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Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review

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Abstract. In searching both for food to produce eggs and for suitable oviposition sites, females of aphidophagous ladybirds must be adapted to exploit prey that vary greatly in their occurrence and abundance over both space and time. A simple model of ladybird searching and oviposition behaviour emerged in the 1950s: adult ladybirds are highly mobile in traversing the landscape, but become less active and produce more eggs as their rate of aphid consumption increases. The net result is that most eggs tend to be laid at sites of high aphid density. Laboratory and field experiments and observations over the past several decades have generally supported this basic model, although the linkage between ladybird dispersal activity and local aphid density often appears to be relatively weak. Not all ladybird eggs are laid in patches of high aphid density. Females use resources from limited prey consumption to produce eggs in modest numbers. They may thus be prepared to lay some eggs quickly when they succeed in finding aphids in high numbers, but otherwise they may have little choice but to lay these eggs in suboptimal sites. Upon locating patches of high prey density, females are faced with the decision of how long to remain. The basic model raises the possibility that these females become passively trapped at such patches until local aphid density collapses. Recent studies, however, suggest that detection of oviposition-deterring pheromones may promote earlier departure from prey patches. Females may also have an innate tendency to disperse throughout their lives regardless of local conditions, as a bet-hedging strategy to spread their eggs widely over space. Additional studies are needed to evaluate further the degree to which females actively determine and vary the rhythms of dispersal and reproduction in response to the unpredictable and short-lived nature of populations of their aphid prey.

INTRODUCTION

Aphids have distinctive features that make them highly suitable in some ways and highly challenging in others as prey for insect predators. On the one hand, aphids are small and soft-bodied, and they often occur at high densities in reasonably discrete patches (which may vary in extent from the population associated with a single, isolated plant to that associated with an agricultural field that may encompass several to many hectares). On the other hand, local aphid populations tend to be both ephemeral and unpredictable over both space and time. Aphidophagous predators must be adapted with appropriate tactics and strategies to exploit the opportunities and overcome the challenges posed by this particular group of prey.

One critical set of tactics is that associated with the searching decisions of female predators, who determine through their oviposition choices the settings in which their offspring will forage (upon hatching, these offspring will search within local habitats with their own, distinctive set of tactics; Ferran & Dixon, 1993). The activity of females can be viewed as ultimately directed towards laying as many eggs in as effective a manner as possible (in contrast, the activity of males is likely dominated by the issue of where best to find multiple females with whom to mate; e.g., Honěk, 1985; Hemptinne et al., 1996, 1998). I review the topic of female activity here for aphidophagous ladybirds (Coleoptera: Coccinellidae) in particular. As adults, ladybirds must feed on prey to gain the nutrients to be used for egg production. Thus females must forage to gather sufficient food both to produce eggs and to maintain themselves while also seeking out those places most suitable for oviposition.

The searching behaviour of female ladybirds clearly reflects the ephemeral nature of local aphid populations. As revealed by mark-recapture studies (Davidson, 1924; Ives, 1981a; Ives et al., 1993; Osawa, 2000; van der Werf et al., 2000), adult ladybirds often do not remain long in any given location, but instead appear to move frequently between sites and habitats throughout the breeding season. In this regard, ladybirds appear to conform only loosely to the general flight-oogenesis syndrome characteristic of many insects in which migratory activities as a youthful adult precede reproductive activities during a sedentary life thereafter (Johnson, 1969; Dingle, 1972). Hodek et al. (1993) note that the dispersal flight of ladybirds from overwintering sites is a step-wise process (i.e., a process punctuated by periods of foraging in local areas between periods of flight) that gradually transforms into trivial flight (i.e., short-range dispersal or appetitive flight among foraging and oviposition sites). The generally high mobility of ladybirds is further reflected in a distinct kind of migratory flight recognized by Hodek et al. (1993), termed hectic trivial flight, in which large numbers of newly molted adult ladybirds may abandon their larval habitat if local aphid abundance has been driven to low levels; swarms of such adults may disperse far and wide in search of better foraging conditions.

