Nutritional Benefits of Cannibalism for the Lady Beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) When Prey Quality is Poor

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ABSTRACT   Cannibalism, a widespread phenomenon in nature, can both reduce competitors and introduce a high-quality food into the cannibal's diet. We investigated the dietary benefits of cannibalism for larvae of the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas). Cannibalism might benefit the larvae by allowing cannibals to take advantage of prey-detoxification already completed by the victim or the different, and perhaps more diverse, feeding history of the victim. In two laboratory experiments we reared *H. axyridis* larvae with aphid prey, and with or without conspecifics to consume, and recorded larval development and survivorship. In the first experiment, we fed groups of *H. axyridis* larvae an aphid species of intermediate quality, *Aphis nerii* (Boyer deFonscolombe), and prevented or permitted consumption of conspecifics of varied quality— conspecific victims had either fed upon the same intermediate quality food as the focal individual or had fed upon a high quality food. Cannibalism increased survivorship and shortened development time, and eating conspecifics that had fed upon higher-quality food further shortened early development. In a second experiment, we reared groups of *H. axyridis* larvae with one or both of two aphid species of poor (*Uroleucon* spp.) or intermediate [*Aphis fabae* (Scopoli)] quality, and either permitted or prevented cannibalism. Larvae could complete development when fed both conspecifics and the intermediate quality aphid, but not on any other diet. Overall, when mixed with other foods, cannibalism allowed *H. axyridis* larvae to develop on prey that were otherwise nutrient deficient or toxic.

KEY WORDS   multicolored Asian lady beetle, generalist predator, aphid, cannibalism, dietary-mixing, Coccinellidae

CANNIBALISM IS WIDESPREAD among generalist predators (Polis 1981, Rosenheim et al. 1995, Rosenheim 1998). Cannibalistic feeding carries several potential costs, including the loss of inclusive fitness if relatives are consumed (Bauer 1987; Breden and Wade 1989; Agarwala and Dixon 1993; Pfennig et al. 1993, 1994; Pfennig 1997, 1999; Joseph et al. 1999) and the risk for injury or disease transmission during the attack (Elgar and Crespi 1992, Pfennig 1997). However, the ubiquity of cannibalism among generalist predators (Polis 1981, Rosenheim 1998) suggests that cannibalism must have benefits that offset these costs. It has been proposed that cannibals gain by eliminating a competitor while simultaneously obtaining a meal (Polis 1981, Elgar and Crespi 1992, Pfennig 1997).

Cannibalism rates may increase when food is rare (Polis 1981, Elgar and Crespi 1992) but many predators are cannibalistic even when food is abundant (e.g., Hopper et al. 1996, Wagner and Wise 1996, Wagner et al. 1999). When other prey are abundant but of low quality, conspecifics might be a valuable food source by acting as bio-accumulators, concentrating valuable resources, or as bio-filters, eliminating toxic or low-quality compounds. Thus, cannibalism may be a food-mixing strategy, with conspecifics representing a relatively high-quality food. Adaptive food mixing is well-documented in herbivores (e.g., Belovsky 1984, Dearing and Schall 1992, Bernays et al. 1994, Guglielmo et al. 1996, Bernays and Minkenburg 1997), but less is known about food mixing in generalist predators (Bernays 1993). The appearance of cannibalistic feeding in domestic animals that are otherwise noncannibalistic, when fed abundant but nutritionally deficient food (Polis 1981), supports the notion that cannibalism can be a strategy to remedy nutrient deficiencies. Cannibalism in the graminivorous beetle *Tribolium castaneum* (Herbst) seems to fill a similar role, allowing the beetles to develop in flour that is otherwise insufficient to support development (King and Dawson 1973; Via 1991, 1999).

We have been investigating the ecological advantages of cannibalism under variable food quality for the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas). This predator was introduced into the southeastern United States for biocontrol of aphids (Tedders and Schaeffer 1994, De Quattro 1995), and the beetles have rapidly become one of the most common coccinellids in agricultural and natural ecosystems in

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Kentucky (Potter et al. 1995). In their native range in Japan, *H. axyridis* adults and larvae are cannibalistic, with adult on egg, larva on egg, and larva on larva cannibalism well documented in the field (Osawa 1989, 1992a, 1992b, 1993). The recent North American colonists are similarly cannibalistic (Joseph et al. 1999, Wagner et al. 1999).

