Ecological Entomology (2004) **29**, 27–34

Using food for different purposes: female responses to prey in the predator *Coccinella septempunctata* L. (Coleoptera: Coccinellidae)

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Abstract. 1. Although predatory insects often feed on diverse prey, their reproductive activity may be linked most strongly to a more restricted range of prey. The propensity of adult females of the ladybird beetle, *Coccinella septempunctata* L., to attack two natural prey species, pea aphids [*Acyrthosiphon pisum* (Harris)] and alfalfa weevil larvae [*Hypera postica* (Gyllenhal)], was compared, and the degree to which ladybird egg production depends on consumption of aphids vs. weevils was assessed.

2. *Coccinella septempunctata* females more readily attacked aphids than weevil larvae. This was true regardless of whether females had fed previously on aphids or on weevil larvae.

3. When females were provided with few to many aphids daily, or few aphids plus an excess number of weevil larvae, their rates of egg production depended primarily on the number of aphids consumed.

4. Addition of weevil larvae to diets of limited numbers of aphids increased egg production, but only modestly. Thus, consumption of weevil larvae may have served mostly for self-maintenance, thereby enabling females to use for egg production more of the nutrients and energy obtained from limited consumption of aphids.

5. The females' linkage of egg production primarily to aphid rather than weevil consumption may be adaptive, as their offspring are much less able as larvae to survive and mature on a diet of weevils rather than aphids.

Key words. Aphidophagous, Coccinellidae, diet, oviposition, predation, prey quality, reproductive strategy.

Introduction

Although many predatory insects appear to be opportunistic generalists in their diets, the suitability of different prey for the predator's growth and reproduction can vary widely (e.g. Strohmeyer *et al.*, 1998; Eubanks & Denno, 2000; Michaud, 2000; Stamp, 2001). Thus Hodek (1962) distinguished broadly between essential prey (those that support both immature growth and development, and adult reproduction) and alternative prey (those that in the absence of essential prey, serve simply as a source of energy and nutrients to maintain the predator). Focusing on adult predators, Dixon (2000) further distinguished between nursery prey, patches of which may elicit predator oviposition, and the broader category of food prey consumed by the predators to sustain themselves.

These distinctions are well-illustrated by ladybird beetles (Coleoptera: Coccinellidae) that prey especially on aphids (e.g. Hodek, 1973; Gordon, 1985; Hodek & Honěk, 1996; Dixon, 2000). Although some species in this group have relatively broad diets and reproduce readily upon consuming non-aphid prey (e.g. Putnam, 1957; Schanderl *et al.*, 1988; Hazzard & Ferro, 1991; Munyaneza & Obrycki,

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1997; Phoofolo & Obrycki, 1997), others appear more narrowly tied to aphids and reproduce little if at all unless aphids are present in their diet (e.g. see reviews by Hagen, 1987; Hodek & Honěk, 1988). Adults of the genus *Coccinella*, for example, consume larvae of Coleoptera and Lepidoptera, but females become reproductively inactive when these prey serve as the sole diet (Richards & Evans, 1998; Evans, 2000). Reproduction by these predators is enhanced, however, when a diet of aphids in limited supply is supplemented with larvae of the alfalfa weevil [*Hypera postica* (Gyllenhal)] (Evans *et al.*, 1999).

Here it is examined how the availability of alfalfa weevil larvae influences the reproductive output of females of *Coccinella septempunctata* L. This Palearctic species has now also become abundant throughout North America (e.g. Schaefer *et al.*, 1987; Maredia *et al.*, 1992; Elliott *et al.*, 1996). Both in North America (e.g. Evans & England, 1996) and its native range (e.g. Yakhontov, 1934; Honěk, 1980), it occurs commonly in alfalfa fields where it feeds on larvae of the alfalfa weevil as well as on pea aphids [*Acyrthosiphon pisum* (Harris)]. Larvae of the univoltine alfalfa weevil are most abundant in spring and early summer. Adult ladybirds can be observed frequently in the field feeding on the larvae at this time, although such prey use may arise largely from opportunistic attacks upon encounter as the predators search alfalfa primarily for aphid prey. The propensity of adult females of *C. septempunctata* to attack alfalfa weevil larvae vs. pea aphids is assessed here first; the contribution of weevil consumption to egg production by this predator when aphid availability is limited is assessed thereafter. Weevil consumption may either indirectly or directly enhance egg production. It may do so indirectly by enabling a female to meet her nutrient and energy needs for self-maintenance (as suggested by Hodek, 1962 and Dixon, 2000). This would free her from devoting to such needs nutrients and energy obtained from consuming a limited number of aphids; instead she could produce more eggs to the extent set by the quantity of aphids consumed. Alternatively, aphids in the diet may serve to stimulate ladybird reproductive physiology (e.g. by providing specific nutrients not present in alternative prey such as weevils). Once such is stimulated, however, a female may consume other prey not only to meet her maintenance needs, but also to increase directly her egg production.