The key questions facing a searching female ladybird can be summed up simply: when and where in the course of her wanderings should she reproduce? An elegantly simple model of ladybird reproduction emerged in the 1950s (Putman, 1955; Banks, 1956; Dixon, 1959) which has served since as the standard general explanation for when and where ladybird eggs are laid. In this model, females produce more eggs and become less active as they consume more aphids. The net result is that eggs tend to be laid near aphids. This result is of fundamental significance, as it appears to reflect that these predators have evolved in their life histories, behaviors and body forms and functions such that for most species, the availability of abundant young aphids as prey appears to be critical for survival of their offspring (e.g., Dixon, 1959, 1970; Wratten, 1973). I therefore first review the literature of the past several decades that bears on this simple model before considering additional questions raised and addressed by recent research.

SUPPORT FOR THE BASIC MODEL

The basic tendency of females to lay more eggs as they feed more has been demonstrated in the laboratory for various species over the years (e.g., Ives, 1981b; Mills, 1981; Hemptinne et al. 1992). Simple laboratory experiments have also revealed that in comparison to adults starved for varying lengths of time, well-fed adult ladybirds are less active and spend less time walking (Frazer & Gill, 1981; Evans & Dixon, 1986; Nakamuta, 1987). Observations of ladybirds in the field also support this latter point. In cultivated crops such as alfalfa, small grains, and strawberries, well-fed individuals appear to become immobile at the bases of host plants, whereas hungry individuals actively search the upper canopy (Frazer & Gilbert, 1976; Frazer & Gill, 1981; Frazer & Raworth, 1985). The proportion of time spent walking on the foliage or the soil surface by adults (both sexes combined) of *Hippodamia convergens* Guerin-Meneville, *H. tredecimpunctata tibialis* (Say), and *Coleomegilla maculata* (DeGeer) in stands of barley and wheat was inversely related to aphid density (Elliott et al., 2000). Similarly, Honěk (1985) found that a higher percentage of females of *Coccinella septempunctata* L. actively searched the vegetation in alfalfa with low aphid numbers than in beans with high aphid numbers (males were much more active than females in beans with high aphid numbers; apparently their activity level was more influenced by search for mates than for prey). Finally, Takahashi (1993) observed greater activity of *C. septempunctata brucki* Mulsant in open plots of alfalfa with low aphid density than in caged pots of alfalfa with high aphid density.

Even when active, the tendency of adult ladybirds to remain in an area is influenced by their feeding behavior. Thus, as is true for many predators (Curio, 1976), the rate of prey encounter also influences adult behavior in that adults search more intensively within a local area following prey encounter (Nakamuta, 1982, 1991). Hence the decreased level of activity, combined with more area-restricted searching behavior that is associated with relatively high rates of prey encounter and capture, results in predators remaining in the local area until eggs are laid rather than drifting away as they continue to search the substrate. This general process can account, for example, for the experimental results of Wetzler & Risch (1984), who compared the loss of marked individuals of *C. maculata* from experimental patches of corn with few or many aphids. The authors modeled such loss as a diffusion process with the rate of diffusion lower at higher local prey density (see also Andow & Risch, 1985, who concluded that adults of *C. maculata* encountered prey less frequently and hence emigrated more rapidly from polycultures of corn, bean and squash than from corn monocultures). Kareiva & Odell (1987) explored the basic issue from a related angle, using field observations of foraging individuals of *C. septempunctata* (e.g., rates of reversal in foraging direction along linear arrays of host plants as a function of hunger) to parameterize quantitative models of movement. These authors were thus able to demonstate how aggregation of predators (and ladybirds in particular) at local patches of high density can arise as an epiphenomenon of the independent searching behaviours of individuals. Such aggregation of walking predators at local areas of high prey density may depend on habitat structure; one important consequence is that ladybirds may be less able to prevent local aphid outbreaks in patchy versus more continuous stands of plants (Kareiva, 1987).

