

Heritability and fitness consequences of cannibalism in *Harmonia axyridis*

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ABSTRACT

We examined environmental (food levels) and genetic (heritability and evolvability) influences on the expression of cannibalism in larvae of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). In conjunction, we examined potential fitness consequences of cannibalism under different levels of food availability by measuring time of larval development and size at adult. Using a full-sib design, we split broods into food environments that differed by five-fold and measured rates of cannibalism by third instar larvae on first instar conspecifics. Surprisingly, there was significant genetic variation in the expression of cannibalism in response to increased prey levels. Some families exhibited a decrease in cannibalistic behaviour, some an increase, while some families did not alter their cannibalistic rate in response to different food levels. In the low food environment, there was a strong genetic basis for the expression of cannibalism with a heritability significantly different from zero. In the higher food environment, heritability was not significantly different from zero. However, evolvabilities for cannibalism were similarly high for both food level environments. Fitness consequences also depended on food levels. Larvae from the low food environments reduced their development time by approximately 1 day when they cannibalized an average of one first-instar conspecific larva. Although in the higher food environment rates of cannibalism did not decrease significantly, development times remained unaffected. Our results suggest significant genetic variation in the expression of cannibalism within a natural population of *H. axyridis* and selection favouring cannibalism under low food environments but not when prey levels are high.

Keywords: beetle foraging behaviour, Coccinellidae, evolvability, genetic variation, ladybird beetle, power analysis, quantitative genetics.

INTRODUCTION

Cannibalism has been recognized as a common form of size-selective predation in many organisms (Fox, 1975a; Polis, 1981; Elgar and Crespi, 1992). It has been suggested that natural selection may favour cannibalistic behaviour because the cannibal can enjoy two advantages over the non-cannibal: (1) the direct metabolic gain from eating a conspecific,

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and (2) the indirect gain from reducing the number of potential competitors (Polis, 1981). However, cannibalism can be disadvantageous as well. Individuals that are cannibalistic can reduce their inclusive fitness if they cannibalize siblings (Hamilton, 1964a,b). Also, cannibals can suffer an increase in mortality from injurious unsuccessful attacks (Polis, 1981) or being infected by pathogens contracted from eating diseased conspecifics (Pfennig *et al.*, 1991).

Generally, when theoretical ecologists consider a cannibalistic species, they consider cannibalism a foraging strategy equally exhibited by all individuals in the population (e.g. Gabriel, 1985; Diekmann *et al.*, 1986; Cushing, 1991; Crowley and Hopper, 1994). Most variation in expression of cannibalism is considered a function of environmental conditions (i.e. a decrease in abundance of alternative prey or an increase in density of conspecifics) rather than a result of genetic variation in cannibalistic behaviour. However, for cannibalism to continue to evolve there must be variation in the propensity to exhibit cannibalism, this variation must have a genetic basis, and there must be variation in fitness associated with the variation in being cannibalistic (Fisher, 1958).

Few studies have examined the genetic variation and heritability of cannibalism. The best known is a series of quantitative genetic studies of cannibalism in the flour beetle *Tribolium confusum* (summarized in Stevens, 1994). In *T. confusum*, Stevens and colleagues artificially selected for laboratory strains of cannibalistic beetles and examined associated effects on life-history traits such as longevity, fecundity and age at first reproduction. These studies revealed that cannibalism is a trait that can be inherited in a Mendelian genetic fashion and selection, albeit artificial selection, can increase the expression of cannibalism in a population. Unfortunately, the logistical demands of such a quantitative genetic study of cannibalism have probably hindered studies on other organisms, particularly when using natural populations. While inter-population variation in cannibalism has been described in other species (e.g. snails: Bauer, 1994), to date no studies have reported the genetic variation, heritability and potential fitness consequences of cannibalism within a natural field population.

