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Life history response of a predatory ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), to food stress

Basant K. Agarwala,[1] Hironori Yasuda[2,]* and Satoru Sato[2]

[1] Ecology and Biodiversity Laboratories, Department of Life Science, Tripura University; Suryamaninagar, Tripura West 799130, India
[2] Faculty of Agriculture, Yamagata University; Tsuruoka, Yamagata 997–8555, Japan

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Abstract

The ladybird beetle, *Harmonia axyridis* (Pallas), was studied under laboratory condition to reveal the effect of food stress on phenotypic changes in life history traits that reflect larval and adult performance. Two food environments (abundant and limited food availability) were used as experimental treatments. When the food was limited, larvae grew slowly. Surviving adults were smaller, and their pre-reproductive period was considerably prolonged, reproductive life span and fecundity were reduced, and longevity was increased. On limited food supply, adults had reduced efficiency of converting food into eggs in comparison to adults provided abundant food supply. The relationships between lifetime fecundity and female longevity suggested that for both food levels, there were two groups of individuals with one group showing a positive correlation and the other group a negative correlation between reproduction and longevity. Life history responses to food stress, and the trade-off between fecundity and female longevity, are discussed.

Key words: Food stress; *Harmonia axyridis*; life history; phenotypic change; predatory ladybird

INTRODUCTION

Life history theory assumes that resources often become limiting and environment is frequently heterogeneous in space and time (Stearns, 1976, 1992). Consequently, animals should vary in their structure, function or behaviour so as to maximize their fitness in particular circumstances. The amount of food available is one of the most fundamental factors determining an animal's potential fitness. Variation in food availability has the potential to affect the developmental and reproductive performance of animals. Natural populations of many taxa, including gastropods (Spight and Emlen, 1976), lizards (Andren and Nilson, 1983), birds (Hussell and Quinney, 1986) and mammals (Duquette and Millar, 1995) all show modifications in their reproductive performance in response to variation in food supply.

Larval growth and adult fecundity are important life history traits in aphidophagous ladybirds that are strongly affected by foraging in seasonal, patchy habitats. In the field, aphid populations are highly ephemeral and this impacts the development and reproduction of ladybirds and hence their fitness. Larvae of ladybirds with limited food supply developed into smaller adults (Kaddou, 1960; Smith, 1965; Kawauchi, 1990; Ng, 1991; Agarwala et al., 2001). Laboratory studies have shown that fecundity decreases with maternal size and food availability to females in a wide range of taxa: copepods (Ebert et al., 1993), polychaetes (Qian, 1994), gastropods (Cheung and Lam, 1999), sea-urchins (Thompson, 1982), insects (Grill et al., 1997), and predatory ladybirds (Hodek and Honek, 1996; Obrycki et al., 1998). When deprived of food, a female can curtail energy expenditure for either maintenance or for reproduction. If energy for maintenance is reduced, then life-span becomes shorter. How females balance their reproduction and longevity as food level varies has been emphasized by Reznick (1985). However, no such studies

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* To whom correspondence should be addressed at: E-mail: hyasuda@tds1.tr.yamagata-u.ac.jp
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have been reported in predatory ladybirds of aphids.

In this study, we have examined experimentally the effect of variation in the amount of food on larval performance and reproductive traits of a widely distributed and polyphagous species of a predatory ladybird, *Harmonia axyridis* (Pallas). The aim of the study was to reveal the phenotypic response by larvae and adult females of *H. axyridis* when deprived of food. We examined changes in larval and adult performance as measured by the size (i.e. fresh weight) of larvae and adult females, the duration of development, larval growth rate, lengths of pre-reproductive and reproductive periods, fecundity and adult longevity. We also analyzed the relationship between lifetime fecundity and female longevity at two levels of food availability.

