Formosan Entomologist
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【Research report】

胡桃金花蟲(Gstrolina depressa)族群密度與死亡率關係之研究【研究報告】

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Abstract

摘要

　　以生命表研究胡桃金花蟲之野外族群動態，分析其死亡過程中之關健因子（key factor）及密度依變性（density dependence）。幼蟲三齡期的死亡為關鍵因子，而捕食性瓢蟲Ailicaria hexaspilota 為導致死亡的主要原因，且其過程密度逆依變性。

Key words:
關鍵詞: 胡桃金花蟲、生命表、關鍵因子、密度依變性。

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A Study of the Relationship between Population Density and Mortality for the Walnut Leaf Beetle, *Gastrolina depressa*

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ABSTRACT

In order to elucidate the population dynamics of the walnut leaf beetle, *Gastrolina depressa*, life tables were developed, and key factors as well as the density dependence of mortality were analyzed. *G. depressa* 3rd larval instar mortality was the key population dynamics factor and hinged on the presence of *Aiolocaria hexaspilota* larvae. The inverse density dependence predation mechanism for 3rd instar *G. depressa* larvae was attributed to the predatory preferences /capabilities of *A. hexaspilota* and to a time lag mechanism between the hatching of predator and prey.

Key words: *Gastrolina depressa*, life table, key factor, density dependence, *Aiolocaria hexaspilota*.

胡桃金花蟲(*Gastrolina depressa*)之族群密度與死亡率關係之研究

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摘　　要

以生命表研究胡桃金花蟲之野外族群動態，分析其死亡過程中之關鍵因子（key factor）及密度依變性（density dependence）。幼蟲三齡期的死亡為關鍵因子，而捕食性瓢蟲 *Aiolocaria hexaspilota* 為導致死亡的主要原因，且其過程呈密度逆依變性。

關鍵詞：胡桃金花蟲、生命表、關鍵因子、密度依變性。

Introduction

From 1985 to 1989, field studies were carried out on the population dynamics of the walnut leaf beetle, *Gastrolina depressa,* a notorious pest that causes serious damage to walnut tree in mountainous areas of central Japan.

Chang and Morimoto (1988) studied *G. depressa* aggregation both in the laboratory and in the field and found that mortality factors were directly related to colony size. The major source of egg mortality results from *Aiolocaria hexaspilota*, a predator that tends to focus mainly on the larger sized egg masses. Consequently, the mortality rate of the 1st instar *G. depressa* larvae decreases with an increase in colony size. The larval stages are preyed upon by *A. hexaspilota* and *Panorpa japonica*, both of which tend to be quite thorough in their consumption of a colony.

One factor of gradation on *Hyphantria cunea* population is that predation often occurs in an inversely density-dependent manner, which may help the population to either increase or decrease depending respectively, on whether there are few or many individuals of the species initially present (Itô and Miyashita, 1968). In these cases, birds and long--legged wasps play the most important predator roles. Richards and Waloff (1961) compiled a life table for *Phytodecta olivacea*. They found that 78–99% of the total number of eggs laid died in either the egg stage or shortly after hatching and that 71–88% of these deaths were due to a chasing bug which was irrelevant to *P. olivacea* population density.

In this article, *G. depressa* life tables were constructed in order to assess the relative importance of the various mortality factors for each developmental stage. Life table data was subjected to key–factor analysis in order to evaluate the density relationships of the mortality processes.

Materials and Methods

Field censuses were carried out in a number of locations in Honshu, Japan: 1) Shinshu University campus (denoted hereafter as "the campus"), Ina, Nagano prefecture (1985 to 1988); 2) the Ozawa district, 2 km south of Shinshu University (1986 to 1988); 3) Nakajima, Tamagashi and the Okayama University campus, Okayama prefecture (1988) and 4) Tamagashi, the Okayama University campus (1989).

Note that *G. depressa* adults had to be introduced into the census tracts of the campus in 1985 and 1986, Ozawa in 1986; and Okayama (Tamagashi and the Okayama University campus) in 1988 and 1989 since we were unable to find any naturally occurring specimens at these localities. Also note that when observing

the predator–prey relationship in Tamagashi and at the Okayama University campus (1989), 1st instar *A. hexaspilota* larvae were released during the 1st and 2nd larval instar periods of *G. depressa*.