We initiated a quantitative genetic study of cannibalism in natural field populations of the ladybird beetle *Harmonia axyridis* (Coccinellidae). Ladybird beetles are a suitable organism for this type of study because both larvae and adults exhibit cannibalism (Stevens, 1992), and their life cycle can occur within approximately 30 days. *Harmonia axyridis*, an Asian species of ladybird beetle, was first introduced to the United States in 1916 for the biocontrol of aphids (Gordon, 1985; Dreistadt *et al.*, 1995). In the USA, these beetles feed on a variety of aphid species found on agricultural plants (e.g. corn, tomatoes, tobacco), ornamental plants (roses), ornamental and fruit trees (e.g. apple, poplar and black locust). Since becoming established in the USA, local densities of *H. axyridis* can become dramatically high (Potter *et al.*, 1995). In their native habitat in Japan, field studies indicate that egg cannibalism in *H. axyridis* may be a major mortality factor regulating population densities (Osawa, 1992b, 1993). Theoretical work has also argued that cannibalism is a foraging strategy that can allow predators to overcome periods of food stress (van den Bosch *et al.*, 1988; Crowley and Hopper, 1994), a particularly advantageous behaviour for a colonizing species such as *H. axyridis*.

Our goals in this study were to: (1) estimate the genetic and phenotypic variance of larvae-larvae cannibalism in *H. axyridis*; (2) determine if prey abundance could influence the expression of cannibalism; and (3) attempt to identify potential fitness consequences of being cannibalistic.

METHODS

Animal husbandry

We formed a laboratory population of penultimate larvae and adult *H. axyridis*, collected in the field during June and July 1996 in Fayette and Scott Counties, Kentucky, to generate the larvae used in our experiment. Animals were housed individually in 100-mm petri dishes with water and *ad libitum* aphid (*Myzus persicae*) prey. Ladybird larvae and adults were maintained in an environment-controlled chamber set at 24°C and a 16:8 light:dark cycle.

If a field-collected female produced no eggs within 2 weeks, she was assumed to be unfertilized or sperm-depleted. These females then mated in the laboratory. Field-collected larvae were allowed to mature to adulthood and, upon reaching sexual maturity (2 weeks after adult moult), allowed to mate. Males and females were haphazardly paired for mating. Females were each paired with a male until a successful mating was observed. A successful mating was distinguished by the male giving a distinctive 'waggle' during copulation, which is thought to indicate sperm transfer (Osawa, 1994). After mating, females were isolated and given aphids *ad libitum* until eggs were laid, approximately 7–14 days post-copulation. After egg clutches were laid, the females were isolated from the clutch to eliminate the potential for egg cannibalism. Twenty-four hours after eggs hatched, the larvae were robust enough to be handled for movement to experimental treatments.

Experimental manipulations

We reared larvae individually under one of two conditions: high (HIGH) or low (LOW) prey. LOW prey levels were approximately 8–12 aphids per larva provided at hatching with no additional aphids added until third instar. HIGH food levels were approximately 45–55 aphids per larva provided at hatching with no additional aphids added until third instar. The third instar of *H. axyridis* is unambiguously defined by the development of distinctive orange pigmentation on the larval thoracic region.

At the third instar, larvae were further split into two additional treatments: larvae provided with an opportunity for cannibalism (C) and larvae not provided with an opportunity for cannibalism (NC). Thus, from the third instar to adult there were four treatments, no cannibalism in LOW and HIGH food environments (LOW-NC and HIGH-NC) and cannibalism in LOW and HIGH food environments (LOW-C and HIGH-C).

Traits measured

We measured the effects of food level on rate of development, size and expression of cannibalism. Development and size have been shown in previous studies of *H. axyridis* to be influenced by the quality of the diet and genetics (Ueno, 1994; Grill *et al.*, 1997).

Rate of development was determined for early and late instar stages. We measured time spent in early development by checking each larva daily and recording the days from emergence from the egg to third instar. Late development was scored as the number of days from third instar to adult eclosion.

