DENSITY DEPENDENCE DEPENDS ON SCALE; AT LARVAL RESOURCE PATCH AND AT WHOLE POPULATION

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Summary

A previous study (Tuda and Shimada, 1993) has shown that the equilibrium population size of the azuki bean beetle was lower at 32°C than at 30°C and that this difference was due to a reduced maximum population size of emerged progeny through inside-bean process. In this paper, these results were analyzed further on the scale of the individual bean where interaction among larvae took place. Per-bean numbers of deposited eggs, hatched eggs, and emerged adults have been recorded at seven different parental densities under the two temperature conditions.

Three individual-bean-scale process hypotheses that may explain the reduced maximum emergence density on the whole population scale are suggested: (1) a lower maximum emergence per bean at 32°C than at 30°C, if the bean scale and the whole-population scale share the same density-dependent pattern in adult emergence, (2) a limited range of hatched egg number per bean at 32°C, resulting from the adult oviposition process outside beans, and (3) different patterns of density-dependent emergence between the two different scales.

This study showed that the inside-bean pattern of responses on the bean scale was a simple saturated curve at 30°C, but one with a discontinuous decline at higher hatched egg densities at 32°C. On the contrary, during outside-bean process, the peak number of hatched eggs decreased on this scale as observed on the whole-population scale. I discuss why the extracted factor of inside-bean process on the whole-population in the previous study could not be applied to the bean-scale pattern.

KEYWORDS: spatial scale, resource patch, intraspecific competition, temperature, *Callosobruchus chinensis*, density-dependent response.

Introduction

Ecological processes occur at neither a single spatial scale nor a single organizational level (Andrewartha and Birch, 1954; O'Neill et al., 1986). In flying insect species, for example, a female's oviposition site and a larval resource patch may differ

in spatial scale simply because of the different dispersal strategies of these life stages. Furthermore, a pattern observed at a population level may not be analogous to one at an individual level because of interactions among individuals at the higher level (Łomnicki, 1988; Levin, 1992). Ecological studies should, in nature, cover multiple spatial scales and organizational levels (Levin, 1992).

Recently, in order to apply lower scale information to higher ones for purposes of prediction, scaling-up problems have received considerable interest (Iwasa et al., 1987; Iwasa et al., 1989; Steele, 1989; Levin, 1992; Rastetter et al., 1992). On the other hand, scaling-down for the purpose of understanding detailed mechanisms is in common use. However it is rarely demonstrated systematically in ecology as such. If an observed pattern is unique to a particular scale, misunderstandings may arise when description of pattern on one scale is applied to other scales (Steele, 1989; Peters, 1991; Levin, 1992; Rastetter et al., 1993).

We have observed that the equilibrium size of a laboratory population of the azuki bean beetle was lower at 32°C than at 30°C (Tuda and Shimada, unpublished). The analysis on the whole-population scale showed that the smaller equilibrium population size resulted from the reduced maximum population size of emerged progenies that have experienced inside-bean processed such as larval development and competition (Tuda and Shimada, 1993; also the upper panel in Fig. 1a). Although the peak density of hatched eggs decreased this did not contribute to the change in equilibrium population size as much as did the reduced maximum density of emerged progeny (Fig. 1a).

Individual beans are a more appropriate scale than the whole population to examine inside-bean process because beans form distinct habitats and resource patches for the bean beetle larvae. Three hypotheses on bean-scale processes are plausible to explain the reduction in maximum emergence density observed on the whole-population scale (Fig. 1b-d). Firstly, if a density-dependent pattern of emerged adults on the bean scale is analogous to the one on the whole-population scale, the primary cause on both scales is a lower maximum emergence density at 32°C (Fig. 1b). The temperature rise has reduced the maximum number of hatched eggs on the whole-population scale (Tuda and Shimada, 1993; also the lower panel in Fig. 1a), although both scales might share the analogous pattern of density-dependent emergence as in the first hypothesis. The second hypothesis is a lower number of hatched eggs on the individual bean, resulting from the reduced hatched eggs during outside-bean process, or egg deposition, at 32°C (Fig. 1c). Finally, a pattern on the bean scale can be quite different from one on the whole-population scale. The third hypothesis explaining the smaller equilibrium population size is based on this difference in density-dependent emergence patterns between these two scales (Fig. 1d). Notice in the last case, the extracted factor on the whole-population scale could not be applied to the bean scale.