All individuals were inspected and censuses were carried out twice daily except in 1988 at the campus and in Ozawa, where they were conducted only once a day. *G. depressa* eggs were found laid in batches on the undersides of host plant leaves. All egg masses were labeled and counted under magnification where the distinction between physiological failure (embryonic death) and incomplete fertilization (no embryonic development) was clearly visible. The number of live and dead *G. depressa* for all developmental stages in addition to mortality factors and predators were recorded. Predators were observed attacking the egg masses, larvae and pupae and indirectly inferred, as in the case of adult *A. hexaspilota*, from red excretions remaining on partially devoured eggs. Note that whenever *A. hexaspilota* larvae were observed wandering amongst those of *G. depressa*, the number of dead larvae of the latter were attributed to this predator. A few dead *G. depressa* larvae were found sticking to the leaves of the host plant. The cause of death was probably due to disease and was categorized as the result of an unknown factor.

In order to identify the key mortality factor for the *G. depressa* species, the Podolar and Rogers method (1975) was employed. This method consists of plotting a particular developmental stage's mortality factor (k_i) against the total mortality (K) of the immature insect, so that the regression coefficient (b_i) of ki can be found. The b_i determined by the largest k_i represents the key mortality factor.

Results and Discussion

Life tables and the mortality factors

of the various *G. depressa* developmental stages

G. depressa life tables were constructed for the campus, Ozawa, Nakajima, and Tamagashi/Okayama University campus and correspond to Tables 1, 2, 3 and 4, respectively.

Egg stage

The major causes of *G. depressa* egg mortality were attributed to physiological failure and predators. In the predator category, *A. hexaspilota* adults were the most important mortality factor both on the campus and in Ozawa. In 1991, Chang *et al.* proposed that the physiological failure of an entire egg mass may be due to an abnormal sex–ratio condition found only in central Japan. In the Okayama district, no physiological egg mass failure was found instead, mortality hinged on the presence of adult *A. hexaspilota*.

Larval stage

On the campus (except in 1985) and in Ozawa, predators such as *A. hexaspilota* larvae and the scorpion fly, *P. japonica* were the major causes of *G. depressa* larval mortality. The kissing bug, *Sphedanolestes impressicollis*, was also found in Ozawa contributing highly to larval mortality, in contrast, the number and diversity of Okayama predators were relatively low.

Pupal stage

The major causes of *G. depressa* pupal mortality were attributed to predators such as *A. hexaspilota* larvae, *P. japonica* and various types of spiders. In addition, many dead pupae were found and categorized as dying of an unknown factor.

Adult stage

The adult sex ratio extremely favored females over males being: 131/23 (1986) and 55/17 (1987) on the campus and 165/21 (1986) and 247/24 (1987) in Ozawa. In Okayama on the other hand, this ratio was nearly 1:1 being: 25/25 (Nakajima), 361/395 (Tamagashi), 670/704

Table 1. Life tables of *G. depressa* on walnut trees at the Shinshu University campus (the campus) in 1985, 1986, 1987 and 1988

X dxF	1985			1986			1987			1988		
	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$
Egg	2096			3460			20442			6866		
physi. failure*		887	42.3		1121	32.4		3019	14.8		604	8.8
A. hexaspilota		0	0.0		897	25.9		7929	38.8		3752	54.7
other predators		51	2.4		66	1.9		2697	13.2		1076	15.6
Unknown		145	6.9		3	0.1		2167	10.6		550	8.0
Total		1083	51.6		2087	60.3		15812	77.4		5982	87.1
L1	1013			1373			4630			884		
A. hexaspilota		0	0.0		29	2.1		447	9.6		41	4.6
P. japonica		76	7.5		40	2.9		1000	21.6		178	20.1
Other predators		32	3.1		0	0.0		204	4.4		81	9.2
Unkown		262	25.9		190	13.9		1092	23.6		286	32.4
Total		370	36.5		259	18.9		2743	59.2		586	66.3
L2	643			1114			1887			298		
A. hexaspilota		0	0.0		32	2.9		296	15.7		4	1.3
P. japonica		120	18.7		115	10.3		294	15.6		84	28.2
Other predators		13	2.0		20	1.8		100	5.3		3	1.0
Unknown		107	16.6		163	14.6		261	13.8		87	29.2
Total		240	37.3		330	29.6		951	50.4		178	59.7
L3	403			784			936			120		
A. hexaspilota		0	0.0		153	19.5		482	51.5		50	41.7
P. japonica		74	18.4		122	15.5		106	11.3		63	52.5
Other predators		24	5.9		10	1.3		35	3.7		0	0.0
Unknown		102	25.3		94	12.0		131	14.0		2	1.6
Total		200	49.6		379	48.3		754	80.5		115	95.8
Pupa	203			405			182			5		
A. hexaspilota		0	0.0		179	44.2		71	39.1		0	0.0
P. japonica		5	2.5		31	7.7		2	1.1		0	0.0
Other predators		13	6.4		5	1.2		18	9.9		1	20.0
Unknown		29	14.3		36	8.9		19	10.4		4	80.0
Total		47	23.2		251	62.0		110	60.4		5	100.0
Adult	156(92.6%**)			154(95.6%)			72(99.7%)			0(100.0%)		
Sex ratio(Female / male)				131 / 23			55 / 17			0 / 0		

* Physiological failure.