In previous experiments (Evans *et al.*, 1999), these different possibilities were not distinguished. In the two experiments presented here, these possibilities were assessed by comparing egg production among females of *C. septempunctata* L. provided with few to many aphids, or few aphids but also an excess supply of weevil larvae. If consumption of weevils serves to promote egg production directly as well as indirectly (i.e. by contributing to self-maintenance), females may lay as many or more eggs when provided with few aphids but numerous weevils, as when provided with many aphids. On the other hand, females that consume few aphids may produce relatively few eggs regardless of whether weevils are also available, if the latter prey serve merely as alternative prey *sensu* Hodek (1962). In this case, the maximum benefit of consuming weevils would be the release from maintenance to egg production of the full amounts of nutrients and energy provided by the small number of aphids also consumed. Overall, these two experiments with differing levels of aphid and weevil availability for the predators enabled the determination of whether egg production by *C. septempunctata* depends primarily on the rate of aphid consumption even when other prey are also available.

Materials and methods

Insects

Overwintered adults of *C. septempunctata* were collected from alfalfa fields near Logan, Utah, in May 2000 during the latter part of the first crop of alfalfa. They appeared free of disease and were unparasitised (rates of parasitism of this species in these fields in May 1998–1999 were estimated at less than 1%; E. W. Evans, unpubl. data). Thereafter the adults were maintained on a diet of pea aphids in an incubator at cool temperature (13 °C, LD 14:10 h) for two to several weeks before being used for experiments. Pea aphids were collected from broad bean (*Vicia faba* L.) grown in the greenhouse. Alfalfa weevil larvae as well as aphids were used in experiments; the weevils were collected in alfalfa fields in late May and early June, and refrigerated until use.

Behavioural observations

To prepare for observations of individual predators exposed to prey, females were removed from the incubator with cool temperature and placed as paired individuals in Petri dishes (9 cm diameter) in a second incubator at 22 °C, LD 14:10 h. For the next 3 days, they were provided with either pea aphids of mixed ages, or weevil larvae (fourth instar). In either case, prey were provided in excess. Prey were then withheld from all predators for one additional day. Thereafter, females were observed after placing them individually in Petri dishes (5 cm diameter) that had been stocked immediately before with five prey individuals. One female of each pair was placed randomly with five adult pea aphids, and the other female with five weevil larvae (fourth instar). Thus, females were observed attacking prey for four treatment combinations of prey (aphids or weevils) provided prior to observations × prey (aphids or weevils) provided during observations. One hundred and twenty females (i.e. 30 females for each treatment combination) were selected initially for the experiment. Two females died, however, while being fed aphids prior to observations. Thus, only 29 females were observed for the treatment combinations: aphids provided prior to observations × aphids or weevils provided during observations.

Predator–prey encounters were observed under ambient conditions (21–24 °C) on a laboratory bench exposed to windows and daylight. Each female was observed for a maximum of 10 min as she searched, and the number of encounters with prey (i.e. instances in which the predator physically contacted the prey) was recorded. Many encounters were brief; the predator moved away from the prey within 2 s or less (if the predator physically contacted an individual prey after she had previously contacted and moved away from that prey, this was scored as another encounter). Predators that made a clear effort to attack the prey (i.e. predators that remained with the prey and attacked it for at least two seconds) were observed for up to 10 min once the attack began.

Egg production on varied diets

Two experiments were conducted with *C. septempunctata* adults kept as mixed pairs (male and female) in Petri dishes (9 cm diameter) at 22 °C, LD 14:10 h. Pairs were placed in these conditions 1 week prior to the start of an experiment, and were fed pea aphids in excess daily during this week. By the start of the experiment, all females had mated and were actively producing eggs.