Rather than leave a local area by wandering off during a relatively undirected search of the plant substrate (the duration and effectiveness of which may be influenced in part by the nature of the substrate itself; e.g., White & Eigenbrode, 2000), many individuals will emigrate by flying away. Such flight may occur more readily as local prey density drops. Thus, although ambient temperature accounted for most variation in emigration rates from the experimental plots of alfalfa and oats of Ives (1981a), residual variation in the emigration rate of *Coccinella californica* (Mannerheim) (both sexes combined) appeared to be inversely related to local aphid density. Although this was not true for *Coccinella trifasciata* Mulsant, Ives failed to recapture any marked individuals of this species in study plots of alfalfa once aphid densities dropped below a minimum level (0.3 aphids/terminal) suggested by studies of Frazer & Gilbert (1976) as necessary for the adult to remain satiated. Similarly, van der Werf et al. (2000) recorded a particularly high rate of departure of marked adults of *C. septempunctata* from alfalfa plots in one of three similar experiments in which resident aphid density was unusually low. Elliott et al. (2000) found that the frequency of short flights (< 2 m) of *H. convergens*, *H. tredecimpunctata tibialis*, and *C. maculata* in stands of barley and wheat increased with decreasing aphid density. Curiously, this relationship did not emerge for longer flights (most of which were so long that the observer was unable to track the movement and final destination of the beetle), although longer flights were observed less frequently than short flights (and hence the investigators had less information on which to build statistical models). Elliott et al. (2000) speculate that their regression results for longer flights were dominated by seasonal effects (i.e., calendar date, which reflects seasonal trends in aphid abundance), thus masking the importance of local aphid density.

Based on repeated visual censusing, Ives et al. (1993) calculated an average tenure time of adults of *C. septempunctata* and *Hippodamia variegata* (Goeze) upon release into plots (5 × 10 and 5 × 5 m) with scattered individuals of fireweed (*Epilobium angustifolium* L.) that were manipulated experimentally to harbor varying numbers of aphids (*Aphis oenotherae* Oestlund). The results indicate that the length of stay of individual beetles before they dispersed from the plots into which they were released was positively related to aphid density (and dispersion) within plots. At a finer spatial scale, Ives et al. (1993) also recorded the time to departure (residence time) of individually marked adults of the two ladybird species from individual fireweed stems. Residence time of females (but not males) was positively correlated (although weakly so) with aphid density on individual stems, with some females remaining up to six days on a single stem. In shorter-term experiments with potted bean plants, Minoretti & Weisser (2000) also found that residence time of individual adults of *C. septempunctata* on individual plants was positively related to the number of aphids present on a plant.

The direct linkage of local reproduction with reduced flight activity as the result of high feeding rates has been addressed by various authors, particularly those interested in long-range dispersal or migration. Rankin & Rankin (1980), for example, documented through laboratory studies that the presence of mature ovaries in overwintered or young second generation females of *H. convergens* following sufficient feeding is associated with suppression of the tendency for sustained flight activity. Similarly, Okuda et al. (1986, p. 220) reported that flight tendency of *C. septempunctata* "drops to near zero when the beetles are in the breeding sites in the 2nd half of May, and when chorionated eggs are to be found in the ovary". Nedvěd et al. (2001) found that *C. septempunctata* collected in mid-September from hibernation sites initiated ovarian maturation if they were provided aphids, and had reduced tendency to fly in comparison to females that were starved or fed honey only. The tendency of female ladybirds to engage in short-range dispersal by flight during the breeding season also appears inversely related to their reproductive condition. Thus, Honěk (1985) found that flight was almost entirely restricted to males among individuals of *C. septempunctata* on beans heavily infested with aphids; as females matured sexually, their flight activity dropped markedly (see also Honěk, 1990). Similarly, Takahashi (1993) observed only males to fly in cages covering potted plants; aphid densities were high in these cages, and females were actively laying eggs in high numbers.