**Toatl mortality from egg to emergence.

(Okayama University campus) in 1988 and 79/111 (Tamagashi), 74/85(Okayama University campus) in 1989. Total *G. depressa* mortality was higher on the campus and in Ozawa than in Okayama; results which are heavily skewed at the former two localities due to failure of egg masses to develop.

Matsura (1976) investigated the effect of the predator, *A. hexaspilota* larvae, on the survival rate of *G. depressa*. His study was conducted in the field and focused on the average rate of *G. depressa* adult emergence on walnut trees. The results showed that 0.68% and 3.67% of eggs made it to the adult stage and that

Table 2. Life tables of *G. depressa* on walnut trees on the Ozawa in 1986, 1987, and 1988

X d_xF	1986			1987			1988		
	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$
Egg	1789			10572			2971		
physi. failure*		657	36.7		1600	15.1		911	30.7
A. hexaspilota		337	18.8		4839	45.8		849	28.6
other predators		55	3.1		332	3.2		276	9.3
Unknown		10	0.6		1133	10.7		212	7.1
Total		1059	59.2		7904	74.8		2248	75.7
L1	730			2268			723		
A. hexaspilota		7	1.0		152	6.7		10	1.4
P. japonica		0	0.0		305	13.4		17	2.3
Other predators		2	0.3		95	4.2		28	3.9
Unkown		206	28.2		489	21.6		214	29.6
Total		215	29.5		1041	45.9		269	37.2
L2	515			1627			454		
A. hexaspilota		36	7.0		62	3.8		17	3.7
P. japonica		0	0.0		84	5.2		96	21.1
Other predators		10	1.9		98	6.0		4	0.9
Unknown		52	10.1		289	17.8		101	22.3
Total		98	19.0		533	32.8		218	48.0
L3	417			1094			236		
A. hexaspilota		93	22.3		183	16.7		40	16.9
P. japonica		0	0.0		53	4.8		37	15.7
Other predators		23	5.5		121	11.1		20	8.5
Unknown		50	12.0		275	25.1		118	50.0
Total		166	39.8		632	57.7		215	91.1
Pupa	251			462			21		
A. hexaspilota		37	14.7		71	15.4		3	14.3
P. japonica		0	0.0		35	7.6		2	9.5
Other predators		6	2.4		61	13.2		4	19.0
Unknown		22	8.8		24	5.2		3	14.3
Total		65	25.9		191	41.4		12	57.1
Adult	186 (89.6%**)			271 (97.4%)			9 (99.7%)		
Sex ratio : Female / male	=165 / 21			247 / 24			9 / 0		

* Physiological failure.

**Toatl mortality from egg to emergence.

these figures were related with the presence of *A. hexaspilota* larvae. He also noted that the effectiveness of predator larvae in controlling *G. depressa* larval population becomes more pronounced at later developmental stages.

From field observations, we know that *A. hexaspilota* adults seek out walnut trees where eggs of *G. depressa* have been lain; first preying on and then laying their eggs around *G. depressa* eggs. Over time, both *A. hexaspilota* and *G. depressa* larvae develop, the former preying more and more frequently on the latter. According to laboratory experimental results, the average prey consumption rate of 1st, 2nd, 3rd and 4th instar *A. hexaspilota* larvae per day (in terms of 1st

Table 3. Life tables of *G. depressa* on walnut trees in Nakajima, Tamagashi and at the Okayama University campus in 1988