In this study, I focus on the individual-bean-scale process and assess what reduces the maximum emergence population size during larval development inside beans. I

show that, at 32°C, few adult offspring emerge when the number of hatched eggs per bean exceed a certain threshold. Integration of this discrete pattern into the higher scale, over all beans as a whole population, masks the different patterns between
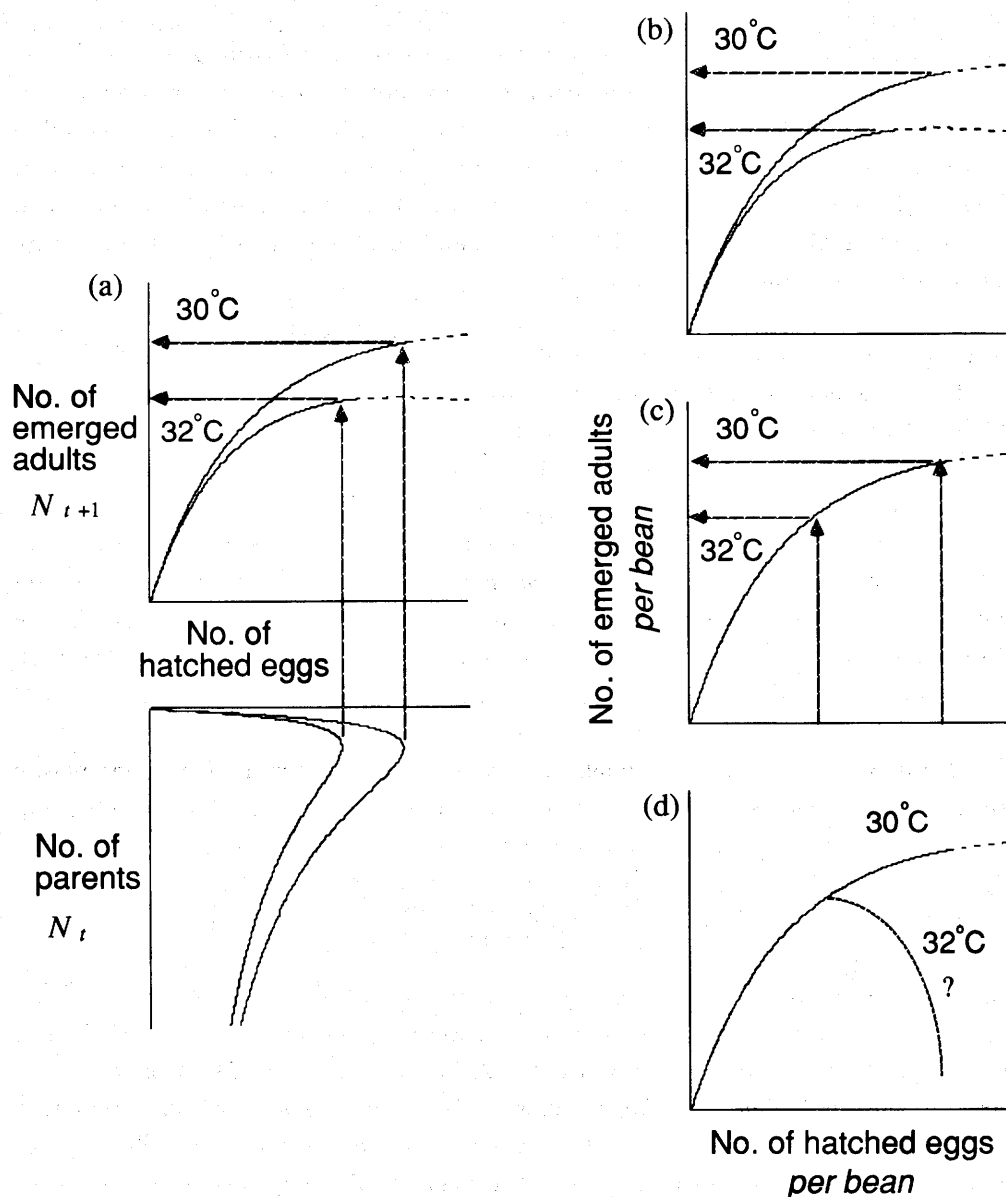