A particularly striking case of the linkage between local reproduction and activity is suggested by the studies of Honěk (1978, 1980), who found large differences in the percentage of females that were gravid at any given time among populations of *C. septempunctata* from nearby fields of alfalfa and barley, and even among local areas within a large alfalfa field. The reproductive status of females at a given site reflected local prey conditions (the percentage of gravid females increased with increasing aphid density). These results presumably reflect that females become quite sedentary as well as reproductively active upon consuming prey in large numbers; hence dispersal of individuals between sites may have been asymmetric, with net migration to sites with many aphids where ladybirds settled in to reproduce.

Overall, then, the basic model has been supported by the observations of researchers over the past several decades. This provides a general understanding of natural patterns of ladybird reproduction. Thus, although eggs of aphidophagous ladybirds are sometimes apparently laid far from aphids (e.g., Banks, 1954), most eggs appear to be laid near aphids. Dixon (1959), for example, reports that 81% of egg masses of *Adalia decempunctata* (L.) were found within a few centimeters of the nearest aphid on lime trees even though aphids were absent from most of the leaves. Evans & Dixon (1986) found that gravid females of *C. septempunctata* were stimulated to oviposit by the odor of aphids or their honeydew; this may contribute to the often close proximity of ladybird eggs to aphids.

Other factors, however, may frequently cause eggs to be laid in more scattered fashion in the general vicinity of aphid colonies, but presumably still close enough to aphids to enable hatching larvae to find their prey. Sakuratani & Nakamura (1997), for example, report that females of *C. septempunctata* that feed on aphids associated with herbaceous plants in winter on the Osaka Plain, Japan, do not lay their eggs on the plants themselves but instead oviposit nearby on various materials (e.g., metal, wood and concrete substrates) that have higher surface temperatures than the aphid-infested plants (see also Takahashi, 1989). This behaviour is likely highly beneficial in enabling eggs to develop relatively rapidly even at the low ambient winter temperatures. As mentioned also by the authors and as discussed in more detail below, this strategy of laying eggs at modest distance from aphids may also serve to minimize egg cannibalism, often a major source of mortality of ladybird eggs (Mills, 1982; Osawa, 1989; Agarwala & Dixon, 1992; Yasuda & Shinya, 1997; Cottrell & Yeargan 1998a, b; Schellhorn & Andow, 1999). Another interesting example is that of *Pullus impexus* (Muls.), in which females lay eggs among or nearby autumn colonies of *Adelges piceae* (Ratz.). The eggs do not hatch until the following year, whereupon larvae feed on the spring generation of the aphid (Delucchi, 1954).

Given the basic model of ladybird behaviour, the proximity with which ladybird eggs are laid near aphids can also be expected to vary with the hunger level of a female ladybird as well as the level of her commitment to egg production. Thus, well-fed females may lay eggs near aphids, but less well-fed (and more active) females may be less likely to do so. This may account, for example, for the very interesting but somewhat puzzling data of Banks

(1956) concerning the distribution of ladybird eggs among bean stems in plots infested with aphids (*Aphis fabae* Scop.). Early in the season, when relatively few stems were infested with aphids, Banks found no association between the presence of eggs and aphids on individual stems. Later in the season when all stems were infested, eggs were laid most frequently on stems with most aphids. Banks states (p. 55) that "the correlation of numbers of egg batches with numbers of aphids when the infestations are well advanced is explained by the concentration of the adult Coccinellids on well-infested stems where they would tend to stay to feed on the Aphids and probably to lay their eggs". As to why a similar explanation might not apply earlier in the season, perhaps the rate of aphid consumption at that time is sufficient to enable limited egg production but insufficient to prevent ladybirds from moving frequently among plants (many of which have few or no aphids) as eggs mature.