We performed two laboratory experiments designed to address whether cannibalism allows *H. axyridis* to develop on foods that are otherwise inadequate for development, and whether the diet of the conspecifics used as food affect the cannibal's development. In both experiments, larvae were provided with one or two species of aphids that *H. axyridis* feeds upon in the field. To assess the potential value of cannibalism, some larvae were provided with dead conspecific larvae as a nutritional supplement. In the first experiment, we varied the quality of the conspecific larvae used as supplemental food by raising the food supplement larvae on either high or low quality foods. In our second experiment, all focal individuals received the same quality conspecifics, but we varied the quality of the aphid that we also provided. We measured the effects of these food treatments on larval *H. axyridis* survivorship, development time, and growth.

Materials and Methods

In May and June 1997 we collected the aphids *Aphis nerii* (Boyer de Fonscolombe), *Aphis fabae* (Scopoli), and *Uroleucon* spp. from several sites within 50 km of Lexington, KY. We collected *Aphis nerii* (Boyer de Fonscolombe) from honeyvine milkweed, *Ampelamus albidus* (Nutt.), *Aphis fabae* from curley dock, *Rumex crispus* (L.), and *Uroleucon* from an unidentified goldenrod (*Solidago*) species in the summer of 1997. We chose these aphids because we found *H. axyridis* adults, eggs, and larvae on plants where these aphids were present. *Aphis nerii* and *Aphis fabae* are known to be mediocre foods for other ladybirds (Banks 1955, Pasteels 1978, Hodek and Honek 1996), and we therefore expected them to be of intermediate quality for *H. axyridis;* we were uncertain of the quality of the *Uroleucon* spp. We brought all aphids back to the laboratory and stored them at −20°C.

Larvae used in these experiments were F_1 progeny, derived from several hundred adults collected from the University of Kentucky Spindletop Research Farm (Lexington, KY, USA), and were reared at 22°C. We separated all larvae used in our experiments from their siblings at the first instar and housed them individually in 100-mm petri dishes containing moist cotton plugs. We conducted all experiments in these petri dishes and began the food treatments 1 d after the larvae were separated. We changed the cotton and dishes as needed to maintain ad libitum water and prevent the growth of mold.

The purpose of our study was to investigate the potential nutritional benefits of eating conspecifics, not the behavior of cannibalism itself. We did not ask whether *H. axyridis* would eat live conspecifics, which we have documented elsewhere (Joseph et al. 1999, Wagner et al. 1999), but rather whether eating conspecifics provides nutritional benefits, and whether the benefits depend on the other sources of food. Although we did not quantify the behavior of a focal individual eating a conspecific, there were no qualitative differences compared with the behavior of cannibals eating live conspecifics observed in our previous studies (Joseph et al. 1999, Wagner et al.1999). Furthermore, where the diets overlap, the results we see using food previously frozen is equivalent to what we find with live prey or conspecifics, at least in its differential effects on growth, survival and development of larvae (Joseph et al. 1999, Wagner et al. 1999).

Experiment 1: Manipulation of Quality of Conspecifics as Food. In the first experiment we investigated how variation in the diet of the conspecific provided as food influenced growth and development of focal individuals. We reared the conspecifics to be used as food to the second instar on either the same diet as their eventual cannibal, or on a higher quality diet (below), froze for storage, then thawed before being offered to the cannibals.

We assigned 30 individually housed larvae to each of three diets: (1) *Aphis nerii* aphids only, (2) *A. nerii* + second-instar conspecifics that had fed on *A. nerii*, or (3) *A. nerii* + second-instar conspecifics that had fed on *A. mellifera* (L.). Aphids were offered ad libitum. We offered a single conspecific to each larva, every other day starting on the first day of the experiment. Although we did not measure consumption rates directly, we needed to replenish aphids of each species daily, indicating that larvae were eating the aphids. Although aphids were replenished each day, aphids from the previous day were never totally consumed between feedings, and thus aphids were always available to the larvae. Conspecifics were always consumed entirely.