Fig. 1. (a) A diagram that explains one-generation response at two different temperatures, 30°C and 32°C, previously studied on the whole-population scale (Tuda and Shimada, 1993). The upper panel shows the inside-bean process and the lower panel shows the out-side-bean process. Diagrams (b), (c), and (d) explain the three hypotheses on individual-bean-scale processes that could reduce the maximum density of emerged adults on the whole-population scale.

temperatures.

MATERIALS AND METHODS

Laboratory Population and Environments

I used strain jC of the azuki bean beetle *Callosobruchus chinensis* (L.). Adults lay eggs on beans and, on hatching, the larvae burrow into the bean. After development they emerge out of the beans. The azuki bean *Vigna angularis* var. *dainagon* was used as a resource of *C. chinensis*. Detail history of the strain and condition of beans were described by Tuda and Shimada (1993). Two environmental cabinets were controlled at 30°C and 32°C respectively with 70% R.H. and 24L : 0D. Ranges of temperature fluctuation were within ±0.5°C.

Experiment on the Individual-Bean Scale

In this experiment, I followed the procedure adopted by Tuda and Shimada (1993). Cultures to examine outside- and inside-bean processes were independently chosen, based on Tuda and Shimada's (1993) assumption that these two processes are independent.

Two, 8, 32, 64, 128, 256 and 512 adults of newly-emerged *C. chinensis* were collected and introduced into a four-compartment Petri dish (Falcon No. 1009: 90 mm in diameter, 15 mm in depth) with 5 g of beans in one of these compartments. These dishes were placed under either of the two different temperature conditions. About 18 days later, when all parent adults had died and eggs had hatched, hatched and unhatched eggs on each bean were recorded.

Beans were then put individually into wells of compartmentalized clear plastic boxes (Nunclon delta SI 1/75: 24 wells) to record adult emergence. Emerged offspring from these beans were counted after about five weeks from the onset of the experiment.

RESULTS

Outside-Bean Response

The number of eggs deposited on a bean were significantly less at 32°C than at 30°C at parental density treatment of 2, 8, 32, 64 and 128 (Table 1). Conversely, at parental densities higher than 256, numbers of deposited eggs were significantly larger at 32°C than at 30°C (Table 1). There was no difference in the hatchability of eggs between the two temperatures at parental density 64 where density of hatched eggs reached a peak ($t = -0.630$, df$=52$, $P=0.53$).

The number of hatched eggs for each bean plotted against the number of deposited eggs for various parental densities is shown in Figure 2. At low (2, 8, 32) and high (512) parental densities (Fig. 2a, b and d at 30°C, a, b and d at 32°C) the number of hatched eggs was significantly correlated with the number of deposited eggs

Table 1. Total number of deposited eggs on a bean at parental densities of 2, 8, 32, 64, 128, 256 and 512.

| Parental density | Temperature | | | | Statistics | |
| | 30°C | | 32°C | | | |
	Mean (n)	SD	Mean (n)	SD	U	P
2	3.72 (25)	1.06	1.88 (26)	1.03	585.5	*
8	9.08 (24)	1.61	6.77 (26)	1.80	526.0	**
32	27.88 (25)	4.99	22.28 (29)	4.37	586.0	**
64	48.30 (27)	5.57	34.89 (27)	4.62	577.0	**
128	57.50 (28)	7.16	43.72 (29)	5.78	770.5	**
256	57.57 (28)	7.87	78.46 (26)	14.00	672.5	**
512	67.36 (25)	9.78	78.50 (26)	15.70	485.0	*