Size, estimated as pronotum width, was measured at two different developmental stages – third instar and adult. We measured pronotum widths from video images using a 8500 PowerMac and the public domain NIH Image video analysis software (available at <http://>

rsb.info.nih.gov/nih-image/). Measurements were made to the nearest 0.01 mm and previous studies have indicated this method has a high repeatability ($r = 0.98$; Grill *et al.*, 1997).

We conducted cannibalism assays immediately after third instars were measured. We assayed the cannibalistic propensity of larvae by placing each third instar larva in an empty 100-mm petri dish with a moistened cotton wick and three non-sib first-instar larvae. At 10, 20 and 30 min, the dishes were surveyed and the number of first instar larvae cannibalized were recorded. All larvae were assayed only once. This provided a measure of cannibalism that varied from 0 to 3 eaten.

After assaying for cannibalism, all larvae were switched to identical food treatments. Thus, from the third instar to pupation, all larvae in all treatments were provided with aphids *ad libitum*. The shift in food level was done to maximize larval development and ensure all larvae survived to adult pupation.

Quantitative genetic analyses

We used a full-sib design to quantify genetic influences on cannibalism and fitness-related traits. Genetic variances, heritabilities (Becker, 1992) and evolvabilities (Houle, 1992) within each treatment were derived from variances calculated from analyses of variance correcting for unequal sample sizes per family (Becker, 1992; Houle, 1992). To determine if the estimates of heritability were significantly different from zero, 95% confidence intervals (CI) for heritability were also calculated based on an F formula (Becker, 1992). The genetic coefficient of variation (CV_G) or evolvability (Houle, 1992) has been proposed as an alternative to heritability as a measure of genetic variation. Evolvability is calculated as $100 \times (\sqrt{V_G}/\bar{X}_{\text{trait}})$ and gives an indication of the potential for selection to change the mean of a trait. Because of the diversity of environmental and genetic influences on different traits which can confound interpretations, comparison of evolvability coefficients will be restricted to within traits and not between traits (Houle, 1992).

Statistical analysis

All analyses were performed using STATISTICA (Version 5.1 1997; StatSoft, Inc.). We were interested in both the environmental treatments (food level, cannibalism) and genetic influences (family effects) on all of the dependent variables. Each family required 24 siblings for the experiment to give six sibling replicates for each of the four treatments (HIGH-C, HIGH-NC, LOW-C, LOW-NC). Because of logistical constraints, not all of the variables were measured for all larvae. Thus, for a family to be included in an analysis, a minimum of two of the six larval replicates per treatment were required. Because logistic constraints prevented measuring all variables on all larvae, the number of families available for specific analyses varied.

Adult size differs between the two sexes in *H. axyridis* (Hodek, 1996). However, it is not possible to determine the sex of larvae; therefore, we corrected for sex differences after individuals emerged to adults. All adult traits were standardized to a common (female) mean (see Grill *et al.*, 1997). There was no significant difference in a 1 : 1 sex ratio at the end of the experiment (Fisher's exact test; HIGH food level: $n = 152$, $P = 0.89$; LOW food level: $n = 153$, $P = 0.67$).

Differences in development time and size at third instar were analysed using a mixed-model, two-way analysis of variance with food level and family as factors. Family was

considered a random effect and was evaluated using the interaction term as the mean square error term (Fry, 1992). Similarly, the effects of family, food and cannibalism on development time (third instar to adult) and adult size were analysed with family as a random factor and food and cannibalism as fixed factors in a separate mixed-model analysis of variance.

RESULTS

Environmental and genetic effects on early growth

The LOW and HIGH food levels were effective in creating environments with different levels of resource available for larval growth (Fig. 1). Larvae raised in the LOW food environment took significantly longer to reach third instar ($F_{1,321} = 48.38$, $P < 0.001$) and were significantly smaller ($F_{1,155} = 79.8$, $P < 0.001$) than larvae reared in the HIGH food environment. The LOW food larvae took 7% longer to reach third instar (Fig. 1A) and were 16% smaller than their siblings in the HIGH food environment (Fig. 1B).