X dxF	Nakajima			Tamagashi			Okayama Univ.		
	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$
Egg	5518			3735			4917		
A. *hexaspilota*		2823	51.2		495	13.3		0	0.0
Diptera		13	0.2		344	9.2		21	0.4
Unknown		1093	19.8		671	18.0		2100	42.7
Total		3929	71.2		1510	40.0		2121	43.1
L1	1589			2225			2796		
A. *hexaspilota*		347	21.8		0	0.0		0	
Spiders		2	0.1		7	0.3		21	0.0
Unknown		312	19.6		296	13.3		518	0.8
Total		661	41.5		303	13.6		539	18.5
L2	928			1992			2257		19.3
A. *hexaspilota*		382	41.2		6	0.3		0	
Spiders		0	0.0		7	0.4		28	0.0
Unknown		81	8.7		186	9.7		248	1.2
Total		463	49.9		199	10.4		276	11.0
L3	465			1723			1981		12.2
A. *hexaspilota*		265	57.0		0	0.0		0	0.0
Spiders		10	2.1		106	6.1		75	3.8
Unknown		71	15.3		294	17.1		328	16.5
Total		346	74.4		400	23.2		403	20.3
Pupa	119			1323			1578		
A. *hexaspilota*		44	37.0		0	0.0		0	0.0
P. *japonica*		0	0.0		15	1.1		0	0.0
Spiders		2	1.7		201	15.2		64	4.0
Unknown		23	19.3		351	26.5		140	8.9
Total		69	58.0		567	42.9		204	12.9
Adult	50(99.1%*)			756(79.8%)			1374(72.1%)		
Sex ratio : Female / male=25 / 25				361 / 395			670 / 704		

*Toatl mortality from egg to emergence.

instar *G. depressa* larval weight) are 2.7, 21.4, 47.3 and 129.0, respectively. Note that 4th instar *A. hexaspilota* larvae consumed extremely high amounts of prey.

Key-factor analysis and the population density dependence of *G. depressa* mortality factors

The Key-factor analysis proposed by Varley and Gradwell (1960) was applied in order to evaluate the effect of mortality at each developmental stage (k_i) in terms of the total mortality (K) of the immature insect. Due to the similarity of curve k_3 to that of the total K (see Fig. 1), it would seem that 3rd instar mortality is a key factor on *G. depressa* population dynamics. The results of the Podolar and Rogers method also substantiated this supposition (Table 5).

In order to determine the density dependence of mortality, the total mor-

Table 4. Life tables of *G. depressa* on walnut trees in Tamagashi and at the Okayama University campus in 1989

X d_xF	Tamagashi[1]			Okayama Univ.[2]		
	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$
Egg	4959			3011		
A. hexaspilota		228	4.6		0	0.0
Unknown		735	14.8		547	18.2
Total		963	19.4		547	18.2
L1	3996			2464		
A. hexaspilota		476	11.9		0	0.0
Spiders		14	0.4		0	0.0
Unknown		456	11.4		280	11.4
Total		946	23.7		280	11.4
L2	3050			2184		
A. hexaspilota		1221	40.0		161	7.4
Spiders		13	0.4		0	0.0
Unknown		171	5.6		433	19.8
Total		1405	46.1		594	27.2
L3	1645			1590		
A. hexaspilota		829	50.4		587	36.9
Spiders		15	0.9		0	0.0
Unknown		327	19.9		405	25.5
Total		1171	71.2		992	62.4
Pupa	474			598		
A. hexaspilota		252	53.2		425	71.1
P. japonica		25	5.3		0	0.0
Spiders		4	0.8		0	0.0
Unknown		3	0.6		14	2.3
Total		284	59.9		439	73.4
Adult	190(96.2%*)			159(94.7%)		
Sex ratio : Female / male=79 / 111				74 / 85		

*Total mortality from egg to emergence.

1) The lst instar *A. hexaspilota* larvae were released during the lst developmental stage of *G. depressa* larvae.

2) The lst instar *A. hexaspilota* larvae were released during the 2nd developmental stage of *G. depressa* larvae.

tality value (K) associated with each developmental stage (k_i) of *G. depressa* was plotted against its log. A positive regression coefficient (b>0) means that k_i is density dependent, whereas a negative value (b<0) is associated with inverse density dependence (Varley and Gradwell, 1963). Note that these values were not significant except for k_3 where the mortality of the 3rd instar is inversely

density dependent (b=−0.66, p<0.01).

The log of the total number of *G. depressa* killed by predators was plotted against the log of those found dead in each developmental stage in order to determine the density dependence of mortality due to predation. The regression coefficient results (b values) for the total number of *G. depressa* eaten by predators are shown in Fig. 2. Note that in the egg,