*: $P<0.01$,   **: $P<0.001$

at both temperatures (Table 2). At middle parental densities 64, 128 and 256 (Fig. 2b and c at 30°C, b and c at 32°C) there was no or only a weak correlation between numbers of deposited eggs and of hatched eggs within parental densities (Table 2).

Inside-Bean Response

The number of adults emerging per bean is plotted against the number of hatched eggs per bean in Fig. 3. Parental densities that share a similar bean-scale pattern are grouped together. At middle (32, 64, 128, and 256) parental densities, peak emergence of 12 to 13 existed around 20 hatched eggs at both temperatures (Fig. 3b). Pooling emergences from 19 to 22 hatched eggs, the average numbers of emerged adults around the peak were not different between the two temperatures (7.92, $n=25$, at 30°C; 7.07, $n=15$, at 32°C) ($U_{15,25}=217.0$, $P=0.40$). However, the decline in adult emergence at higher densities of hatched eggs was steeper at 32°C than at 30°C. Very few adults emerged at hatched egg densities per bean higher than 25 (Fig. 3b). At low (2 and 8) and high (512) parental densities, except for 2 beans, the range of hatched eggs per bean was limited to 15. Adult emergence patterns at 32°C were

Table 2. Spearman's rank correlation between the numbers of deposited eggs and of hatched eggs per bean at parental densities of 2, 8, 32, 64, 128, 256 and 512.

| Temperature Parental density | 30°C | | | 32°C | | |
	r_s	df	P	r_s	df	P
2	0.452	25	*	0.668	26	***
8	0.865	24	***	0.790	26	***
32	0.926	26	***	0.923	27	***
64	0.011	27		0.214	27	
128	−0.392	28	*	0.043	29	
256	0.121	25		−0.338	26	
512	−0.604	25	**	−0.765	26	***

