 4 or later (gate III), and pupation followed one day later, the developmental profiles of the larvae were compared by the ratio of gate I, II, and III larvae.

For crossing experiment, five females from one group and five males from the other group, which had exhibited characters specific to respective group during the last larval instar in isolated rearing, were crossed and the larvae from five egg batches obtained were mixed for further rearing at different densities.

RESULTS

Sensitive periods for density

A field-collected group2, RY, showing a weak response to density in body colour was used in the experiment. As shown in Fig. 1, final instar larvae reared in crowded conditions throughout larval development (A) showed a slightly melanized body colour (score 2.7), ca 30 sec of feigned death and consisted of both gate I and II larvae. These characters were essentially the same as in the larvae which were only isolated during the final instar (B). When larvae were isolated from the third (E) or fourth larval instar (D), the characters at the final instar clearly differed from those of the crowded larvae: body colour was yellowish brown (score 1.6), the duration of feigned death was 170 sec, and no gate I larva was observed. When isolated larvae were again exposed to crowded conditions during the fifth instar (F) or when isolation was started from this instar (C), the three characters mentioned above were intermediate between those reared in crowded and isolated conditions. These results indicate that antepenultimate and penultimate larval instars are sensitive to density and that exposure to crowded conditions during these two instars alone is sufficient to manifest the phase characters in the final instar.

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2 Group names were abbreviated by the initial of predominant body colour of crowded larvae, followed by the initial of colour of isolated larvae shortly after final ecdysis as follows: Y, yellowish brown; R, rust brown; B, black.
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Fig. 1. Effects of isolated and crowded rearing initiated at different larval instars as illustrated in the lower scheme on three phase characters of last instar female larvae (group RY) in *S. litura*. Top: ratio of individuals with feeding periods of 3 days (gate I), 4 days (gate II), and 5 days or longer (gate III) at 25°C. Middle: left ordinate, grade of black colouration from 1 (yellowish brown), 3 (rust brown) to 5 (totally blackened); right ordinate, the duration in seconds of feigned death, when dropped from a height of 30 cm. Values are averages with S. D. (n=30).

Fig. 2. Comparison of the effects of isolated (I) and crowded (C) rearing conditions on three phase characters of the last instar female larvae in five groups of *S. litura*. All larvae were individually isolated in the last larval instar. Values are averages with S.D. (n=30). For others, see Fig. 1.
Occurrence of groups exhibiting different responses to density

Typical responses of phase characters to density observed in *S. litura* larvae originating from different egg masses are shown in Figs. 2 and 3. The BY group showed the most prominent difference in all of the three phase characters when reared in isolated and crowded conditions. Conversely, both crowded and isolated larvae of BB group were highly melanized (ref. Fig. 3), showed a rather quick recovery from feigned death and developed mostly to gate II animals. The rust brown colour of isolated BR group larvae changed to black under crowded conditions, but they showed neither faster recovery from feigned death, nor accelerated development, most of them becoming gate III animals (Fig. 2).

The RY group, which was used for the experiment in Fig. 1, exhibited altered feeding period and behaviour in response to density as in the BY group, however, it showed only a slight change in colour from yellowish brown in isolation to rust brown in crowded conditions (Fig. 2). The phase characters of the final group YY in Fig. 2 were not affected by rearing density, as with the BB group, but, in contrast to the latter, the larvae exhibited a yellowish brown colour (ref. Fig. 3), quickly recovered from feigned death and developed slowly (gate III), under both isolated and crowded conditions.

Evidence for genetic control of phase characters

Figure 4 shows the body colour of last instar larvae obtained from isolated and crowded conditions of the YY and BR groups used in Fig. 2, and their F1 hybrids. Further, as shown in Fig. 5, colour scores graded on a scale of 1 to 5 were influenced considerably by density in the BR group, but only slightly in the YY group. In addition, the F1 progenies showed intermediate scores under both conditions and a comparison of their behaviours revealed the following: as shown in Fig. 6, the YY group quickly recovered from feigned death, while the BR group showed a rather sluggish recovery, the duration of this behaviour not being influenced by density in both groups. F1 progenies gave intermediate values for this trait compared to their parents, and were also unaffected by density.