Experiment 2: Manipulation of Quality of Aphids as Food. In the second experiment, we randomly assigned *H. axyridis* larvae to one of three diets: (1) the *Uroleucon* species only, (2) *Aphis fabae* only, or (3) *Uroleucon* + *A. fabae*. We combined these food-quality treatments with one of two cannibalism treatments in a complete 3×2 factorial design: (1) conspecifics offered or (2) no conspecifics offered. Again, we provided aphids ad libitum, and conspecifics were always completely consumed.

Common Reference Treatments. Each experiment included two reference treatments: (1) conspecifics only and (2) homogenized *Apis mellifera* pupae. We added the conspecific-only treatment to reveal the ability of *H. axyridis* to develop as a pure cannibal. In the first experiment, the conspecifics-only treatment received ad libitum second-instar larvae that had fed upon *A. nerii.* In the second experiment, cannibals received ad libitum newly hatched (so they had not fed) first-instar larvae. The second reference food, *A. mellifera* pupae, provided a standard that approximates maximum growth rate. *A. mellifera* pupae are often used as food in empirical studies of coccinellids and have been shown to provide a high quality diet for *H. axyridis*, equivalent to or better than most other

foods including many aphids (Niijima et al. 1986, Pre-ziosi et al. 1999).

Data Collection and Statistical Analyses. In both experiments we measured survivorship at each stage from third instar to adult. We also measured stage-specific development time (days from hatch to third instar, third to fourth instar, fourth instar to pupa, and pupa to adult) and total development time (days from hatch to adulthood). We measured size at third instar (pronotal width) and as adults (pronotal width, abdomen width). Measurements were made on live subjects using digital image analysis and National Institutes of Health (NIH) Image software (see Grill et al. 1997). All data are presented as means ± 1 SE.

We performed analysis of variance (ANOVA) using the general linear model in SYSTAT (Wilkinson et al. 1996). In the first experiment, we conducted a two-way ANOVA with food quality and conspecifics as factors. In the second experiment we used a one-way ANOVA followed by a series of planned contrasts. In the first planned comparison we contrasted a diet of *A. nerii* to *A. nerii* supplemented with conspecifics (*A. nerii* alone versus pooled *A. nerii* + conspecifics fed *A. nerii* and *A. nerii* + conspecifics fed *A. mellifera*). In the second planned comparison we contrasted the effects of the conspecific victims that had been reared on different diets (*A. nerii* + conspecifics fed *A. nerii* versus *A. nerii* + conspecifics fed *A. mellifera*).

To examine performance relative to a high-quality food, we compared those treatments containing a sufficient sample of individuals surviving to adulthood ($n \geq 5$) to the *A. mellifera* treatment. In these latter analyses we compared rate of development and adult size.

Results

Effects of Variation in Diet on Survivorship. In the first experiment we varied the quality of conspecifics provided as supplemental food to *H. axyridis* larvae (Fig. 1). The supplemented conspecific food increased survivorship, and the increase did not depend on the quality of the supplemental food. While no larva survived to third instar on a diet composed solely of conspecifics fed *A. nerii*, 18% survived on a diet of *A. nerii* alone. Combining conspecifics with aphids increased survivorship. Forty four percent survived on *A. nerii* + conspecifics fed *A. nerii*, 40% survived on a diet of *A. nerii* + conspecifics fed *A. mellifera*, and 85% survived on a diet of *A. mellifera* alone. A monotypic diet of *A. nerii* permitted survival to adulthood. However, any type of cannibalism increased survivorship to adulthood.