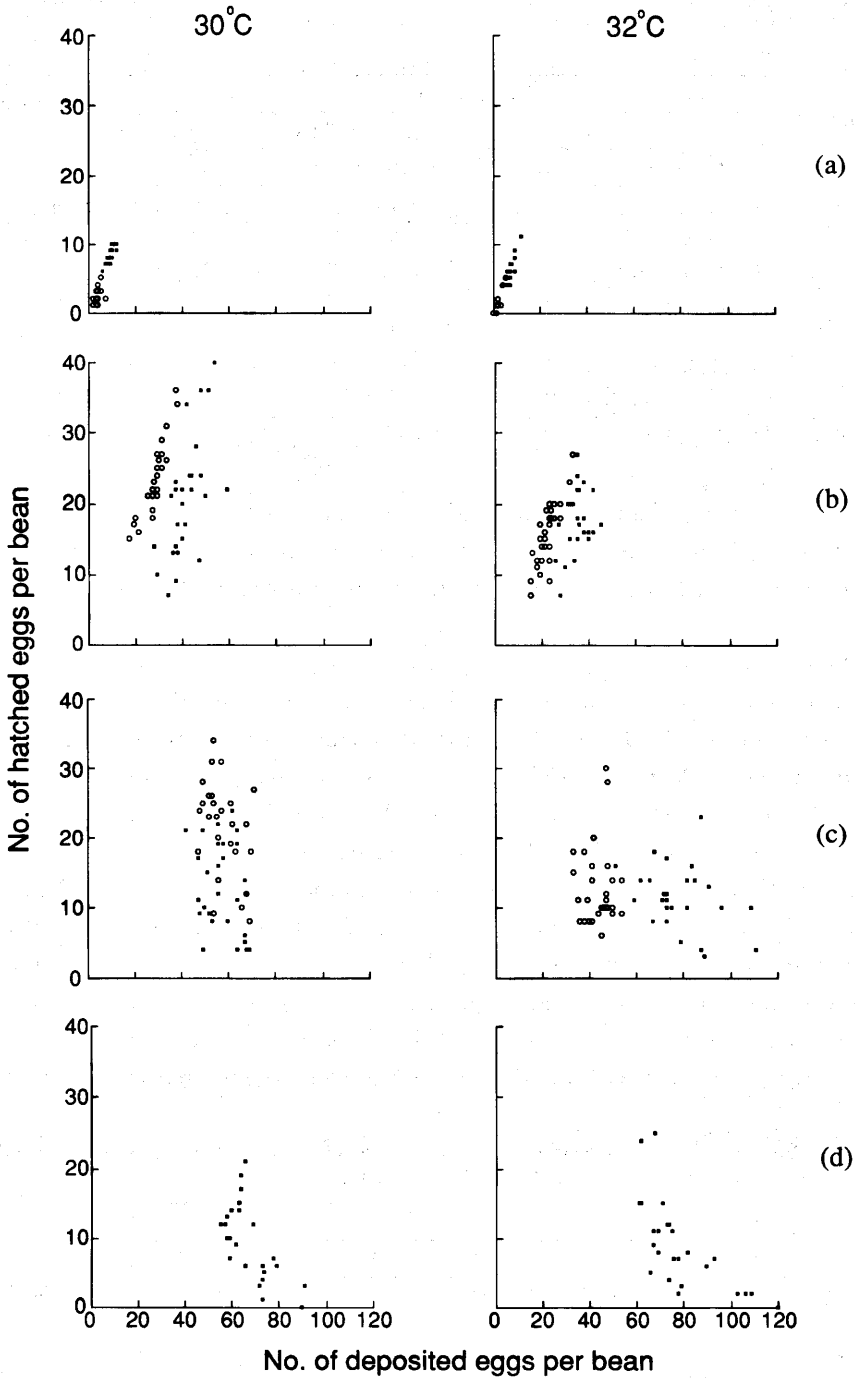*: $P<0.05$,   **: $P<0.01$,   ***: $P<0.001$