MATERIALS AND METHODS

Insect materials. Males and ovipositing females of overwintered populations of *H. axyridis* were collected in early summer of 2000 from three trees of *Hibiscus syriacus* located within an area of about 1.5 square km on the campus of Yamagata University, Tsuruoka, Japan (38°43′N, 139°49′E). Six pairs of these beetles were kept in a ventilated plastic box (6 cm×17.5 cm×11.6 cm) at 22±1°C and 16 h photoperiod, and supplied an excess of live pea aphids, *Acyrthosiphon pisum* (Harris), that had been reared in a greenhouse on bean plants, *Vicia faba*. These beetles readily ate pea aphids and females laid clusters of eggs on paper towels (Agarwala et al., 2003). Egg clusters from these females were transferred for rearing to 9 cm Petri dishes (one cluster per dish) lined with filter paper in the bottom that was slightly dampened every 12 h. Adults reared from eggs were put in the ventilated plastic box. This stock was maintained in the laboratory for two generations. In the third generation, ten virgin females were chosen randomly from the stock at emergence and kept individually on *ad libitum* food in separate 9 cm Petri dishes with a male beetle of similar age. They were allowed to mate and lay eggs. The beetles used in the experiments were the offspring of these individuals.

Larval performance. In one experimental treatment, each larva was provided with abundant food. In the other experimental treatment, each larva experienced a reduced food supply until it emerged as an adult female and laid its first batch of eggs. A preliminary study showed that individual larvae of *H. axyridis* provided with 30 pea aphids per day had pre-pupal fresh weight of 46.87±2.34 mg (mean±SE, $n=14$), whereas larvae provided with five pea aphids per day had 38.01±3.04 mg ($n=12$). Most larvae that were provided only three pea aphids per day died before becoming fourth instars and the few remaining individuals died in the pupal stage. Larvae provided 35 pea aphids per day did not differ significantly in their pupal weight (48.02±2.67 mg, $n=14$) from those provided 30 aphids ($t=1.14$, df=26, $p=0.27$). In view of these results, two food environments were used in experiments: (1) a limited food supply consisting of five aphids per larva per day, and (2) an abundant food supply consisting of 30 aphids per larva per day. As they developed, larvae were provided aphids as follows to match their increasing food requirements: first instar larvae were offered second instar aphids, second instar larvae given third instar aphids, and third and fourth instar larvae and adult females were offered fourth instar and adult aphids in 1 : 1 ratio.

Ladybird larvae were checked for molting every 12 h. Individual larvae were weighed at birth (<8 h old), at the pre-pupal stage, and upon emergence as an adult (<1 day old). Aphids were replaced every 24 h, and the fresh weight of aphids eaten every 24 h by each larva was determined by multiplying the numbers eaten by the mean weight of that aphid instar. Aphids of each instar were weighed to the nearest 0.01 mg using a Sartorius Microbalance R 200D: first instar=0.11±0.01 mg, second instar=0.57±0.18 mg, third instar=1.02±0.23 mg, fourth instar=1.78±0.30 mg, adults (<1 day old)=2.70±0.46 mg ($n=40$, for each stage). The "food conversion efficiency" was measured as the body weight of the pre-pupae (37.32±2.89 mg, mean±SE, $n=22$, for limited food, 47.48±1.66 mg, $n=22$, for abundant food) minus the body weight of the first instar larvae (0.29±0.03 mg, $n=22$, for limited food, 0.30±0.02 mg, $n=22$, for abundant food) divided by the weight of prey consumed. The weight of prey consumed was the total number of prey consumed multiplied by the average weight of the prey. The study was performed on forty larvae in each food environment. As a result, the study produced sixteen females that be-

Table 1. Development time and survivorship during each developmental stage when *H. axyridis* larvae were provided with a limited or abundant food supply (pea aphids) in Petri dishes

Developmental stage	Development time (mean±SE) in days [*n*]		Survivorship (%)	
	Limited food[a]	Abundant food[a]	Limited food[a]	Abundant food[a]
First instar	2.25±0.16 (a) [40]	3.62±0.18 (b) [40]	92.5 (a)	95.0 (a)
Second instar	2.12±0.13 (a) [37]	2.12±0.13 (a) [38]	83.8 (a)	97.4 (a)
Third instar	2.75±0.16 (a) [31]	2.87±0.13 (a) [37]	80.4 (a)	100 (b)
Fourth instar	6.25±0.16 (a) [25]	3.25±0.16 (b) [37]	96.0 (a)	97.3 (a)
Pupa	7.50±0.27 (a) [24]	6.75±0.16 (b) [36]	100 (a)	100 (a)
Total	20.75±0.31 (a) [24]	18.75±0.25 (b) [36]	60.0 (a)	90.0 (b)

[a] Dissimilar letters in parenthesis following means in a row indicate significant difference at $p<0.05$ by Student's *t*-test for developmental time and χ^2-test for survivorship.

came reproductively active in each food environment.