The first experiment began 2–3 weeks after adults had been collected from the field. Ten pairs of *C. septempunctata* were assigned systematically to each of four diets provided daily during the experiment: (1) five aphids (predators were provided with adults of the pea aphid in this and other treatments), (2) five aphids plus 20 alfalfa weevil larvae (fourth instar), (3) 10 aphids, or (4) 20 aphids. Females were paired with males throughout the experiment to promote a high level of reproductive activity. Females of *C. septempunctata* eat greater quantities of prey than do males but the two sexes are similar in their relative consumption rates of aphids and weevil larvae (E. W. Evans, unpubl. data). Each pair of *C. septempunctata* was transferred to a new Petri dish each morning, and provided with new prey. The numbers of eggs laid by females were recorded three times throughout each day for 15 days (based on casual observations made before and during the experiment, it was assumed that eggs were fertile). In the few instances in which cannibalism occurred, the number of eggs consumed by adults was determined (and included in the total count) from the egg remains or yellow spot left behind. Males (but not females) that died during the experiment were replaced.

The second experiment began 5–6 weeks after adults were collected from the field. Procedures identical to those of the first experiment were used, except that pairs were provided with more aphids. Thus, 10 pairs of *C. septempunctata* were assigned systematically to each of the following four diets provided daily: (1) 10 aphids, (2) 10 aphids plus 20 alfalfa weevil larvae (fourth instar), (3) 20 aphids, or (4) 30 aphids.

Statistical analyses

Chi-square analyses (Daniel, 1978) were used to compare percentages of females from different treatment combinations that attacked a prey during 10 min of observation. For females that attacked a prey, the number of encounters with prey that occurred before the predator attacked, and the time that the predator spent feeding on the prey, were examined with two-way ANOVA (with Type III sums of squares for unbalanced design) for effects of prey (aphids or weevils) provided prior to vs. during observations, and for their interaction (SAS Institute, 1998). To homogenise variances among treatment combinations, the number of encounters was transformed by taking the square root prior to analysis.

The number of eggs produced on differing diets in the two experiments was examined by using multivariate repeated measures analysis following square root transformation (SAS Institute, 1998). For each experiment, egg counts were combined into five 3-day periods (e.g. the first to third day) prior to analysis (this was done to retain sufficient degrees of freedom in the analysis; Von Ende, 1993). Data were omitted for females that died during experiments. In the first experiment, these individuals included one female from a pair provided with five aphids plus weevils each day, and two females from pairs provided with 10 aphids each day. In the second experiment, they included one female from a pair provided with 10 aphids each day, and two females from pairs provided with 10 aphids plus weevils each day. Because the design was therefore unbalanced, Type III sums of squares were used in analyses.

Results

Behavioural observations

When *C. septempunctata* females were exposed to prey for 10 min, a higher percentage of individuals attacked a pea aphid than attacked a weevil larva (Fig. 1a). This was especially evident for females that had previously fed on aphids (Fig. 1a; $\chi^2 = 15.82$, $P < 0.0001$). A similar but less pronounced pattern was evident for females that had fed previously on weevil larvae (Fig. 1a; $\chi^2 = 6.67$, $P = 0.001$). A higher percentage of females attacked the prey (both weevils and aphids) when they had previously fed on weevil larvae rather than on aphids. This was most striking when weevils were offered as prey (Fig. 1a; $\chi^2 = 14.34$, $P = 0.0002$). A similar but less striking pattern occurred when aphids were offered as prey (Fig. 1a; $\chi^2 = 5.65$, $P = 0.017$).

Among females that attacked a prey, fewer encounters tended to occur with aphids than with weevils before the predator attacked; this was true both when predators had fed previously on aphids and when they had fed previously on weevil larvae (Fig. 1b; two-way ANOVA, effect of prey type offered: $F_{1,83} = 3.44$, $P = 0.067$; interaction of effects of prey type offered and prey type consumed previously: $F_{1,83} = 0.33$, $P = 0.56$). For a given type of prey (aphid or weevil), more encounters with the prey occurred before an attack when the predator had previously been fed aphids than when the predator had previously been fed weevil