ADDITIONAL QUESTIONS

As noted at the outset, successful reproduction by aphidophagous ladybirds seemingly requires that females locate and oviposit at local aphid populations of high density, as the immature stages have low success in attacking aphids and therefore need to exploit such populations to successfully mature (Dixon, 1959, 1970; Wratten, 1973). The basic model is useful in explaining in a general way how it comes about that eggs are often laid under these circumstances. Nevertheless, the basic model leaves some important questions unanswered. These questions arise primarily because local aphid populations of high density are typically both unpredictable and ephemeral in their occurrence, and ladybird adults exploiting these prey must consequently be highly mobile in moving frequently from opportunity to opportunity (e.g., Hagen, 1962; Evans & Youssef, 1992; Osawa, 2000). I focus on two questions here: how much should a female engage in egg production before she has located a prey patch of high density, and how much should a female engage in local oviposition once she has located such a prey patch?

Reproduction when prey density is low. In regard to the first question, it appears that a female ladybird moves fairly rapidly through the environment while encountering aphids in low numbers. During this time, should she use some of the energy and nutrients that she obtains from the relatively few prey consumed to begin producing eggs, or should she instead devote all of these resources to her own self-maintenance and her ability to disperse? In this regard, a female ladybird seemingly is subject to a fundamental trade-off between finding suitable, ephemeral patches as rapidly as possible, and exploiting them most effectively once found. Given that local populations of aphids occur at high densities for only limited periods of time (often in part because other predators also discover and exploit them heavily), a female ladybird may be under considerable selective pressure to lay eggs as soon as possible upon encountering such a prey patch. This may favor females that devote some of their limited resources to producing eggs even as they search for suitable sites to oviposit. But such a commitment may compromise that female's searching ability. With nutrients and energy shunted to egg production, she will have less fuel to burn to support her searching effort. In addition, the energetic cost of searching may be high if she is carrying eggs (at the extreme, a female with abdomen swollen with eggs may be physically unable to fly).

We need additional studies to determine how females act in light of this seeming trade-off. The available evidence suggests that females invest in producing some eggs even as they seek out optimal sites at which to oviposit. One can consider, for example, the detailed studies of aphid consumption and egg production by females of *C. trifasciata* and *C. californica* conducted by Ives (1981b). These females begin producing eggs at very low rates of aphid consumption (i.e., low rates in comparison to the maximal rates of which they are capable); egg production rises linearly thereafter with increasing aphid consumption. Thus they produce eggs in constant ratio to the amount of food available to them. Presumably then, they may often find themselves ready to lay these eggs under conditions of limited prey availability; this may be the necessary consequence as they seek to be prepared to oviposit quickly upon discovery of local patches with more favorable prey conditions.

Perhaps even more striking is that ladybirds will produce eggs even when aphids are absent. Although primarily aphidophagous, many ladybird species consume a variety of other foods, including eggs and larvae of several orders of insects (Hodek, 1973; Gordon, 1985; Hagen, 1987; Hodek & Honěk, 1996). These prey are usually thought to be alternative foods (sensu Hodek & Honěk 1996) that serve primarily to maintain the predator but not support reproduction. As Dixon (2000) notes, given the dependence of their offspring on an abundant supply of aphids, one might suppose that aphidophagous ladybirds would require aphids as essential foods in their diet to elicit and sustain egg production (Dixon describes as nursery prey those aphid species that elicit ladybird oviposition when the predators encounter prey patches suitable for their offspring). For many species (e.g., *Coccinella* and *Hippodamia* spp.), it indeed appears to be the case that aphid consumption is required to stimulate egg production, as revealed by lack of success in efforts to develop artificial diets (Racioppi et al., 1981; Hagen, 1987; Hodek & Honěk, 1988). It is therefore intriguing that *Coccinella* spp., for example, will engage in limited egg production when feeding on non-aphid prey (Coleopteran and Lepidopteran larvae) supplemented with sugar water as a substitute for the plant nectar these predators are known to consume in the field (Richards & Evans, 1998; Evans et al., 1999; Evans, 2000). One interpretation is that females are investing to a limited degree in egg production even in the absence of aphid prey, to enhance their ability to oviposit quickly upon locating patches of high aphid density.