In the second experiment we varied the quality of the aphid food provided to *H. axyridis* larvae (Fig. 2). Individuals fed a diet of just *Uroleucon* or *Uroleucon* combined with conspecifics did not survive to the third instar. Other food types supported growth and development to at least the third instar; 37% of the individuals reared on *A. fabae* survived to the third instar, although none of these individuals survived to adulthood. Consuming conspecifics when reared on *A.*
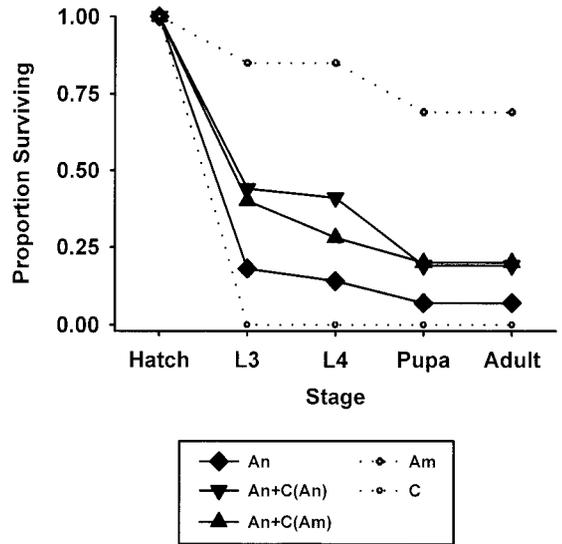

Fig. 1. Larval survivorship in experiment 1. Larvae allowed to consume conspecifics were more likely to complete development than those fed only *Aphis nerii*, although survivorship was low in all treatments including aphids. No larva completed development on conspecifics as the only prey. An, *Aphis nerii* only; An+C(Am), *Aphis nerii* and conspecifics that ate *Apis mellifera*; An+C(An), *Aphis nerii* and conspecifics that ate *Aphis nerii*; Am, *Apis mellifera*; C, conspecifics only.
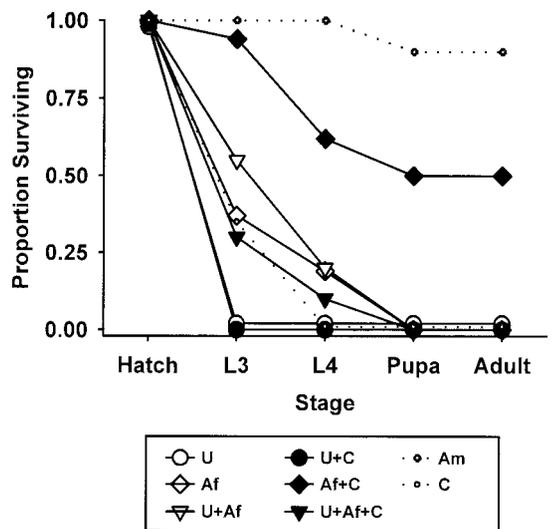

Fig. 2. Larval survivorship in experiment 2. Among the diets that included aphids, larvae only completed development on *Aphis fabae* + conspecifics. No larva completed development on a diet including *Uroleucon*, or on a diet of conspecifics only. U, *Uroleucon*; Af, *Aphis fabae*; U+Af, Uroleucon and *Aphis fabae*; U+C, Uroleucon and newly hatched conspecifics; Af+C, *Aphis fabae* and newly hatched conspecifics; Af+U+C, *Aphis fabae* and *Uroleucon* and newly hatched conspecifics; Am, *Apis mellifera*; C, conspecifics only.
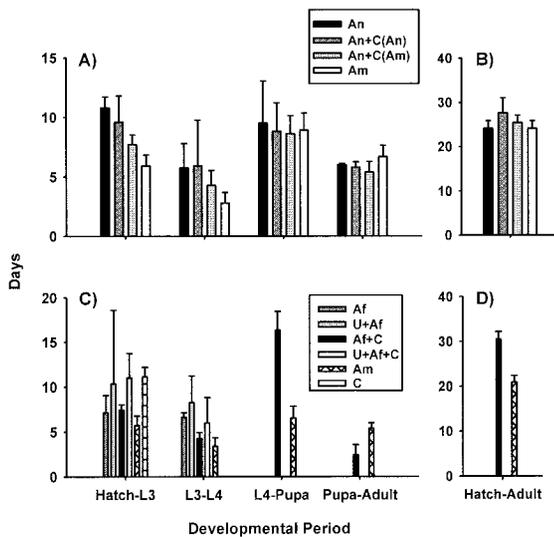
Fig. 3. Effects of aphid quality and cannibalism on (A) stage-specific development time (days from hatch to third instar, third to fourth instar, fourth instar to pupa, and pupa to adult) and (B) total development time (days from hatch to adulthood) in experiment 1, and (C) stage-specific and (D) total development time in experiment 2. In experiment 1 we varied the quality of conspecifics offered as cannibalism victims. Cannibalism shortened early development; consuming high-quality conspecifics further increased the rate of early development. In experiment 2, we varied the quality of aphid prey. Cannibalism facilitated larval development on the intermediate-quality aphid *Aphis fabae*, but development was slower than when larvae fed on the high-quality food *Apis mellifera*. Cannibalism did not mediate the negative effects of feeding on the low-quality aphid *Uroleucon*. For treatments not presented, no larva survived to the third instar. Data are presented as means ± 1 SE.