Table 5. K-k relationship in the key-factor analysis

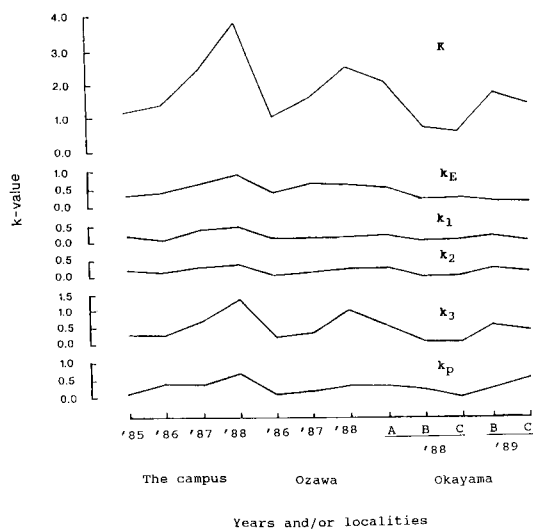| k	b	r^2
k_E	0.211	0.61
k_1	0.121	0.75
k_2	0.077	0.54
k_3	0.405	0.95
k_p	0.152	0.55

Fig. 1. Key-factor analysis of G. depressa populations. A: Nakajima, B: Tamagashi, C. the Okayama University campus.

1st instar, larval, pupal and immature stages, predation occurs in a density-dependent manner (b>1). On the other hand, in the 3rd instar larval stage, predation is inversely density dependent (b<1). The b value results for A. hexaspilota predation on each developmental stage of G. depressa are shown in Fig. 3. Note that b>1 in all developmental stages except that of the 3rd larval instar (b<1).

The results of the Varley and Gradwell analysis as well as those of the Podolar and Rogers method suggested that G. depressa 3rd instar larval mortality is the key population dynamics factor and that mortality of this develop-

mental stage hinges on the presence of A. hexaspilota larvae, in particular, 4th instar larvae.

The 3rd instar *G. depressa* larval inversely density-dependent mortality mechanism

In the course of investigating the inversely density–dependent mortality relationship between A. hexaspilota and G. depressa, the 1st instar larvae of the former were released in Tamagashi and at the Okayama University campus in 1989, in conjunction with the appearance of the 1st and 2nd larval instars of G. depressa. The concurrence of G. depressa and A. hexaspilota populations is shown in Fig. 4, while the life table of G. depressa is shown in Table 4. Note that when 1st instar A. hexaspilota larvae were released during the 1st developmental stage of G. depressa larvae, as was the case in Tamagashi, the population densities of the 1st–2nd and 3rd–4th instars of the former almost concurred exactly with those of the 1st–2nd and 3rd–pupal instars of the latter. In contrast, if 1st instar A. hexaspilota larvae were released during the 2nd developmental stage of G. depressa larvae, as was the case at the Okayama university campus, the population densities of the former did not parallel those of the latter. Nevertheless, the mortality rate due to predation at both localities increased as A. hexaspilota and G. depressa larvae developed.

