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Effects of Aggregation on the Survival and Development on Different Host Plants in a Papilionid Butterfly, *Luehdorfia japonica* LEECH

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Abstract Effects of aggregation on the survival and development in a papilioid butterfly, *Luehdorfia japonica*, were tested by rearing individuals in the laboratory from egg to adult stage in varying group sizes on 3 different host plants. Survival rate and developmental rate were enhanced by larval aggregation on each host plant. Aggregation also synchronized larval development. The magnitude of these effects varied with host plant species supplied and probably depended on the different suitability of the plants. Effects were most pronounced when the larvae were fed on *Asarum caulescens*, but less so when *Heterotropa takaoi* was used.

Introduction

Many insects lay eggs in clusters and the newly hatched larvae usually form aggregations. Breeding experiments in the laboratory have thus far generally indicated that the benefits of aggregation are enhanced survivorship and increased development. Larvae reared in large groups usually fare better than those maintained in small groups or in isolation (see MORIMOTO, 1972, 1979; IWAO, 1968, for reviews). In some studied species these beneficial effects are pronounced when larvae are supplied less suitable food plant (IWAO, 1959; MIZUTA, 1977).

The aim of the present study is to test the effects of aggregation on the larval survival and development in a papilionid butterfly, *Luehdorfia japonica*, on different host plants. *L. japonica* is univoltine, emerging in spring and laying eggs in clusters of 1 to over 20 (averaging around 10) (FUJISAWA *et al.*, 1964; ISHIDA, 1982; ITÔ *et al.*, 1982) on the fresh growth of the larval host plant, which may be any of a number of species of wild gingers. The larvae which hatch from one egg cluster aggregate on the underside of the leaf, and feed and rest synchronously until they have entirely consume the host plant leaves, which usually happens during the 3rd instar. At this stage individuals disperse in search of new plants, and the original group breaks up. Fresh plants are colonized by small groups or individuals. Plants colonized by several larvae are eaten rapidly and further migration occurs, hence 5th instar larvae are almost always solitary.

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Materials and Methods

To test the effects of aggregation and host plant, I reared larvae in different group sizes on different host plants. Laboratory stock was obtained from the field by collecting *L. japonica* eggs laid on *Heterotropa takaoi*, growing in a suburb of Kanazawa City, Ishikawa Prefecture. The hatchlings were provided with fresh leaves of one of the following 3 species of wild gingers: *Asarum caulescens* (henceforth abbreviated as Ac) from a suburb of Kanazawa (a stock collected and cultivated by Dr. H. KIMURA in the Herbal Garden of Kanazawa University), *H. nipponica* var. *natadera* (Hn) from Komatsu City and Yamanaka Town, and *H. takaoi* (Ht) from Kanazawa City.

Ac, a deciduous perennial herb whose leaves are thin and relatively hairy, is known to me a larval host plant of *L. japonica* at only 1 locality in Kanazawa, and it is very sporadically a host plant in the other districts as well, despite its wide distribution over the central and western Japan (HIURA, 1978). It is reported that *L. japonica* larvae fed on this plant have lower survival and developmental rates than those fed on another wild ginger, *Heterotropa blumei* (KITAMURA, 1969). The *Heterotropa* species are evergreen perennials, and Hn has thicker and harder leaves than Ht. Hn is endemic to the southern part of Ishikawa Prefecture and northern Fukui Prefecture and a common host plant of the butterfly in these regions, but it does not occur in Kanazawa where the eggs for the experiment were collected. Ht is widely distributed in the central part of Honshu and the commonest host plant of the butterfly in Ishikawa Prefecture, as well as in many other localities. I chose these 3 plants expecting more pronounced effects of aggregation when larvae were fed on Ac (may be less suitable as suggested by KITAMURA, 1967) or Hn (tough-leaved) than when Ht was used as food.