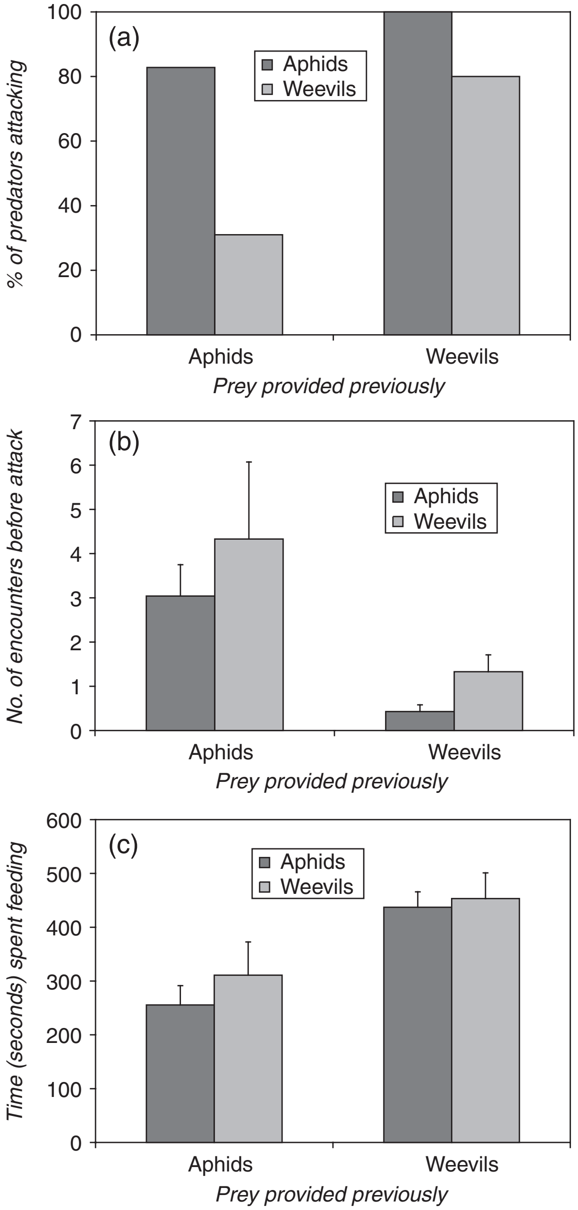

Fig. 1. Results of encounters with prey when females of *Coccinella septempunctata* that had fed previously on pea aphids or alfalfa weevil larvae were placed with five pea aphids (fully shaded bars) or five weevil larvae (dappled bars). (a) Percentage of females that attacked an aphid or a weevil larvae within 10 min after being placed with the prey. (b) Mean number of encounters with prey (+ 1 SE) that occurred before a female attacked an aphid or a weevil larva for those females attacking within the first 10 min. (c) Mean length of time (in seconds, + 1 SE) that females that attacked spent feeding on aphids or weevil larvae.

larvae (two-way ANOVA, effect of prey type consumed previously, $F_{1,83} = 20.39$, $P < 0.0001$).

In all but two cases, attacking predators succeeded in subduing the prey and consuming it for at least 20 s (in the two exceptions, females spent only 5 and 11 s attacking weevils before abandoning them). Females that attacked aphids and females that attacked weevils spent similar amounts of time feeding on the prey; this was true both of females that had fed previously on aphids and of females that had fed previously on weevils (Fig. 1c, two-way ANOVA, effect of prey type offered: $F_{1,83} = 0.63$, $P = 0.43$; interaction of effects of prey type offered and prey type consumed previously: $F_{1,83} = 0.19$, $P = 0.66$). Females that had fed previously fed on weevils, however, spent longer consuming prey (aphids or weevils) than females that had fed previously on aphids (Fig. 1c, two-way ANOVA, effect of prey type consumed previously: $F_{1,83} = 13.02$, $P = 0.0005$).

Egg production on varying diets

Pairs of *C. septempunctata* adults in both experiments consumed all aphids (or on rare occasions, almost all aphids) provided each day (the dry weight of an aphid was 0.6–0.7 mg). Those pairs that were also provided with weevil larvae consumed these prey as well; pairs killed a mean (+ SE) of 5.9 + 0.5 weevils per day in the first experiment, and 5.8 + 0.8 weevils per day in the second experiment (the dry weight of a weevil larva was 2.2–2.6 mg; predators usually did not consume fully the entire carcass of weevils killed, however). Egg production in the first experiment dropped rapidly to very low levels when pairs were provided with five aphids daily, especially when this diet was not supplemented with weevils (Fig. 2). Egg production when pairs were provided with 10 aphids daily also dropped after the first 3 days, but remained much higher for the remainder of the experiment than that of pairs provided with five aphids plus weevils. Egg production was high throughout the experiment for pairs provided with 20 aphids daily. These differences in egg production among females led to a significant interaction between treatment and time (multivariate repeated measures analysis, interaction of treatment × time: Wilks' $\lambda = 0.337$, $F_{12,79} = 3.38$, $P < 0.001$).