The total number of G. depressa in each developmental stage were plotted against those that were consumed by A. hexaspilota and the results are shown in Fig. 5. Note that in Tamagashi, the maximum number of G. depressa killed by A. hexaspilota occurred during the former's 2nd larval instar stage, while at the Okayama University campus, predation was heaviest during the 3rd larval instar stage. Also note that while G. depressa population density at the Okayama Uni-
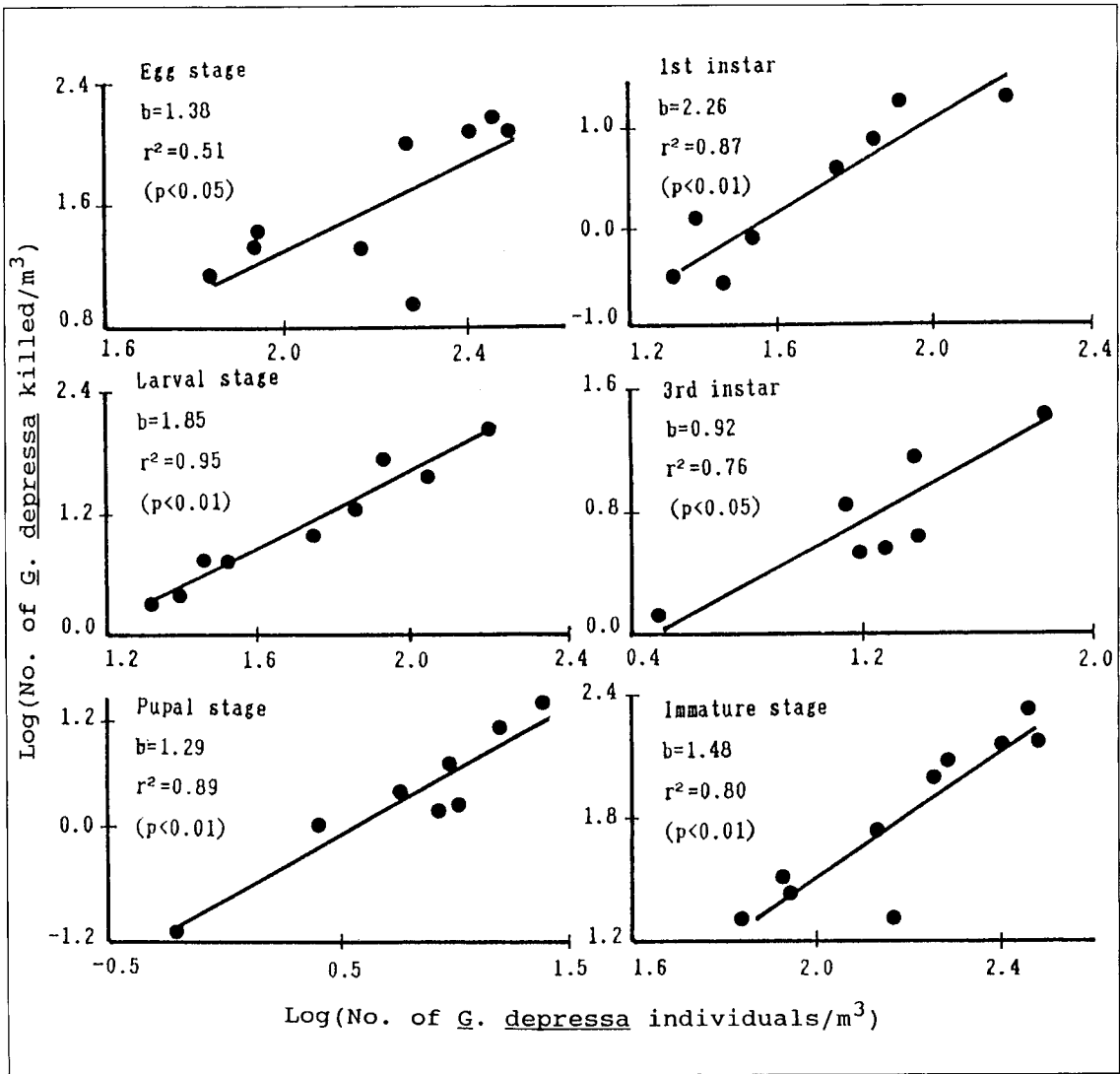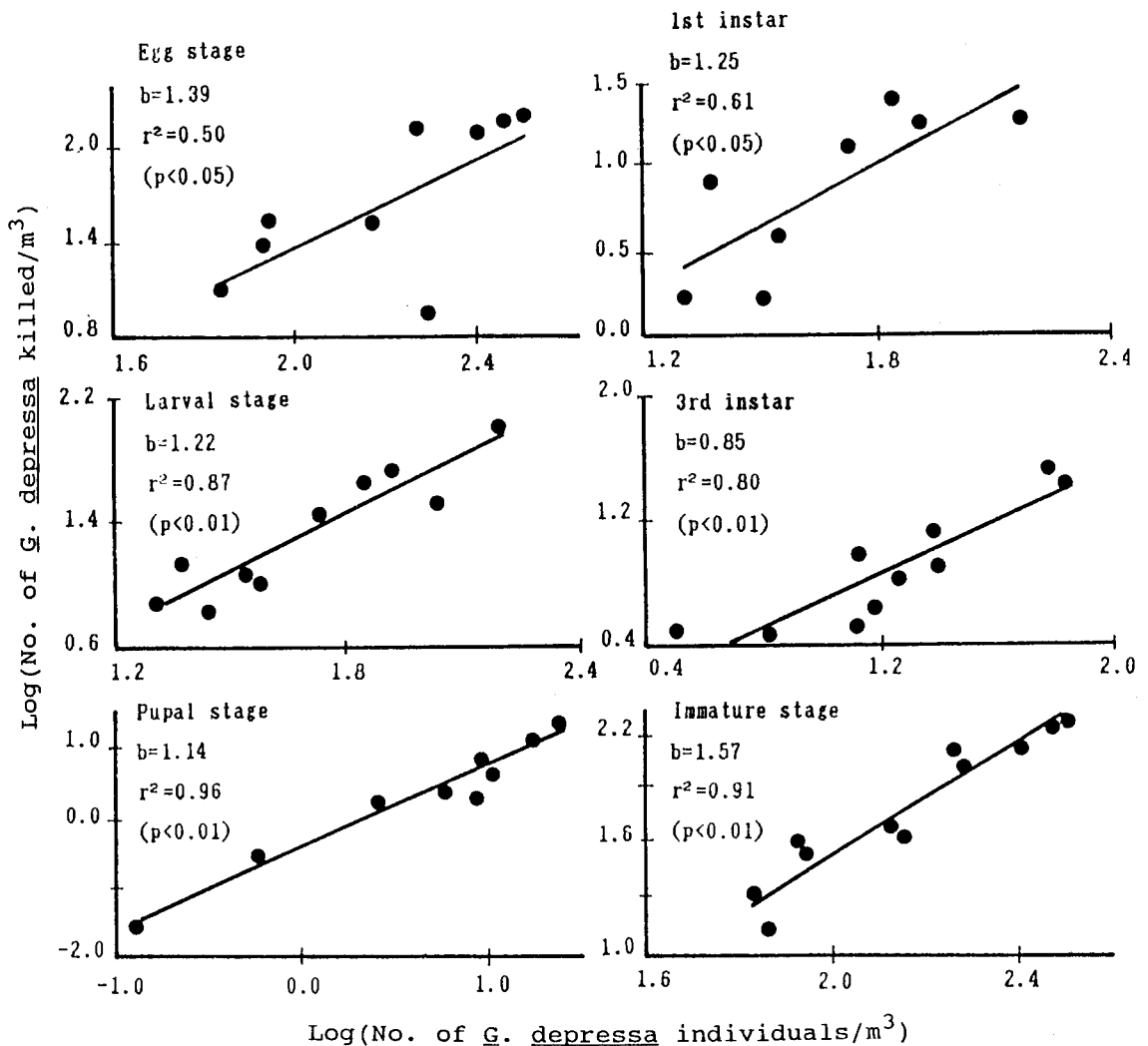
Fig. 2. Relationship between the number eaten by predators and the number of individuals of *G. depressa*.
P shows the level of significance of correlation coefficient (r).