Food levels also affected the amount of genetic influence on early larval growth rate and size (Table 1). Development time exhibited a strong genetic basis regardless of food level. In both the LOW and HIGH food environments, heritability in development time was above 0.8 and significantly different from zero. In contrast, the genetic influence on size at third instar varied with the environment. In the LOW food environment, genetic basis of size was nominal with a heritability value not differing from zero. In contrast, the HIGH food environment resulted in a strong correlation between genotype and phenotype for size at third instar with $h^2_{(\text{HIGH})} = 0.92$. Evolvabilities for development time were similar for both

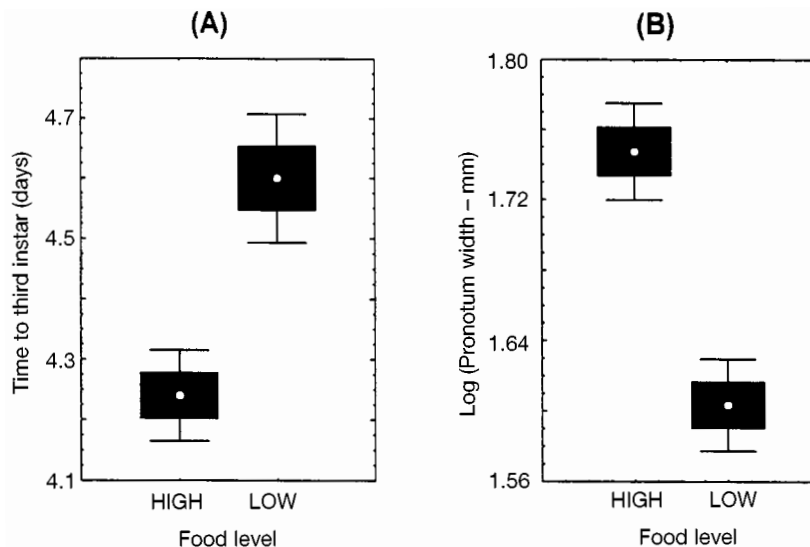


Fig. 1. (A) Effect of food on developmental time from first to third instar prior to cannibalism assay. The LOW food level (10 aphids per larva) resulted in significantly smaller third instar larvae than the HIGH food level (50 aphids per larva). (B) Size of larvae at third instar prior to cannibalism assay. Box represents 1 s.e.; bars represent 2 s.e.

Table 1. Means, heritabilities and evolvabilities of *Harmonia axyridis* traits under different food levels (heritability coefficients in **bold** are significantly different from zero based on the 95% CI)

Character	Mean $\pm$ S.E.	Number of families	Adjusted family sizes	h^2	95% CI for h^2 (lower)–(upper)	Evolvability (CV _G)
LOW food environment						
Time to third instar (days)	4.6 $\pm$ 0.05	27	8.3	1.14	(0.85)–(1.46)	19.2
Size at third instar (log(mm))	1.6 $\pm$ 0.01	13	7.8	–0.04	(–0.16)–(0.30)	N.E.
Cannibalism rate (# eaten/30 min)	1.06 $\pm$ 0.06	32	4.3	0.49	(0.17)–(0.89)	54.1
Time to adult (days)	15.0 $\pm$ 0.15	26	6.3	0.62	(0.33)–(1.01)	10.6
Size at adult (log(mm))	1.0 $\pm$ 0.01	26	5.4	0.54	(0.24)–(0.95)	5.4
HIGH food environment						
Time to third instar (days)	4.3 $\pm$ 0.04	27	8.4	1.15	(0.86)–(1.46)	14.8
Size at third instar (log(mm))	1.72 $\pm$ 0.01	15	7.2	0.92	(0.52)–(1.41)	1.7
Cannibalism rate (# eaten/30 min)	1.01 $\pm$ 0.08	32	4.3	0.22	(–0.04)–(0.59)	45.4
Time to adult (days)	13.5 $\pm$ 0.16	27	6.4	1.10	(0.79)–(1.42)	17.6
Size at adult (log(mm))	1.02 $\pm$ 0.005	27	5.1	0.67	(0.35)–(1.07)	5.0

N.E. = cannot be estimated because of negative heritability coefficient.

the low and high food environments: 19.2 and 14.8 respectively. Evolvabilities for size at third instar in the LOW food environment were indefinable and low in the HIGH food environment ($CV_{A(HIGH)} = 1.7$).