It is also striking that some ladybirds are much more inclined than species of *Coccinella* to produce eggs when maintained on non-aphid diets; this may reflect that these species are less strictly aphidophagous (and hence may differ fundamentally in their reproductive strategies). The polyphagous species *C. maculata*, for example, produces very large numbers of eggs in the laboratory when it feeds on eggs of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Hazzard & Ferro, 1991; Munyaneza & Obrycki, 1997) or the European corn borer, *Ostrinia nubilalis* (Hubner) (Phoofolo & Obrycki, 1997), foods that it is known to feed on in natural settings. *Harmonia axyridis* (Pallas) produces eggs at high rates when fed eggs of the lepidopteran *Ephestia* (*Anagasta*) *kuehniella* Zeller (Schanderl et al., 1988). The prey is a pest of stored products that this predator would not encounter naturally, but its reproductive response may reflect that it does often exploit similar prey as well as aphids in nature.

Certainly much work remains to be done to understand how females of aphidophagous ladybirds respond reproductively in the field both when encountering aphids at low density and when encountering non-aphid prey in the absence of aphids. At least for those species that are relatively strictly aphidophagous, it appears that females use the resources from limited prey consumption to support modest egg production. Females may often be forced to lay these eggs in suboptimal sites; such is the price they may pay for the opportunity to lay eggs quickly when they succeed in locating more optimal sites.

In this light, one intriguing topic that could benefit from more study is the capacity for egg resorption. Some parasitic Hymenoptera produce eggs continuously as they seek out hosts but are capable of resorbing these eggs if they have not found a host by the time the eggs mature (Doutt, 1964). Such an "egg recycling" strategy would seem well-suited to the lifestyles of aphidophagous ladybirds, but it is not clear how much these predators may engage in egg resorption. Gravid females with mature eggs are able to delay oviposition for a number of hours under adverse conditions, but they do oviposit eventually and show no signs of resorbing eggs at this mature stage of development (Evans & Dixon, 1986; Hemptinne et al., 1992). Similarly, females continue to lay eggs for a couple of days before ceasing altogether to oviposit when switched from an aphid diet to a diet of alternative prey (e.g., Richards & Evans, 1998); presumably these eggs are ones that were far enough along in development at the time of the switch in diet such that resorption is not an option. Additional studies seem well-worth pursuing to determine the degree to which eggs less advanced in development may be "recalled" by female ladybirds when opportunities for oviposition are poor.

Reproduction when prey density is high. Females face another decision once they have found prey patches: How much should they engage in oviposition at the patch before moving on? This topic has been explored in depth by Hemptinne, Dixon, and Kindlmann (Hemptinne et al., 1992; Kindlmann & Dixon, 1993; Dixon 1997, 2000). These authors stress the ephemeral nature of aphid colonies, and theorize that ladybirds should synchronize their oviposition with colony development to exploit a window of best opportunity early in the colony's development. Thus, ladybird eggs may be laid too early if too few young aphids are present for young ladybird larvae to prey on. On the other hand, if eggs are laid too late into colony development, larvae may have insufficient time to mature before the prey colony collapses. In addition, they may be subject to cannibalism or predation from other aphidophagous insects that accumulate at the colony (e.g., Takahashi, 1989; Yasuda & Shinya, 1997). Indeed, the presence of the predators themselves may indirectly speed the collapse of the aphid colony by stimulating the production of alates that disperse (Dixon & Agarwala, 1999; Weisser et al., 1999).

Do temporal patterns of ladybird oviposition at aphid colonies support the egg window hypothesis? In some cases, rates of egg production by ladybird populations appear to reflect directly the current population size of aphids (e.g., Wright & Laing, 1980; Agarwala & Bardhanroy, 1999), but in others eggs do indeed appear to be laid in greatest numbers before aphid numbers peak (Hemptinne et al., 1992; Osawa, 2000). Banks (1955), for example, found that while the number of ladybird eggs laid on bean stems peaked simultaneously with aphid numbers in one field plot, egg numbers peaked a week before aphid numbers in two other plots.