fabae both increased survivorship to the third instar and permitted 50% to survive to adulthood. A combined diet of *Uroleucon* and *A. fabae* aphids was better than a diet of *Uroleucon* alone—55% survived to the third instar—but none of these individuals survived to adulthood. Cannibalism did not improve the mixed *Uroleucon* and *A. fabae* aphid diet. As we have seen in other studies (Preziosi et al. 1999), a diet consisting solely of *A. mellifera* larvae is as good as the best aphid diets, with nearly complete survival to adulthood (Figs. 1 and 2).

Effects of Variation in Diet on Development. More subtle differences were apparent in development time. In the first experiment, development to third instar was dependent on diet (Fig. 3A). There was an overall significant effect of food ($F = 4.239$; df = 2, 24; $P = 0.027$). Allowing individuals to consume conspecifics resulted in significantly faster development time. The contrast of *A. nerii* without conspecifics to *A. nerii* + conspecifics (pooled cannibalism treatments) indicated a significantly increased rate of development when cannibalism occurred ($F = 4.060$; df = 2, 24; $P = 0.05$). However, the diet of the conspecific used as a supplemental food also significantly affected

development. Individuals that ate *A. nerii* + conspecifics fed *A. nerii* developed significantly slower than individuals that ate *A. nerii* + conspecifics fed *A. mellifera* ($F = 4.750$; df = 2, 24; $P = 0.029$).

There were no significant effects of the diet of the conspecific used as a supplemental food on later development of the focal individuals (Fig. 3A). There was no significant difference on development from third to fourth instar between the diets *A. nerii* + conspecifics fed *A. nerii* and *A. nerii* + conspecifics fed *A. mellifera* ($F = 1.141$; df = 1, 16; $P = 0.301$), fourth instar to pupa ($F = 0.006$; df = 1, 8; $P = 0.942$), or pupa to adulthood ($F = 0.848$; df = 1, 8; $P = 0.384$). However, in all cases, individuals reared on *A. nerii* + conspecifics fed *A. mellifera* developed faster. Lack of significance reflects, at least in part, the small number of individuals that survived to pupa or adulthood on all diets including *A. nerii*.

Assuming reduced development time is beneficial, none of the diets that included *A. nerii* compared well with development on *A. mellifera* alone (Fig. 3A). Individuals reared on *A. mellifera* spent significantly less time in the stages from hatching to the third instar ($F = 29.050$; df = 2, 41; $P < 0.001$) or from the third to the fourth instar ($F = 11.409$; df = 2, 37; $P < 0.001$). There was no significant difference between treatments in the time spent between the fourth and the pupal stage ($F = 0.073$; df = 2, 25; $P = 0.929$). Individuals reared on *A. mellifera* spent significantly more time in the pupal stage ($F = 5.713$; df = 2, 25; $P = 0.009$) but less overall time developing to adulthood (Fig. 3B; $F = 5.534$; df = 2, 25; $P = 0.010$).

In the second experiment, we found that adding *Uroleucon* aphids to a diet of *A. fabae* resulted in *H. axyridis* taking significantly longer to develop to the third instar (Fig. 3C). Cannibalism did not overcome this effect, nor did cannibalism shorten early development time on *A. fabae*. A two-way ANOVA of the effects of food (*A. fabae* or *Uroleucon*) and cannibalism (yes, no) showed food had a significant effect on development time ($F = 1.239$; df = 1, 37; $P < 0.001$). Neither cannibalism ($F = 0.036$; df = 1, 37; $P = 0.358$) nor the interaction between food and cannibalism ($F = 0.00036$; df = 1, 37; $P = 0.926$) were significant.