The YY group showed an interesting behaviour: when dropped on the ground, most of the larvae quickly flipped over to normal position, while only a few remained curled up, displaying the typical response of feigned death. On the other hand, larvae of most groups, including the BR group showed predominantly the curling-up behaviour, and rarely flipped over. As shown in Fig. 7, the F1 progenies showed intermediate responses as determined by the ratio of the dropped larvae showing curling-up and flipping-over behaviours.

DISCUSSION

Here, I first reconfirmed that the antepenultimate and penultimate larval instars were sensitive to density with regard to changing body colour, behaviour and feeding period in the last instar larvae of *Spodoptera litura*, as previously reported (Tojo, et al., 1985 a). Further, as suggested by Yamanaka et al. (1975), I could demonstrate the presence of field groups like BB and YY showing no response to density in the characters, which have been accepted to change in a density-dependent manner in this insect. To the extent of my investigation, groups manifesting phase-specific responses, which have
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![Photographs of last instar larvae from isolated (I) and crowded (C) rearing in three groups of *S. litura*.](image1)

![Photographs of last instar larvae from isolated (I) and crowded (C) rearing in YY and BR groups and their F₁ progenies of *S. litura*.](image2)
Fig. 5. Comparison of body colour in last instar female S. litura larvae ($n=30$) from isolated and crowded rearing in YY and BR groups and their $F_1$ progenies.

Fig. 6. Comparison of duration of feigned death in last instar female S. litura larvae ($n=30$) from isolated and crowded rearing in YY and BR groups and their $F_1$ progenies.

been reported in previous papers (Yagi and Kuramoto, 1976; Tojo et al., 1985 a, b; Morita et al., 1988) could only rarely be found. Most of the field groups showed slight changes in body colour, and no difference in either behaviour or feeding duration resulting from rearing density, and exhibited the characters specific to low-density rearing. The predominance of such groups in S. litura may indicate that this species and other species of migratory noctuids are originally adapted to existence at low population densities, as suggested by Gatehouse (1986).

During the course of study, I found an unusual group YY, which exhibited solitary characters even at high density and cryptic yellowish brown colouration at the final instar, but did not feign death when dropped. Behavioural polymorphism has been studied most extensively in Drosophila, in which selection for specific traits has been
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Fig. 7. Comparison of last instar female *S. litura* larvae (n=30) showing curling-up and flipping-over behaviour after isolated and crowded rearing, when dropped from a height of 30 cm in YY and BR groups and their F1 progenies.

shown to produce strains differing in behaviour from the original ones as reviewed by HALL (1983). The simple crossing experiment presented in this article indicates that all three phase characters, i.e., body colour, feeding period and behaviour of *S. litura* are genetically controlled. Therefore, the presence of groups showing an immediate flipping-over behaviour may indicate the occurrence of natural selection for a behaviour related to defense against predators, in quite a different way from feigned death, which is believed to be effective in avoiding their attacks. Further experiments to elucidate the significance of these behavioural differences in this species are expected to be done.

In another phase-polymorphic species, the African armyworm, *S. exempta*, female adults derived from high-density gregarious phase larvae were observed to fly longer than those from low-density solitary larvae (Woodrow et al., 1987). But also, in this species, selection for long-flight has been shown to induce individuals with higher flight performance (Parker and Gatehouse, 1985; Gatehouse, 1986). Discovery of a black *S. litura* group, BB which always shows gregarious behaviour suggests that there may also be genetic variation in flight ability in this species, and perhaps this black group is related to natural selection for high migratory ability. Colour polymorphism is known in many species of insects as reviewed by Fuzeau-Braesch (1985), who cited the work of Nel (1967), having managed to displace phase polymorphism by a process of selection based upon the body colour of *Locusta migratoria*.

Recently, great inherent variation in wing-form responses to density in field populations of the brown planthopper, *Nilaparvata lugens*, has been found, which ranges from populations being highly brachypterous to those being predominantly macropterous, with intermediates responding to density in different ways (Nagata and Masuda, 1980; Iwanaga et al., 1985, 1987; Morooka et al., 1988). Further, Morooka et al. (1988) found a good correlation between wing-form response to larval density and body colour of adults, and were able to produce a strain showing the brachypterous form only by successive selection for yellowish brown individuals, and another one exhibiting nearly all macropterous wing-form in a broad range of density by selection for blackish individuals. Thus, the development of variation in response to density and colour.
polymorphism, as observed in N. lugens, appears to have occurred in S. litura. To elucidate this possibility in S. litura, selection experiments for specific colour are now being planned.

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