Reproduction and longevity of female beetles. Two groups of sixteen adult females that developed as larvae on the limited and the abundant food supply were kept individually in 9 cm Petri dishes on the same respective food treatments. Adult males of similar age obtained from the stock culture were allowed to mate with females in a ratio of 1 : 1 for 2 h at the time of food change every other day, in order to induce oviposition and maintain reproductive vigour of females. This practice was followed till females stopped laying eggs. The number of eggs laid was counted every day when residual food and other contents in each Petri dish were replaced with fresh aphids. Egg cannibalism was not observed during the experiment.

Lengths of pre-oviposition and oviposition periods, fecundity, size of egg clusters, and longevity were recorded for each female beetle in the two food environments. Fresh weight of individual beetles was also recorded at first oviposition, on the 10th day from first oviposition, and, again, at death.

Survival rate was compared between treatments using χ^2-test, while developmental time, biomass of pea aphids eaten, and reproductive characteristics were analyzed by *t*-test. In addition, discriminant test was performed for two groups of adults in terms of fecundity and longevity in each treatment (Fig. 1). All data were analysed using SPSS (version 10.0) software.

RESULTS

Larval performance

On a limited food supply, *H. axyridis* larvae grew more slowly (2.72±0.16 mg/day) but converted food more efficiently into larval weight by gaining more weight per fresh weight of pea aphids consumed (0.21±0.02 mg weight gained per mg consumed) in comparison to larvae that developed on an abundant food supply (growth rate: 3.90±0.25 mg/day; food conversion efficiency: 0.15±0.01 mg weight gained per mg consumed). Larvae provided limited food developed more slowly into adults than those provided abundant food, and suffered significantly more mortality (40%) than those provided abundant food ($\chi^2=9.6$, df$=4$, $p<0.05$; Table 1). The observed difference in duration of development is chiefly attributable to effects on the fourth instar, which took significantly longer to complete development on the low food supply. Larvae provided abundant food consumed more than twice the amount of food consumed by larvae provided limited food (Tables 1 and 2). A fourth instar larva, on average, consumed 93.15 mg of pea aphids in 6.25 days on the limited food supply in comparison to 193.05 mg of pea aphids consumed in 3.25 days on the abundant food supply (Table 2). Adult females at emergence were significantly lighter when they were provided limited versus abundant food as larvae (for limited food, 27.98±1.22 mg, mean±SE, $n=16$; for abundant food, 36.06±1.87 mg, $n=16$, $t=3.8$, $p<0.05$).

Reproductive characteristics and longevity of female beetles

Adult females that were kept on a limited food supply had a longer pre-reproductive period, and a shorter period of reproduction, and they lived a longer life in comparison to females that developed on abundant food supply (Table 3).

Table 2. Biomass of pea aphids eaten by larvae of *H. axyridis* at each developmental stage when kept on limited or abundant food supply in Petri dishes ($n=22$)

Developmental stage	Biomass of aphids eaten (mean±SE) (mg)	
	Limited food[a]	Abundant food[a]
First instar	5.96±0.34 (a)	7.14±0.39 (b)
Second instar	6.37±0.52 (a)	9.81±1.09 (b)
Third instar	20.76±1.03 (a)	38.31±3.83 (b)
Fourth instar	93.15±1.77 (a)	193.05±15.03 (b)
Total	126.15±1.26 (a)	252.80±15.62 (b)

[a] Dissimilar letters in parenthesis following means in a row indicate significant difference at $p<0.05$ by Student's *t*-test.

Females kept on limited food supply produced significantly fewer eggs at first oviposition, in the first ten days of reproduction, and during the entire reproductive period in comparison to females that were kept on abundant food supply (Table 3). Females kept on limited food supply laid egg clusters that were smaller by a factor of 3.22 (7.2±0.6, mean±SE, $n=16$), on average, than the size of egg clusters laid by females kept on an abundant food supply (23.2±1.6, $n=16$, $t=8.9$, $p<0.05$).