Several females of pairs provided with only five aphids daily (with or without weevils) laid no or almost no (only one or two) eggs after the first day (when egg production likely was highly influenced by aphid consumption prior to the experiment). Of the remaining females, those fed weevils as well as five aphids daily laid significantly more eggs from the second day on than did those fed only five aphids daily ($\bar{x} + \mathrm{SE}$: 54.5 + 10.6 vs. 26.3 + 7.4 eggs; $F_{1,13} = 6.39$, $P = 0.025$). Even those reproductively active females that were fed weevils as well as aphids, however, produced many fewer eggs from the second day on than did females of pairs provided 10 aphids per day ($\bar{x} + \mathrm{SE}$: 54.5 + 10.6 vs. 139.9 + 34.9 eggs; $F_{1,14} = 7.26$, $P = 0.017$).

Egg production in the second experiment again rapidly declined when pairs were fed only 10 aphids daily, particularly when this diet was not supplemented with weevils (Fig. 3). Females of pairs fed 20 aphids daily consistently produced substantially more eggs than females of pairs fed 10 aphids plus weevils, and the disparity in egg production between these two treatments increased over time. Females

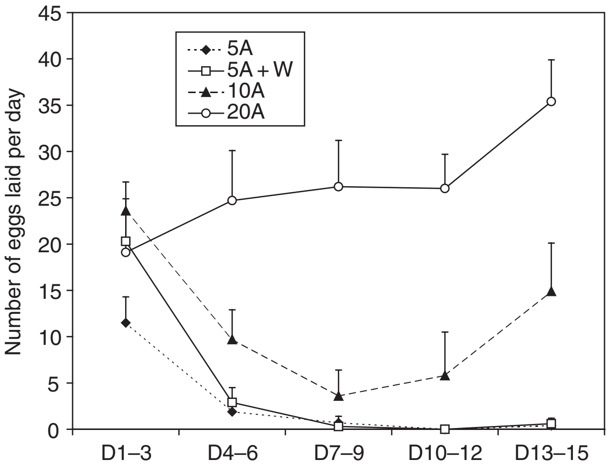

Fig. 2. Mean number of eggs laid per day by a female (+ 1 SE) when paired adults of *Coccinella septempunctata* were provided five ('5A'), 10 ('10A'), or 20 ('20A') adult pea aphids daily, or five such aphids and an excess supply of weevil larvae ('5A + W'). Mean daily egg production is presented for successive 3-day periods throughout the 15-day experiment [e.g. the mean number of eggs laid per day during the first 3 days ('D1–3') of the experiment].

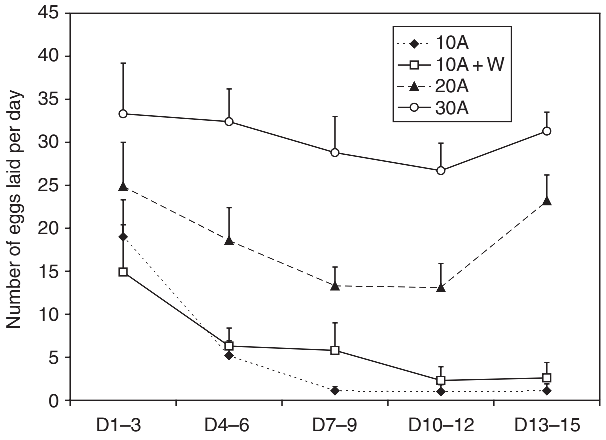

Fig. 3. Mean number of eggs laid per day by a female (+ 1 SE) when paired adults of *Coccinella septempunctata* were provided 10 ('10A'), 20 ('20A'), or 30 ('30A') adult pea aphids daily, or 10 such aphids and an excess supply of weevil larvae ('10A + W'). Mean daily egg production is presented for successive 3-day periods throughout the 15-day experiment [e.g. the mean number of eggs laid per day during the first 3 days ('D1–3') of the experiment].

of pairs fed 30 aphids daily produced greatest numbers of eggs throughout the experiment. As in the first experiment, these differences in egg production among females led to a significant interaction between treatment and time (multivariate repeated measures analysis, interaction of treatment × time: Wilks' $\lambda = 0.49$, $F_{12,79} = 2.04$, $P = 0.03$).