Environmental and genetic effects on cannibalism

Although larvae suffered lower growth in the LOW food environment, they did not exhibit a significantly higher rate of cannibalism than their siblings in the HIGH food environment ($F_{1,250} = 1.04$, $P = 0.31$). Third instar larvae from both environments ate an average of 1.0 ± 0.06 (mean $\pm$ s.e.) first instar conspecifics.

The two-way analysis of variance of the cannibalism data indicated that there was no significant family effect on rates of cannibalism (Table 2; $F_{32,32} = 1.47$, $P = 0.141$), but there was a significant family $\times$ environment (LOW and HIGH food) interaction (Fig. 2; $F_{32,250} = 1.53$, $P = 0.039$). Because of the significant gene $\times$ environment interaction, heritability for cannibalism was calculated separately for the two food environments.

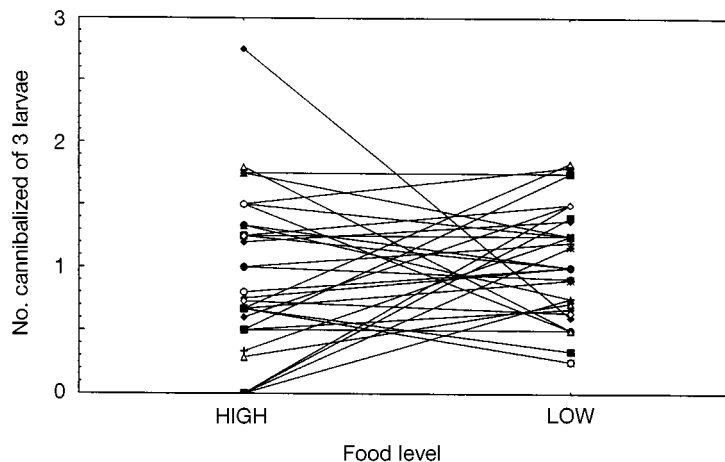


Fig. 2. Mean number of first instar larvae cannibalized by third instar larvae (see p. 378 for details). Each point represents the mean for a unique family. There was a significant sire $\times$ food level interaction for rates of cannibalism.

Table 2. Mixed-model analysis of variance on number of first instar larvae cannibalized by third instar larvae

Effect	d.f. effect	MS effect	d.f. error ^a	MS error	<i>F</i>	<i>P</i>
Food (F)	1	0.729	40.241	1.015	0.717	0.402
Sire (S)	32	1.580	32.000	1.075	1.470	0.141
F $\times$ S	32	1.075	250.000	0.700	1.534	0.039

^a d.f. error computed using Satterthwaite method (Statsoft, Inc., 1995).

Food level determined the level of genetic influence on the expression of cannibalism. In the LOW food environment, heritability for cannibalism was significantly different from zero, $h^2_{\text{(LOW)}} = 0.49$. In the HIGH food environment, heritability estimates were about half of that and the 95% CI overlapped zero (Table 1). Evolvabilities were similar under both environmental conditions ($CV_{A(\text{LOW})} = 54.1$; $CV_{A(\text{HIGH})} = 45.4$).

Environmental and genetic effects on late growth

Although third instar larvae from both the LOW and HIGH food environments were switched to an *ad libitum* food level, the food treatment effects on time of development persisted through the final (fourth) instar and adult pupation. All of the main effects (family, food level and cannibalism) had a significant effect on late development time from third instar to adult (Table 3). Of particular interest was the significant food level $\times$ cannibalism interaction. Larvae raised in the LOW food environments were able to reduce development time by 1 day if they cannibalized conspecifics (Fig. 3). No effect of cannibalism on development time was observed in larvae from the HIGH food environment.