Mean number of eggs produced per fresh weight of aphids consumed by a female of *H. axyridis* per day was significantly higher on an abundant food supply (0.20±0.02, mean±SE, $n=16$), than on a limited food supply (0.12±0.01, $n=16$, $t=3.4$, $p<0.05$).

Figure 1 shows the relationships between lifetime fecundity and female longevity at the two

Table 3. Reproductive characteristics and adult longevity in days (mean±SE) of *H. axyridis* females when kept on limited or abundant food supply of pea aphids ($n=16$)

Biological characteristics	Limited food[a]	Abundant food[a]
Pre-reproductive period (days)	25.9±0.4 (a)	8.4±0.3 (b)
Reproductive period (days)	23.0±1.1 (a)	53.4±3.3 (b)
Fecundity at first day	6.9±1.1 (a)	34.7±2.0 (b)
Fecundity for first ten days	27.2±3.4 (a)	375.7±27.7 (b)
Fecundity in total	166.8±11.2 (a)	1739.9±167.3 (b)
Adult longevity (days)	96.7±3.7 (a)	65.4±4.1 (b)

[a] Dissimilar letters in parenthesis following means in a row indicate significant difference at $p<0.05$ by Student's *t*-test.

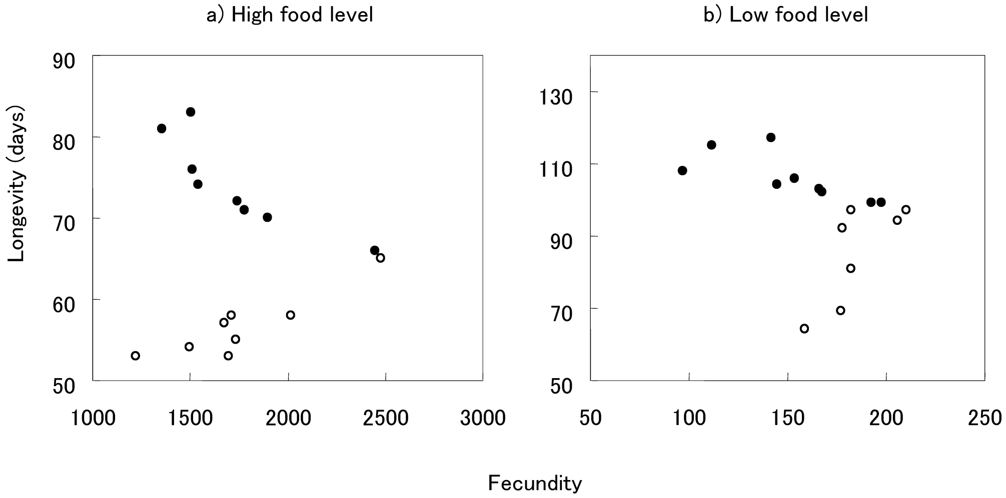

Fig. 1. The relationship between lifetime fecundity and longevity at two food availability. Open and closed circles show relatively short- and long-lived females, respectively.

food levels. In both food levels, females can be categorized into two groups, relatively short- (open circles) or long-lived (closed circles), based on longevity of the most fecund female in each food level (for high food level: Wilks' Lambda$=0.21$, $\chi^2=20.0$, $p<0.001$, low food level: Wilks' Lambda$=0.40$, $\chi^2=11.9$, $p<0.01$). In both food levels, although longevity of relatively short-lived females tended to be longer with increase in their fecundity (for high food level: $r=0.90$, $p<0.01$, $n=8$, low food level: $r=0.75$, $p<0.05$, $n=7$), longevity of relatively long-lived females tended to be shorter with increase in the their fecundity (for high food level: $r=-0.86$, $p<0.01$, $n=8$, low food level: $r=-0.74$, $p<0.05$, $n=9$).

DISCUSSION

Results show large differences in the life history response of the coccinellid at the two food levels. When the environment was food-limited, larval growth was slower and development time was longer, as shown in previous studies (e.g. Kaddou, 1960; Smith, 1965; Kawauchi, 1990; Ng, 1991; Agarwala et al., 2001). In addition, surviving adults under low food availability were smaller, the pre-reproductive period was prolonged, reproductive life span and fecundity were reduced, and longevity was increased. These results clearly reflect that surviving beetles had meager food available for egg production after expending food on basic physiological maintenance.