Because so few individuals developed to adulthood on most diets in the second experiment, we compared the one treatment with relatively high survivorship, *A. fabae* + conspecifics, to the standard food treatment, *A. mellifera* (Fig. 3C). Although survivorship was similar, development from first instar to third instar was significantly shorter in the *A. mellifera* treatment compared with the *A. fabae* + conspecifics treatment ($F = 32.809$; df = 1, 34; $P < 0.001$). The time spent in the period from the third to fourth instar ($F = 7.889$; df = 1,2 8; $P = 0.009$) or fourth instar to pupae ($F = 146.098$; df = 1, 24; $P < 0.001$) was also significantly shorter for the *A. mellifera* treatment. However, the amount of time spent in the pupal stage was significantly longer; over twice as many days for *A. mellifera* compared with *A. fabae* + conspecifics ($F = 44.09$; df = 1, 23; $P < 0.001$). Overall, however, individuals reared on *A. mellifera* developed to adulthood significantly faster than

individuals reared on *A. fabae* + conspecifics (Fig. 3D; $F = 206.205$; df = 1, 23; $P < 0.001$).

Variation in Diet and Effects on Growth. Although development time varied, size was not affected as much by diet in either experiment. In experiment 1, size at third instar was not significantly affected by diet ($F = 2.057$; df = 2, 25; $P = 0.149$). Likewise, in experiment 2, there were no significant effects of food ($F = 0.012$; df = 1, 34; $P = 0.914$), cannibalism ($F = 1.167$; df = 1, 34; $P = 0.288$), or the interaction between food and cannibalism ($F = 0.540$; df = 1, 34; $P = 0.467$) on size of third-instar larvae.

In experiment 1, there were no differences between adult sizes among those that were reared on *A. mellifera* (2.86 ± 0.04 mm) and *A. nerii* + conspecifics fed *A. mellifera* (2.89 ± 0.07 mm; $F = 0.129$; df = 1, 21; $P = 0.723$). Thus, longer development times can, but do not always, result in convergence in adult size. In experiment 2, treatment did have a significant effect on adult size, with individuals reared on *A. mellifera* being larger. Individuals reared on *A. mellifera* had significantly larger pronota (3.11 ± 0.09 mm) than individuals reared on *A. fabae* + conspecifics (2.96 ± 0.03 mm; $F = 17.630$; df = 1, 20; $P < 0.001$). Individuals reared on *A. mellifera* also had wider abdomens (5.30 ± 0.20 mm) than individuals reared on *A. fabae* + conspecifics (4.38 ± 0.35; $F = 63.388$, df = 1, 20; $P < 0.001$).

Discussion

Although *H. axyridis* preys upon many arthropods in North America (Pfannenstiel 1995; LaMana and Miller 1996; Cottrell and Yeargan 1998a, 1998b, 1999), not all of the foods that it encounters and eats are sufficient to sustain growth, development, and survival (Hodek and Honek 1996, Preziosi et al. 1999). Furthermore, like many coccinellids (Hodek and Honek 1996), female *H. axyridis* preferentially oviposit near aphid infestations, apparently without regard to the quality of the aphids as a food resource for the developing larvae (Banks 1955, Hodek and Honek 1996). Previous studies of *H. axyridis* have shown that cannibalism reduces competition and overcomes food limitation (Osawa 1989, 1992a, 1992b, 1993; Wagner et al. 1999). Here we demonstrate an additional benefit of cannibalistic feeding for this species: cannibalism can also allow *H. axyridis* to develop on prey that otherwise are insufficient or of poor quality. Cannibalism by itself is not, however, nutritionally complete. A monotypic diet of conspecifics was the poorest quality food we examined.

Variation in Quality of Aphid Prey. For our studies we chose aphids that we had observed *H. axyridis* eating in the field. We found *H. axyridis* adults, eggs, and larvae on the plants where we collected *Uroleucon*, *A. fabae*, and *A. nerii*. Our initial assumption was that all aphids on which we observed *H. axyridis* feeding in nature would support development to adulthood, even in the absence of alternative food. Contrary to our expectation we found that, in the absence of cannibalism, only *A. nerii* supported full develop-

ment. Beetle larvae could only develop to the third instar on *A. fabae,* and complete development on *A. nerii* was rare (2/28 larvae). Larvae that consumed *Uroleucon* exhibited high mortality, which was only partially offset by the addition of *A. fabae.* Varying diet quality appears to affect development more than size. Different aphid species used as food did not affect the size of larvae at the third instar (early growth) in either experiment, but all diets including aphids yielded development times significantly slower than when larvae were reared on near-optimum food (*A. mellifera* pupae).