Food level and cannibalism effects on development time did not translate into differences in adult size (Table 4). Adult pronotum width was similar in the LOW and HIGH food

Table 3. Mixed-model analysis of variance on effects on larval growth defined as time from third instar to adult pupation^a

Effect	d.f. effect	MS effect	d.f. error ^b	MS error	<i>F</i>	<i>P</i>
Cannibalism (C)	1	18.37	25.25	2.33	7.87	0.009
Food (F)	1	205.86	21.96	3.94	52.19	0.000
Sire (S)	19	18.30	14.85	4.24	4.32	0.003
C $\times$ F	1	18.36	230.00	2.26	8.11	0.005
C $\times$ S	19	2.34	230.00	2.26	1.03	0.421
F $\times$ S	19	4.18	230.00	2.26	1.84	0.019

^a To control for the effect of sex on development time, males were standardized to female development time. Cannibalism and food levels were fixed effects; sire was analysed as a random effect. ^b d.f. error computed using Satterthwaite method (StatSoft, Inc., 1995).

Table 4. Mixed-model analysis of variance for cannibalism effects on adult size (log[pronotum width])

Effect	d.f. effect	MS effect	d.f. error ^a	MS error	<i>F</i>	<i>P</i>
Cannibalism (C)	1	0.001	21.66	0.003	0.40	0.533
Food (F)	1	0.014	19.56	0.006	2.29	0.146
Sire (S)	18	0.018	12.97	0.006	2.87	0.029
C $\times$ F	1	0.000	180.00	0.003	0.00	0.988
C $\times$ S	18	0.003	180.00	0.003	0.89	0.594
F $\times$ S	18	0.006	180.00	0.003	1.92	0.017

^a d.f. error computed using Satterthwaite method (StatSoft, Inc., 1995).

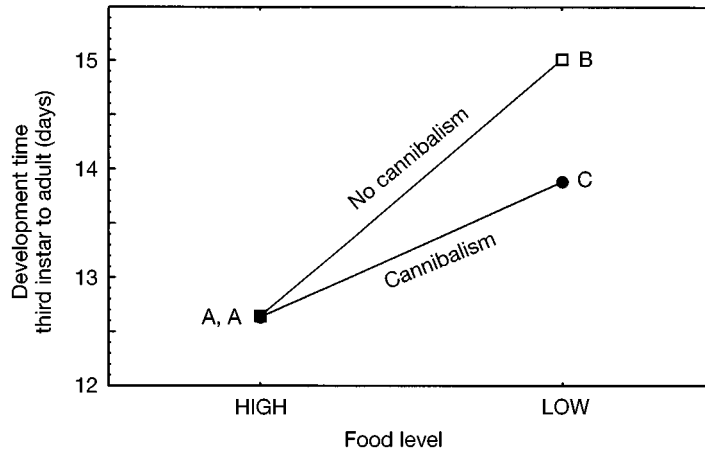


Fig. 3. Growth rate of larvae after cannibalism assay. Although after the cannibalism assay all larvae were fed aphids *ad libitum* from third instar to adult, those larvae that experienced low food levels prior to third instar continued to suffer negative effects on growth rate. Larvae given the opportunity to cannibalize were able to overcome slightly the negative effects of food deprivation on growth by reducing development time by 1 day (LOW-NC versus LOW-C).

environments (2.76 and 2.79 mm respectively) and partaking of conspecifics in their diet had no influence on final adult body size.

The strong genetic influence on late growth was supported by high significant heritability coefficients ($h^2 = 0.54\text{--}1.10$) associated with both late development time and adult size, which were also generally unaffected by food levels. Evolvabilities for both development time from third instar to adult ($CV_{A(LOW)} = 10.6$; $CV_{A(HIGH)} = 17.6$) and size at adult ($CV_{A(LOW)} = 5.4$; $CV_{A(HIGH)} = 5.0$) were independent of food levels.