The effect of food supply on adult longevity has been reported for several insects. Female longevity in the water strider, *Gerris buenori*, nearly doubles when food is scarce (Rowe and Schudder, 1990). However, Blanckenhorn et al. (1995) showed that longevity for both sexes of the water strider, *Aquarius remigis*, increased with food supply. It seems that the relationship between food level and longevity is not so simple since higher food levels did not increase female longevity in the water strider, *A. remigis* (Blanckenhorn, 1994). In the present study, as females provided limited food lived 1.5 times as long as the females with abundant food, it seems that they would spend much energy for maintenance instead of reproduction under limited food availability.

That fecundity is affected by food supply is well known for predatory arthropods (e.g. Kessler, 1971; Blanckenhorn, 1994; Spence et al., 1996). In addition, when food is abundant fecundity increases with body weight in many taxa (e.g. Beck and Connor, 1992; Honek, 1993; Preziosi and Fairbairn, 1996). However, when food is limited the effect depends on the size of the females. For example, fecundity of small individuals of the nursery web spider, *Dolomedes trion*, is unaffected by food availability, whereas large females fail to achieve their reproductive potential when food is scarce (Spence et al., 1996). This suggests that small individuals are no so limited by food, but is scarce or limited for large individuals. In the present study, there was a positive effect of food availability on fecundity, showing that females with abundant food laid 10 times as many eggs over their lifetimes than did females with limited food. This suggests that large females provided abundant food during larval period had enough food to produce the eggs.

Reproduction is known to reduce the longevity of insects (Partridge and Farquhar, 1981; Kaitala, 1987; Rowe and Schudder, 1990; Stearns, 1992; Blanckenhorn, 1994; Blanckenhorn et al., 1995; Dixon and Kundu, 1997). A trade-off between reproduction and longevity has been reported in several species of insects (e.g. Dixon and Kundu, 1997), although Stearns (1992) showed from 22 laboratory studies that there was no clear trade-off. For instance, in water striders, the correlation between fecundity and longevity was insignificant or negative in *A. remigis* (Blanckenhorn, 1994; Blanckenhorn et al., 1995), but positive in *G. thoracicus* (Kaitala, 1987). In addition, the trade-off may only become apparent when organisms are food limited (e.g. Ohgushi, 1996a, b), as is the case for starved planktonic rotifers that show a trade-off between survival and reproduction (Kirk, 1997). In the present study an apparent trade-off between fecundity and longevity was observed in individuals at both food levels with relatively long longevity (as shown also in the ladybird, *Adalia bipunctata*, Hariri, 1966). In contrast, there were positive correlations between fecundity and longevity for individuals with shorter longevity. Although why those shorter lived individuals were present is not revealed in the present study, it might be probably affected by aphid species used in the present study. For instance, Rana et al. (2002) showed that performance of ladybird after consuming certain species of aphids varied in their individuals, suggesting that aphid species used in the present study might be less suitable for ladybird individuals with shorter longevity as a prey. As the trade-off between fecundity and longevity seems rather complex and it might be influenced by food availability, future studies to understand life history responses of organisms should include comparisons of individuals subjected to varying degree of food limitation.

Prey availability in patchy habitat is variable and often unpredictable. This is particularly true of short-lived aphid colonies which are influenced by a number of density-dependent (crowding, competition) and density-independent (climatic and nutritional) factors (Mohammed and van Emden, 1989; Helden et al., 1994). Larvae of aphidophagous predators developing in such patches are likely to face competition for limited food (Dixon, 2000). Variation in adult size at emergence and age at maturity in response to larval growth condition as shown in this study reveals that individuals respond to variable food supplies. The significant increase in the developmental period of fourth instars on limited food supply suggests that the coccinellid larva has a developmental threshold in order to develop into next life history stage.

Environmental variability is a universal feature of biological systems. Environment-induced variations in life history traits play a key role in determining population dynamics. Occurrence of smaller sized predatory ladybirds in the field is common (Obrycki et al., 1998) and this vindicates the prediction that ladybird beetles often live in habitats that are limited by food (Dixon, 1997). Factors that affect prey consumption and reproduction in aphidophagous ladybirds are likely to affect their efficiency as predators and, therefore, influence biological control.

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