The most dramatic drop in egg production by females of pairs provided 10 aphids daily with or without weevils occurred early in the second experiment (Fig. 3). Several females in these two treatments laid no or almost no (four or fewer) eggs after the first 3 days. Of the remaining females, females fed weevils as well as 10 aphids daily laid significantly more eggs from the fourth day on than did females fed only 10 aphids daily ($\bar{x}$ + SE: 81.2 + 19.9 vs. 31.6 + 7.2 eggs; $F_{1,11} = 6.85$, $P = 0.026$). These reproductively active females that were fed weevils as well as aphids, however, produced far fewer eggs from the fourth day on than did females of pairs provided with 20 aphids per day ($\bar{x}$ + SE: 81.2 + 19.9 vs. 204.7 + 24.8 eggs; $F_{1,13} = 8.59$, $P = 0.012$).

Discussion

Although they may attack diverse kinds of prey, predatory insects often show distinct prey preferences in both feeding (e.g. Digweed, 1993; Eubanks & Denno, 2000; Stamp, 2001) and reproduction (e.g. Hoelmer *et al.*, 1993; Richards & Evans, 1998; Spieles & Horn, 1998). *Coccinella septempunctata* in particular is a member of a group of ladybirds that feed on many kinds of prey but appear to specialise in preying upon aphids (Gordon, 1985; Hagen, 1987; Hodek & Honěk, 1996; Dixon, 2000). Previous studies have shown aphidophagous ladybirds to consume more aphids than non-aphid prey when given the choice (e.g. Hussain, 1975; Ouayogode & Davis, 1981; Lucas *et al.*, 1997; but see also Gagné *et al.*, 2002, who found that larvae of *Coleomegilla maculata lengi* Timberlake prefer conspecific eggs over aphids). In the present study, greater percentages of *C. septempunctata* females attacked aphids than attacked weevil larvae, and fewer encounters with aphids vs. weevil larvae occurred before attack. This was true even when females were maintained on a weevil diet prior to observations. Thus, previous feeding experience did not affect the predators' basic tendency to attack aphids more readily than weevils. Similarly, Hagler and Cohen (1991) found that prey preferences of the big-eyed bug *Geocoris punctipes* (Say) did not vary between field-captured individuals and individuals reared in the lab on artificial diet. Hattingh and Samways (1992) also found that feeding history did not influence food choice of the coccinellids *Chilocorus nigritus* (Fabricius) and *C. bipustulatus* (L.), although these species showed no strong preference in any case.

Previous feeding experience influenced the tendency of *C. septempunctata* females to attack prey of both types in the experiment reported here. Thus females that were maintained on a weevil vs. aphid diet prior to observations more readily attacked both weevils and aphids, and fed on both longer. Previous experience in attacking weevils may have increased the propensity of females to attack this prey type (e.g. Bergelson, 1985; Barron, 2001); fourth instar weevils often thrashed in defence when touched and this may have deterred inexperienced females especially from attacking. That the females also attacked aphids more readily, however, suggests that hunger played a part. Thus females that had been provided previously with weevils were likely less satiated during observations than females that had been provided previously with aphids. Overall, the behavioural results reflect the aphidophagous nature of *C. septempunctata* females in indicating that these predators have greater propensity to attack aphids vs. weevils, particularly when they have ample access to aphids.

The aphidophagous nature of *C. septempunctata* females is also apparent in the experimental results for egg production on varying diets. Thus, in both experiments, the number of eggs produced by a female depended primarily on the number of aphids consumed. Females provided with abundant weevil larvae in addition to limited numbers of aphids produced relatively few more eggs than females provided only with limited numbers of aphids. In the first experiment, provision of weevils delayed the rapid collapse in egg production when pairs were placed on a diet of only five aphids each day. Thereafter, females became so inactive reproductively when pairs were provided with only five aphids daily, that consumption of weevil larvae provided little benefit for egg production. Previous studies have similarly documented a minimum rate of consumption or density of aphids to support active reproduction in this and related species (e.g. Honěk, 1978, 1980; Ives, 1981a). The existence and level of such a minimum rate likely reflects the basic trade-off between reproduction and longevity; female ladybirds may be adapted to survive well at low prey densities in part by reducing their reproductive effort (e.g. Valicente & O'Neil, 1995).