In 1979 and 1980, experiments were performed as follows: Hatching larvae were divided into 7 categories, classified by group size (1, 2, or 10 individual(s) per group) and host plant (one of the 3 species of wild gingers above). Between 2 and 14 replicates of each group size/host plant category were established. Data (Table 1) are designated by host plant; thus series A included all group sizes on Ac, series N on Hn, and series T on Ht, respectively. The effects of group size and host plant on survivorship and development were compared. Groups comprised initially 1, 2 and 10 eggs, respectively, and replications of each group class were offered leaves of one of the above 3 host plants. Single individuals (group size 1) or groups of 2 individuals were maintained in cylindrical glass containers (7.5 cm in diameter and 8.0 cm in height). Similar containers were used to rear groups of 10 individuals until they reached the 3rd instar, after which they were placed in a larger container 21.0 cm in diameter and 5.0 cm in height) to avoid overcrowding. To keep the humidity high a piece of moistened filter paper was placed at the bottom of each container. The cultures were kept in a thermostatic chamber set at 24.5±1°C in 1979, but the temperature fluctuated irregularly with a range of ±3°C in 1980 due

Table 1. Percentage of survivors at the 1st moult, pupation and emergence to adults (in terms of initial number of eggs) for *Luehdorfia japonica* reared in groups of 1, 2 and 10 individuals on 3 different wild gingers in 1979 and 1980.

Series	Food plant	Group size	No. of replications	% Survivors at		
				1st moult	pupation	emergence
A	*Asarum caulescens*	1	14	64.2	64.2	57.1
		2	8	87.5	87.5	87.5
		10	4	100.0	100.0	100.0
N	*Heterotropa nipponica*	1	9	100.0	88.9	77.8
	var. *natadera*	2	8	87.5	87.5	81.3
		10	2	100.0	100.0	100.0
T	*Heterotropa takaoi*	1	14	92.9	92.9	92.9
		2	8	100.0	100.0	100.0
		10	4	100.0	100.0	100.0

to equipment malfunction. The number of surviving larvae in each instar was recorded every day until all larvae had pupated or died. Any dead larvae were removed as soon as they were found. In 1979 pupae were weighed about 2 weeks after formation.

Results

1. *Effects on the survival*

Table 1 shows the percentage of the initial hatchlings surviving to the 2nd instar (at the 1st moult), pupation and emergence. In all series survivorship from hatching to emergence was lowest in the isolated larvae, and in series A and N the survivorship of larvae reared in groups of 2 individuals was also reduced. By contrast, no deaths occurred in larvae reared in groups of 10 on any host plant or those in groups of 2 in series T.

Most larval death occurred in the 1st instar may be responsible for an inability on the part of the hatchlings to begin feeding. This may correspond to "establishment mortality" defined by GHENT (1960). Table 2 details the establishment rate of the hatchlings. Individuals which succeeded in becoming established included both those which began feeding immediately upon hatching and those which fed only after a delay of more than 1 day (shorter delays could not be detected as cultures were examined only once per day). Delayed feeding was observed only for isolated larvae and those reared in groups of 2. Hatchlings which failed to establish themselves included those which starved to death without feeding and those which died after minimal feeding which left minute feeding scar(s) along the leaf edge.

Totally 4 individuals died after the 1st moult. Of these, 1 isolated larva in series N started feeding normally but showed delayed development after the 2nd

Table 2. Survival rates and mortality patterns in the 1st instar larvae of *Luehdorfia japonica* reared in different group sizes in 1979 and 1980.

Series	Food plant	Group size	No. of replications	% Larvae that survived to the 2nd instar			% Larvae that died in the 1st instar		
				Without delay*	With delay*	Total	Fed**	Not fed**	Total
A	*Asarum caulescens*	1	14	57.1	7.1	64.3	0	35.7	35.7
		2	8	87.5	0	87.5	6.3	6.3	12.5
		10	4	100.0	0	100.0	0	0	0
N	*Heterotropa nipponica* var. *natadera*	1	9	88.9	11.1	100.0	0	0	0
		2	8	68.8	18.8	87.5	0	12.5	12.5
		10	2	100.0	0	100.0	0	0	0
T	*Heterotropa takaoi*	1	14	92.9	0	92.9	0	7.1	7.1
		2	8	100.0	0	100.0	0	0	0
		10	4	100.0	0	100.0	0	0	0

* Without delay and with delay: Larvae started feeding within a day after hatching and started feeding with a delay of one day or more, respectively.

** Fed and not fed: Larvae fed a minute amount (see text) and not fed at all.

Table 3. Mean duration of the larval stage in *Luehdorfia japonica* reared in different group sizes (1, 2 and 10 individuals) on 3 different wild gingers under a constant air temperature of 24.5°C in 1979.