DISCUSSION

We examined the genetic and environmental contributions to the expression of cannibalism and life-history characters in the ladybird beetle *Harmonia axyridis* (Coccinellidae). Cannibalism in ladybird beetles can occur in three forms: adults eating eggs, larvae eating eggs and larvae eating larvae (reviewed in Hodek, 1996). In the laboratory, we have observed adult female *H. axyridis* to occasionally eat their own eggs when left housed in the same container with their eggs. We have also observed this in the field, but data are lacking on its prevalence. In the field, egg cannibalism by larvae is well documented. Egg cannibalism by larvae can account for up to 60% of the egg mortality and has been proposed to be a major density-dependent factor regulating populations of *H. axyridis* (Osawa, 1989, 1993). Although less is known about inter-larval cannibalism in the field, our laboratory study indicates that larval cannibalism – third instar feeding upon first instar larvae – readily occurs in *H. axyridis*. We found that larval cannibalism was not directly influenced by food availability, but was significantly influenced by genetics and the interaction between food availability and genetics. In response to increased prey levels, some families exhibited a decrease in cannibalistic behaviour, some an increase, and some families did not alter their cannibalistic rate in response to changing food levels (Fig. 2).

In the lower food environment, heritability for cannibalism was high, suggesting that inter-generational changes in expression of cannibalism can occur in response to selection during low food conditions. In contrast, heritability for cannibalism in the high food environment was not significantly different from zero. This could reflect either: (1) previous strong stabilizing selection that has eliminated genetic variation (V_G) or (2) the presence of large phenotypic variation (V_P). In the LOW food environment, the variance components for the heritability estimates were $V_G = 0.33$ and $V_P = 0.67$. In the HIGH food environment, the variance component V_G was similar at 0.23, but there was an approximate doubling in the phenotypic variance, with $V_P = 1.1$.

The increased phenotypic variation in cannibalism within the HIGH food environment therefore reflects local environmental influences. Although it is unknown how these differences arise, factors such as variation in individual hunger level, chance encounter rates with first instar larvae, or variation in foraging activity may have had a greater influence on the expression of larval cannibalism in the HIGH food environment than individual genetics alone.

We also detected potential fitness consequences for being cannibalistic. Cannibalistic larvae in the lower food environment were able to reduce their development time to adults by approximately 1 day – a 6% reduction in development time – compared with their non-cannibalistic siblings. Key factor analysis of field data for *H. axyridis* indicates that, in development from first to fourth instar, larval mortality is high (96%) and density-dependent (Osawa, 1993). Since larval development time in *H. axyridis* decreases with increasing prey consumption (Fig. 1A; see also Honěk, 1996), cannibalistic individuals can reduce their development time, thereby potentially reducing their risk of mortality from predation, cannibalism and parasitism (Osawa, 1992b).

In the LOW food environment, the significant genetic basis of cannibalism combined with the potential fitness advantages on larval growth suggest that when prey levels are reduced cannibalism will evolve. We failed to detect a positive fitness advantage on development time and size of adult for cannibals in the HIGH food environment. Cannibalism can also have negative fitness consequences because cannibals can experience a loss of inclusive fitness from eating a related individual (Hamilton, 1964a,b) or an increased risk of mortality by eating diseased individuals (Pfennig *et al.*, 1991). These factors may be important in selecting against cannibalism in environments where prey levels are high (Osawa, 1992a).