versity campus becomes greater than that in Tamagashi during the 3rd larval instar stage, the number of individuals eaten by *A. hexaspilota* did not follow suit until the pupal stage.

G. depressa mortality at the egg or early larval stages is mainly due to *A. hexaspilota* predation. As Matsura(1976) pointed out, the spatial distribution of the various developmental stages of a *G. depressa* population is contagious. Adult

A. hexaspilota lay eggs on walnut trees where high densities of *G. depressa* eggs or larvae are present. Bearing in mind the above facts, the inverse density–dependent mortality response in the 3rd larval instar of *G. depressa* is postulated as being a result of: (1) a "time lag" or delay mechanism, where the egg laying timing of *A. hexaspilota* adults is such that offspring of a particular developmental stage exist in conjunction with

Fig. 3. Relationship between the number eaten by *A. hexaspilota* and the number of individuals of *G. depressa*.
P shows the level of significance of correlation coefficient(r).

several stages of *G. depressa* larvae; (2) the predatory preference of *A. hexaspilota*, where adults and larvae prey on *G. depressa* eggs and larvae, respectively. It is worthwhile to note that *A. hexaspilota* adults infrequently prey on *G. depressa* larvae, and that the formers' larvae disdain the latters' eggs (Chang, unpublished data). Observations of the feeding patterns of *A. hexaspilota* larvae revealed that 1st instar larvae are almost

functionally unable to catch 3rd instar *G. depressa* larvae. When 4th instar *A. hexaspilota* larvae prey on 1st instar *G. depressa* larvae, they do so with such voraciousness that they come close to eliminating their food supply (Chang, unpublished data). In comparison with their other instar larval stages, 4th instar *A. hexaspilota* larvae consumed more 3rd instar and pupal stage *G. depressa* individuals. The high mortality rate of 1st
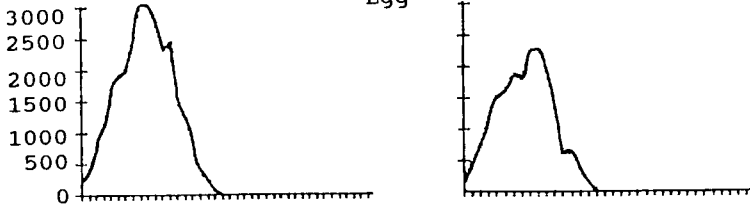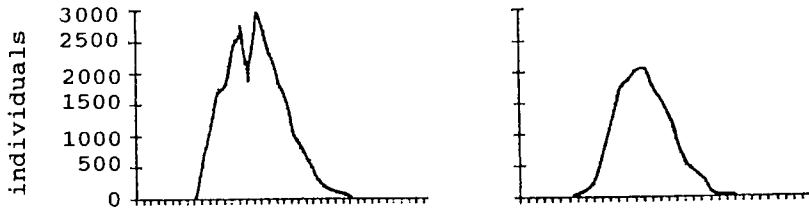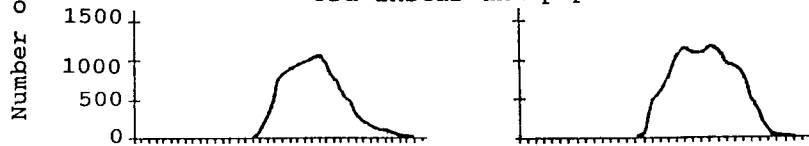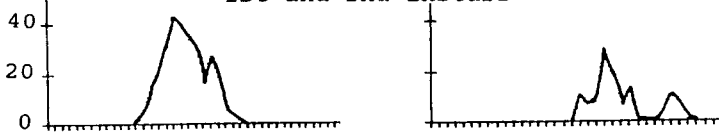
Fig. 4. The concurrence of G. depressa and A. hexaspilota populations in Tamagashi and at the Okayama University campus in 1988. The 1st instar A. hexaspilota larvae were released during the 1st developmental stage of G. depressa larvae in Tamagashi. The 1st instar A.hexaspilota larvae were released during the 2nd developmental stage of G. depressa larvae at the Okayama University campus.