Fig. 2. Outside-bean responses on the bean scale at different parental densities. Relation between numbers of deposited eggs and of hatched eggs of *C. chinensis* is shown at 30°C (left panels) and at 32°C (right panels). Parental densities are (a) low (2 and 8), (b) lower-middle (32 and 64), (c) higher-middle (128 and 256) and (d) high (512). Open circles indicate the lower parental densities in the panel.
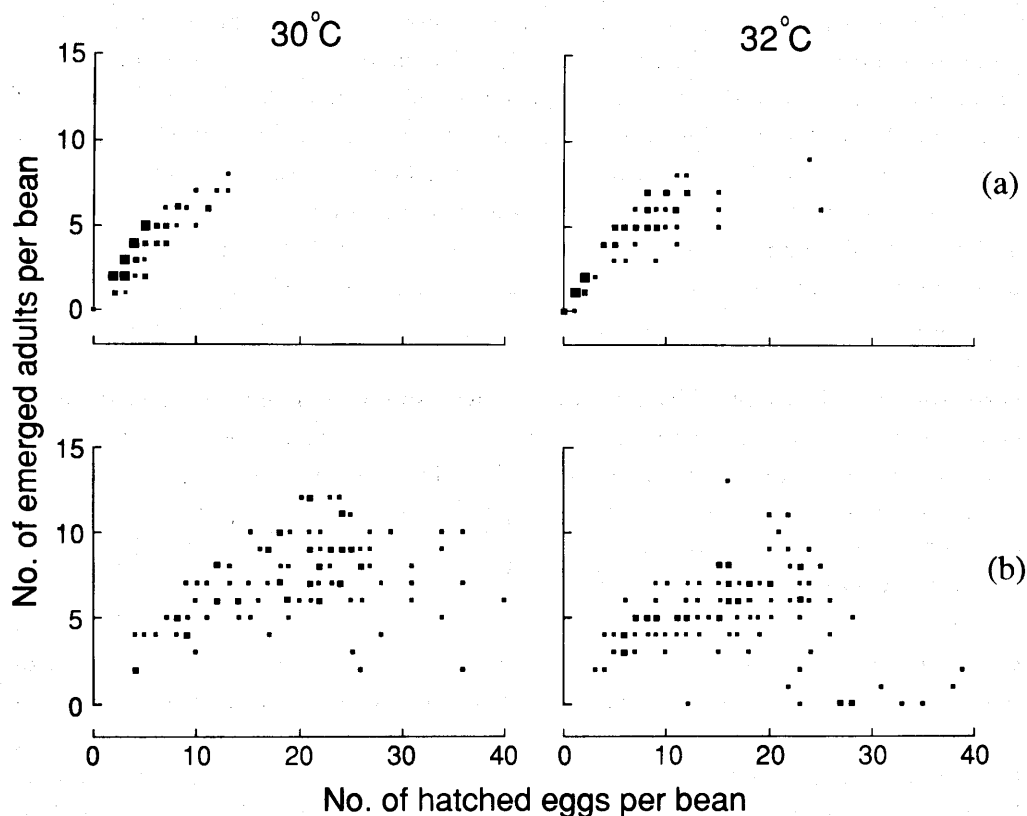
Fig. 3. Inside-bean responses on the bean scale at different parental densities. Relation between numbers of hatched eggs and of emerged adults of *C. chinensis* is shown at 30°C (left panels) and at 32°C (right panels). Parental densities are (a) low and high (2, 8, and 512) and (b) middle (32, 64, 128, and 256). Size of plots shows the number of data at the coordinates; the smallest plot indicates 1 datum, the middle plot 2 to 4 data, and the largest plot indicates ≥ 5 data.

similar to those at 30°C (Fig. 3a).

DISCUSSION

Outside-Bean Response

The number of eggs deposited per bean were reduced by the temperature rise at 64 parents (Table 1 and Fig. 2b) where density of hatched eggs reached a peak on the whole-population scale (the lower panel in Fig. 1a). Per-bean decrease in deposited eggs was a common trend among low-to-middle parental densities (Table 1). Individual female fecundity was reduced by the 2°C rise (82.5 eggs deposited at 30°C and 71.3 at 32°C; Tuda and Shimada, unpublished). Therefore, the reduction in peak density at 64 parents at 32°C on both scales can be explained by the reduced fecundity at individual levels.

There is a novel result obtained by the bean-scale analysis irrespective of temperature conditions (Fig. 2d and Table 2). Hatchability of deposited eggs in *C. chinensis* has been regarded to depend primarily on the parental density because of direct mechanical injury by parents' trampling on eggs (Utida, 1941). At lower parental densities (2, 8 and 32) the number of hatched eggs was positively correlated with the number of deposited eggs per bean within parental densities (Table 2, Fig. 2a and b). Adult trampling on eggs rarely happens at such low densities and thus a constant natural mortality of eggs (ca. 10%) prevails. Therefore, this positive correlation is rather self-evident. At a high parental density of 512, however, the correlation was negative (Table 2, Fig. 2d). Possible causes for this negative correlation may be hatchability reduction by oviposition-deterring substance (Oshima et al., 1973; Yamamoto, 1990) and/or positive correlation between frequencies of ovipositing and of trampling by female adults. Further analysis on individual adult behavior is needed.

Inside-Bean Response

The reduced maximum population size of emerged adults at 32°C was a consequence of the finding that few individuals emerge per bean when the number of hatched eggs exceeded a certain threshold (Fig. 3b at 32°C). Because the number of hatched eggs exceeded this threshold at each of middle parental densities, summing over these range produced lower maximum levels of emergence. This threshold may be due not only to resource depletion but to larval metabolic heat (Utida, 1954; Utida, 1965; Sano, 1967). At high larval densities per bean, the metabolic heat may exceed physiological limit of survival, especially under such a high ambient temperature condition as 32°C.