The data suggest genetic variation in cannibalistic behaviour but the variation in cannibalism may be an indirect result of other genetically controlled factors (behavioural or physiological). Genetic variation in either foraging activity or metabolic efficiency may also lead to differential rates of cannibalism. An increase in foraging activity in response to a decrease in food availability could increase encounters with conspecifics and the opportunity for cannibalism. In a similar vein, a genetic influence on metabolic efficiency could alter larvae's ability to withstand starvation. Under low food conditions, those individuals genetically predisposed for poor metabolic efficiency would be closer to starvation and more likely to attack individuals they encounter. Hunger level has been strongly linked to rates of cannibalism in other predators (Fox, 1975b; Wagner and Wise, 1996, 1997). Although these alternative mechanisms may be the cause of the detected genetic influence on cannibalism, this does not invalidate our conclusions. Regardless of the actual trait (cannibalism, foraging activity or metabolic efficiency), selection will favour the traits which ultimately yield an increase in cannibalistic behaviour during periods of food stress.

Our genetic analysis of adult development and size has yielded results similar to those in previous studies of these traits in *H. axyridis* (Grill *et al.*, 1997). This suggests that opportunity for cannibalism does not provide a fundamentally different environmental effect. Genetic influences on size and development account for a large proportion of the variation even though food environments are important.

Typically, rates of cannibalism are significantly influenced by food availability and hunger level (Fox, 1975b; Polis, 1981), although we failed to detect any changes in the rate of cannibalism between our five-fold food levels. The difference in cannibalism rates between the LOW and HIGH food levels was only 0.05 larvae per 30-min assay. A power analysis (Cohen, 1988) indicated an 89% chance of making a type II error in the cannibalism analysis. However, using power analysis we can also determine how big a difference must exist in cannibalism rates between the LOW and HIGH food levels before we have a reasonable chance (80%, $\beta = 0.2$; Cohen, 1988) of detecting the difference. Based on the sample sizes and variances in the cannibalism analysis, we have an 88% chance of detecting a difference in cannibalism rates of 0.4 larvae per 30-min assay. If there is a real difference between the LOW and HIGH food level cannibalism rates, it is a difference of less than 0.4 larvae per 30-min assay. Although these seem trivially small differences in cannibalism rates, assuming a linear extrapolation of these rates indicates a density reduction of 2.4–19.2 larvae per day from cannibalism alone when levels of field prey approximate the LOW prey density levels.

Ecologists typically consider cannibalism in arthropods to be a foraging behaviour expressed in response to food availability and crowding and not individual genetics (e.g. scorpions: Polis, 1980; notonectids: Orr *et al.*, 1990; odonates: Johansson, 1992, 1993; Hopper *et al.*, 1996; wolf spiders: Wagner and Wise, 1996). Our results indicate that individual genetics can have a significant influence on the expression of cannibalism and that within a population there can be significant genetic variation in the expression of cannibalism. The persistence of the genetic variation in most traits in nature has generated numerous hypotheses (reviewed in Roff, 1992, 1997). In the only other published quantitative genetic studies on cannibalism, Stevens and Mertz (1985; Stevens, 1989) suggested that the persistence of genetic variation in cannibalism within laboratory-selected strains of *Tribolium* is a result of neutral selection or stabilizing selection with numerous adaptive peaks. The presence of a selective advantage for cannibalism when prey levels are low disputes the notion of neutral selection for cannibalism in *H. axyridis*. The presence of high genetic variation in the expression of cannibalism in this population of *H. axyridis* may reflect variation in local ecological conditions resulting in numerous adaptive peaks.

The dominant prey of *H. axyridis* is aphids, which are often characterized by localized large-scale fluctuations in population densities (Dixon, 1985; Wellings and Dixon, 1987). Coccinellids frequently maximize egg laying during periods of peak aphid density (Banks, 1955; Dixon, 1970), but within an entire season female ladybird beetles may experience large temporal or spatial variations in patch quality when ovipositing eggs. Since ladybird beetles can produce multiple clutches within a season, each brood can experience selection for or against being cannibalistic depending upon local prey densities. Large environmental heterogeneity may result in differential selection (Levine, 1953) on cannibalism, thereby maintaining genetic variation in the expression of cannibalism. Future comparative studies with natural populations of other cannibalistic species may help to evaluate the roles temporal and spatial variation in prey abundance have in (1) regulating selection for cannibalism and (2) maintaining genetic variation in cannibalism.

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