Females remained more active in egg production throughout the second experiment when pairs were provided with a minimum diet of 10 aphids daily. Consumption of weevil larvae modestly enhanced egg production as the second experiment progressed. In neither experiment, however, did females produce as many eggs when abundant weevil larvae and a limited number of aphids were provided as when twice as many aphids (but no weevils) were provided. The modest increase in egg production when weevils were available may reflect that females consumed these prey primarily to gain nutrients and energy for self-maintenance. They then could devote to egg production more nutrients and energy as set by aphid consumption than could females whose limited diet of aphids was not supplemented with weevils.

Both predator and prey condition likely influenced absolute rates of egg production in the two experiments. Females of pairs fed 10 and 20 aphids daily laid fewer eggs in the second experiment than in the first. This may reflect adverse effects of prolonged storage at cool temperature prior to the start of the second experiment, or greater age of the females (e.g. Dixon & Agarwala, 2002). When pairs were provided with 30 adult pea aphids daily, rates of egg production were similar to those reported previously for *C. septempunctata* (Hodek & Honěk, 1996) but nonetheless may have reflected that pea aphids reared on broad beans are less nutritious for *C. septempunctata* than pea aphids reared on alfalfa (see Giles *et al.*, 2002).

Why do *C. septempunctata* females not use the opportunity to produce more eggs when aphid numbers are low but weevils are abundantly available? Similarly, why do females of *Coccinella* spp. become reproductively inactive when limited solely to non-aphid diets of larvae of Coleoptera and Lepidoptera (Richards & Evans, 1998; Evans, 2000)? Aphids may possess specific nutrients required for ladybird reproduction that are lacking or present only in small amounts in alternative prey (e.g. see Hagen, 1987). Furthermore, as noted by Dixon (2000) in his discussion of nursery prey, the behaviour of female ladybirds in this regard may be adaptive. Larvae of *C. septempunctata* are much less able to survive and mature on a diet of weevil larvae than on a diet of pea aphids (Kalaskar & Evans, 2001). By not producing large numbers of eggs through consumption of weevil larvae when only few aphids are present, a female may avoid placing her offspring in an unfavourable environment. In contrast, by setting her rate of egg production primarily by her rate of consumption of aphids, a female may succeed in placing her offspring in environments that are relatively well-suited for their development. Her ability to do so is further enhanced by her tendency to become less active as her rate of aphid consumption increases (e.g. Banks, 1956; Dixon, 1959; Frazer & Gill, 1981; Nakamuta, 1987). Thus, a female that encounters and consumes aphids at low rates may continue to disperse through the environment in search of suitable oviposition sites even as she is maturing small numbers of eggs (e.g. Ives, 1981b; Ives *et al.*, 1993; van der Werf *et al.*, 2000). In contrast, at higher aphid densities and rates of consumption, flight activity of females drops markedly and they lay eggs locally at high rates (Honěk, 1985; Takahashi, 1993; but see also Hemptinne *et al.*, 1992; Dixon, 1997).

Thus the relative specialisation of lady beetles such as *C. septempunctata* on aphid prey, as reflected both in the greater propensity of females to attack aphids vs. weevils and in the primacy of aphid consumption in promoting egg production, may have its ultimate basis particularly in factors and constraints associated with larval foraging (e.g. see Dixon, 1959, 1970; Wratten, 1973). In attacking prey such as weevil larvae, adults may use the energy and nutrients gained primarily for self-maintenance. They may thereby also reap a modest benefit indirectly in egg production when such is limited by aphid availability.

Acknowledgements

We thank Andrew Nelson for maintaining aphid cultures and assisting with experiments, and two referees and the associate editor for commenting on the manuscript. Financial support was provided by the U.S.D.A.-N.R.I. (99-35302-8104) and the Utah Agricultural Experiment Station.

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Accepted 28 July 2003