instar *A. hexaspilota* larvae may be due to food shortages and as a result, relatively few survive to develop further. As there are fewer predators present, their overall consumption rate of *G. depressa* decreases (Table 4 and Fig. 4).

It takes relatively few 4th instar *A. hexaspilota* larvae to drastically reduce

(●) Tamagashi (▲) Okayama University campus

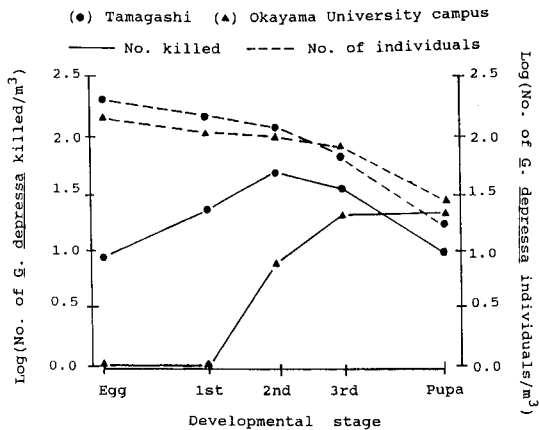―――― No. killed   ---- No. of individuals

Fig. 5.   Changes of the number eaten by *A. hexaspilota* and the number of individuals of *G. depressa* in immature stage in Tamagashi and at the Okayama University campus in 1989. (Refer to Fig. 4)

the entire *G. depressa* larval population. This situation sets the scene for mass starvation of any subsequently hatching *A. hexaspilota* and may explain the reason why 3rd instar *G. depressa* larvae are not consumed by large numbers of predators (recall that predation occurs in an inversely density–dependent manner).

Acknowledgments

References

Chang, K. S., and N. Morimoto. 1988. Life table studies of the walnut leaf beetle, *Gastrolina depressa* (Coleoptera: Chrysomelidae), with special attention to aggregation. Res. Popul. Ecol. 30: 297–313.

Chang, K. S., T. Shiraishi, F. Nakasuji, and N. Morimoto. 1991. Abnormal sex–ratio condition in the walnut leaf beetle, *Gastrolina depressa* (Coleoptera: Chrysomelidae). Appl. Ent. Zool. 26(3): 299–306.

Itô, Y., and K. Miyashita. 1969. Biology of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) in Japan. V. Preliminary life tables and mortality data in urban areas. Res. Popul. Ecol. 10: 177–209.

Matsura, T. 1976. Ecological studies of a Coccinellid, *Aiolocaria hexaspilota* Hope I. Interaction between field population of *A. hexaspilota* and its prey, the walnut leaf beetle; *Gastrolina depressa* Baly). Jap. J. Ecol. 26: 147–156. (In Japanese with English summary).

Podoler, H., and D. Rogers. 1975. A new method for the identification of the key factors from life-table data. J. Anim. Ecol. 44: 85–114.

Richard, O. W., and N. Waloff. 1961. A study of a natural population of *Phytodecta olivacea* (Forster) (Coleoptera: Chrysomeloidea). Phil. Trans. R. Soc. (B) 244: 205–257.

Varley, G. C., and G. R. Gradwell. 1960. Key factors in population studies. J. Anim. Ecol. 29: 399–501.

Varley, G. C., and G. R. Gradwell. 1963. The interpretation of insect population changes. Proc. Ceylon Ass. Adv. Sci. 18(D): 142–156.