Scale Dependency of Inside-Bean Response

The outside-bean responses on the whole-population scale reflected those on the individual-bean scale under both temperature conditions. Bean-scale data on deposited and hatched eggs added information on variability among beans but did not change the pattern observed on population scales; on both scales the maximum level of hatched egg production was reduced by the 2°C temperature rise (the lower panel in Fig. 1a and Fig. 2b). By contrast, the inside-bean responses showed different patterns on the bean scale from those on the population scale. On the population scale, the effect of emergence decline at high larval density, described by parameter value b_L, was far less important than the maximum emergence level (Tuda and Shimada, 1993; also the upper panel in Fig. 1a). On the bean scale, however, an obvious emergence decline was induced around 25 larvae per bean by the 2°C rise (Fig. 3b at 32°C). As a result, the sum of larvae which survived over beans decreased (Fig. 1a, upper). Notice that the average number of emerged adults around the peak on the bean-scale was not reduced at 32°C (Fig. 3b). Peak reduction on the whole-population scale by

the temperature rise was, in fact, the result of extremely high larval mortality at the higher density per bean which is b_L-analogue on the bean scale.

Utida (1975) stated that, in the azuki bean beetle, density-dependent competition is of the scramble type during the process from egg deposition to hatching outside beans, but from hatched larvae to adult emergence inside beans it follows the contest pattern. Compared to his analysis on the whole-population scale, the present study showed competition among hatched larvae on the individual-bean scale can also be of the scramble type as shown in Fig. 3b at 32°C. Toquenaga and Fujii (1990) have also pointed out the inapplicability of description of density-dependent patterns across scales in contest- and scramble-type competition of *Callosobruchus analis* and *C. phaseoli*. I have shown more generally in this study how discrepancy of patterns between scales could arise and that scale-dependency can be different among life stages that belong to different habitat scales, overall and individual beans.

The present study shows that density-dependent responses on the scale of larval resource patches had been masked by integrating these patches into a larger scale, i.e., overall beans as the whole population. "Many holometabolous insects spend most of their lives in or on the plant or animal ... which serves both as food and as a place to live" and the adult is specialized for dispersal (Andrewartha and Birch, 1954). Depending on the different dispersal ability between larvae and adult, an appropriate spatial scale should be chosen when studying such stage-specific responses.

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密度依存はスケールに依存する；幼虫資源パッチと個体群全体において

津 田 み ど り

　アズキゾウムシの個体群サイズは飼育温度32度では30度でより低下し，豆内で発育過程を経た羽化成虫数の最大値の減少がその主要因であることが前報までででわかっている．本論文では，幼虫間相互作用の起こる個々の豆スケールでの解析を進めた．豆当たりの産卵数，孵化卵数，羽化成虫数を7つの親密度について，前述の2つの温度条件下で調査した．

　個体群全体スケールでの最大羽化成虫数の減少をもたらした豆スケールの過程について3つの仮説をたてた．(1) 32度での豆当たり最大羽化成虫数の減少．どちらのスケールにおいても羽化成虫数の密度依存的パターンが同じ場合である．(2) 32度での豆当たり孵化卵数の範囲が狭くなった．両スケールで同じパターンになる場合．(3) 二つのスケール間で羽化成虫数の密度依存的パターンが大きく異なる場合，である．

　本研究により豆スケールでの豆内羽化数パターンは，30度では単純な飽和曲線だが，32度では孵化卵密度の高いところで非連続的な傾きのあることが示された．反対に，豆外の過程では個体群全体スケールでみられたような孵化卵数のピークの減少が豆スケールでもあった．個体群全体スケールで抽出された豆内過程の要因は，豆スケールのパターンには適用できないことを議論した．