Despite the variation in the quality of diets, larvae did not discriminate among the different food-types offered, readily feeding upon all three aphid species or conspecifics that were offered. Even when presented with the opportunity to choose food, the larvae did not recognize *Uroleucon* as a poor-quality food. This was true even though adding *Uroleucon* to their diet significantly decreased the overall value of the diet—*A. fabae* + conspecifics was a superior diet to *Uroleucon* + *A. fabae* + conspecifics. Together, these results seem to confirm what we have observed in the field: *H. axyridis* larvae readily consume aphids they encounter but appear to be unable to differentiate between aphids based on their quality. This lack of discrimination may be caused, in part, by the lack of a co-evolutionary history between *H. axyridis* and the aphids it encounters in its new range in North America.

Benefits of Cannibalism with Poor-Quality Prey. Our results also suggest that consumption of conspecifics can overcome deficient diets and have significant effects on fitness-related characters. Cannibalism increased survivorship on both of the intermediate-quality prey species, *A. fabae* and *A. nerii.* In fact, larval development on *A. fabae* could not be completed in the absence of cannibalism. Adding conspecifics to a diet of *A. nerii* increased egg to adult survivorship 270% and significantly shortened early development time. However, cannibalism only slightly increased survivorship on *Uroleucon,* the aphid of lowest quality. Thus, cannibalism can, but may not always, overcome the negative effects of a poor diet. Cannibalism seems to fill a similar role for the graminivorous beetle *Tribolim castaneum.* In *T. castaneum,* larval cannibalism of conspecific eggs allows larval development in grain flours that are otherwise nutritionally insufficient (Via 1991, 1999).

The value of cannibalism was not only dependent on the cannibal's diet, but also the diet of its victims. Consuming conspecifics with a better feeding history than the cannibal decreased their cannibal's development time by 2 d. This fairly small reduction could be ecologically significant. Osawa (1993) reports 96% mortality before pupation for *H. axyridis* in the field. Cannibalism might therefore act as a means for the cannibal to artificially homogenize the spatiotemporal variation in its feeding environment by combining the results of its own foraging with its victims'. This indirect effect mediated through cannibalism may result from the victims' having accumulated necessary re-

sources or because they filter toxic or harmful substances.

Conspecifics by themselves are not high quality prey. It is only in the presence of other food that conspecifics benefit larval survivorship and growth. Conspecifics as the sole food resource were always insufficient for development. A similar result has been found for another cannibalistic arthropod predator, the wolf spider *Schizocosa* (Toft and Wise 1999), suggesting that conspecifics by themselves might often be a poor quality diet. Although a monotypic diet of conspecifics did not support survival to adulthood, there did appear to be variation in the quality of victims. Larvae were able to reach the third instar on a diet of conspecifics in the second experiment, where newly hatched victims were offered, but not in the first experiment, where the victims were in the second instar and thus had already fed. Although these are separate experiments, it is intriguing that the value of a conspecific to its cannibal might decrease as the victim feeds, especially if the victim feeds on lower-quality prey.

Although the value of dietary mixing for herbivores has been widely studied, less is known about the value of dietary mixing for predatory arthropods (Bernays 1993). Dietary mixing has sometimes been found to increase predator growth and survival (e.g., Greenstone 1979, Uetz et al. 1992), but in other cases dietary mixing has been found to be detrimental. For example, Toft and Wise (1999) found that dietary mixing by the wolf spider *Schizocosa* influenced development. However, the effect was not always positive—inclusion of low quality foods could eliminate the value of higher-quality foods also included in the diet. These results suggest that mixing food can have dietary benefits, but only if relatively nontoxic prey are available in the predators' environment. As nutritionally high-quality and commonly encountered prey, conspecifics might be a particularly rewarding food for generalist predators to include in their diet.

Acknowledgments

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