Series	Food plant	Group size	No. of replications	Duration of larval stage in days (Mean±standard errors)
A	*Asarum caulescens*	1	5	24.6±0.9
		2	2	22.5±0.3
N	*Heterotropa nipponica*	1	8	21.1±0.5
	var. *natadera*	2	6	20.3±0.3
		10	2	20.2±0.2
T	*Heterotropa takaoi*	1	10	19.4±0.3
		2	5	19.3±0.3
		10	1	18.5±0.2

moult and died in the 5th instar. One individual in isolation in series A, another in isolation in series N and one from a group of 2 individuals in series N died in the pupal stage. The latter two (both males) began feeding after a delay and the pupae were underweight (320.4 mg and 370.4 mg; male pupae usually exceeded 400 mg). This presumably corresponds to "maintenance mortality" defined by GHENT (1960), Pupae also tended to be light in isolation in series A and the lowest one (male) was only 284.0 mg.

The survivorship advantage of larval aggregation was found to be the general trend (Tables 1 and 2), but it was less pronounced in larvae feeding on Ht than in those feeding on Hn or Ac.

2. *Effects on development*

Table 3 shows the mean durations of the larval stages and their variation. Since development may be affected considerably by a relatively small change in the temperature (CHAPMAN, 1971), the results obtained in 1980 are not included in the table because of the irregular temperature fluctuations noted above. The mean values suggest that larval aggergation tend to increase developmental rate and to synchronize development. However, these effect were not prominent and, as with survivorship, less pronounced in series T than in series A or series N. In all available comparisons between the same group sizes on different host plants, mean larval durations were in the order series A>series N>series T.

Discussion

The above results suggest that aggregation of *L. japonica* larvae, at least in the early instars, enhanced the survival and developmental rates when they were fed on Ac or Hn. Young larvae from the same egg batch normally start feeding within a few hours of hatching; as soon as an individual begins to feed, all the other members of the group follow suit (pers. obs.; HIRUKAWA, 1981). It has been suggested

(NAKAMURA, 1977) that delayed feeding among individuals in small groups or in isolation may be due to the lower probability of a given larva commencing feeding. However, it seems likely that the presence of other larvae also stimulates feeding. Isolated individuals presumably had difficulty in continuing feeding, possibly because they were weakened after the delay and also because they were forced to feed more on the external leaf tissue which is tough (especially in Hn) and haired (especially in Ac).

The effects of aggregation were less pronounced when larvae were fed Ht. On the basis of both survivorship and development found in larvae bred in the same group sizes on different host plants, it may be concluded that, of the 3 wild gingers used in this study, Ht is the most suitable host plant, while Hn is less suitable and Ac still less so. Varying suitability on a similar basis of several different wild ginger species for *L. japonica* larvae has been previously reported (*e.g.*, KITAMURA, 1969; ITÔ *et al.*, 1975; NAKANISHI, 1977). Increases in survivorship and developmental rate of larger groups was also observed in the breeding experiments of the armyworm, *Leucania unipuncta* (IWAO, 1959) and the oriental tussock moth, *Euproctis flava* (MIZUTA, 1977). As in this study, effects were more pronounced when larvae were fed on less suitable food plant species.

By contrast, OSADA (1978) and ISHIDA and KANO (1980) detected no significant differences in the survival or developmental rates between the immatures of *L. japonica* reared in different group sizes, including isolated larvae. Their results are similar to those of series T (the experiments with Ht) in this study. Failure to detect positive aggregation effects by OSADA (1978) and ISHIDA and KANO's (1980) results could be due to the use of high quality host plant species. When OSADA (1983) used old (overwintered) leaves which the larvae never eat in nature, the survival rates of larvae in isolation and small groups were lower than those of larvae in larger groups, results comparable to those in the experiments with Ac and Hn.

Mild laboratory conditions could also mask the effects of aggregation. In fact ISHIDA (1981) re-examined the effects of aggregation in *L. japonica* by rearing larvae in various group sizes at a stressful low temperature (15°C) and found that the survival rate was only slightly lower in smaller groups than in larger ones. Although ISHIDA (1981) emphasized that the differences between the groups were too small to draw clear concludions, it should be noted that the thermal stress in the field is much greater than in the laboratory, hence differences in the survivorship and developmental rates between different group sizes may be more pronounced. OSADA (1983) found that the survival of *L. japonica* larvae in the field was higher in groups than in isolation, and it was higher in larger groups than in smaller ones. The aggregation may well be an important adaptation for increasing survival of indivivuals under natural conditions.

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