Effective timing of oviposition requires that ladybird females have some means of assessing the status of the prey population, such that they generally restrict oviposition to the best times in terms of the likelihood of their offspring surviving. How might a female predator make such an assessment? Through field observations and clever experiments, Kan (Kan & Sasakawa, 1986; Kan, 1988a, 1988b) addressed this question for syrphid flies, and discovered that these highly visual predators judge the stage of an aphid colony's development particularly by the absence or presence of winged adults. In a similar study of ladybirds, however, Hemptinne et al. (2000) found that gravid females of *A. bipunctata* did not respond in their oviposition behavior either to the age structure of aphid colonies on experimental bean plants, or to the age of the host plants.

Another possibility is that the rate of encounter and overlap with conspecifics and other aphid predators may influence an individual ladybird's tendencies to remain in a patch and lay eggs. As Hemptinne et al. (1992) point out, the presence of conspecific larvae in particular may reflect that the aphid colony is fairly mature and may diminish rapidly in size before offspring can mature. Furthermore, laying eggs in the presence of conspecifics may expose those eggs to cannibalism, and it may lead to competition for food with these individuals. In testing these ideas, Hemptinne et al. (1992) found that females of *Adalia bipunctata* (L.) kept with other conspecific females or larvae (but not heterospecific larvae) had reduced rates of oviposition over experimental periods of nine to twenty-four hours. Furthermore, females became more active when held with conspecific larvae. These results suggest that gravid females may disperse rather than lay eggs in aphid colonies where conspecifics occur.

Similar deterrence of oviposition in response to the presence of conspecific larvae of the lacewing *Chrysopa oculata* Say was discovered by Růžička (1994), who found that the mechanism lay in chemical deterrents laid down in the larval tracks. This basic mechanism appears to apply for ladybirds also (Růžička, 1997; Doumbia et al., 1998; Yasuda et al., 2000), as well as for deterrence of oviposition observed for the aphidophagous cecidomyid fly, *Aphidoletes aphidimyza* Rondani (Růžička & Havelka, 1998). Additional experiments have revealed similar heterospecific as well as conspecific deterrence of oviposition among ladybirds and lacewings; females of individual species vary in their responses, suggesting that a variety of chemicals are used among species to deter oviposition (Růžička, 2001).

The discovery of oviposition-deterrence in the presence of other predators is exciting in suggesting that ladybirds may indeed be surprisingly sophisticated in their reproductive decisions. Additional studies can be pursued to appreciate more fully the nature of this sophistication. An especially interesting question is that of how far a female may disperse before laying eggs after she detects the chemical traces of other predators. Some females may move only a relatively short distance before ovipositing so as to avoid laying eggs in the immediate vicinity of aphids (and the tracks of other predators attacking the aphids). Thus, Takahashi (1989, 1993) observed that in stands of alfalfa infested with aphids, egg batches were laid elsewhere than on the alfalfa itself; Takahashi (1993) suggests that such behavior may be selected for to avoid cannibalism by other females that aggregate on the alfalfa in response to the presence of aphids. Osawa (1989) and Sakuratani & Nakamura (1997) also emphasize the importance of avoiding cannibalism by not laying eggs too close to aphids. The experiments so far completed on deterrence of oviposition have focused on gravid females on the verge of oviposition (and capable of delaying oviposition for only a matter of hours). These females may be unable to disperse far, especially by flying (e.g., Honěk, 1985 and Takahashi, 1993); in delaying oviposition temporarily, they may be seeking sites associated with the patch where the risk of egg cannibalism or predation is reduced. Thus it would seem very much worthwhile to follow up on the intriguing results obtained so far concerning deterrence of oviposition, by studying the response of less well-fed females (such as those newly arriving at an aphid colony) to larval ladybird tracks in the presence of abundant aphids. Will these females remain to feed and develop eggs? Or will they choose instead to disperse in search of an aphid colony at a more suitable stage of development?

The decision to leave a patch even as aphid numbers are still high raises an intriguing issue when one considers how natural selection might act on a female ladybird. Granted that the probability that her offspring will survive may decline as an aphid colony develops, leaving the patch may nevertheless not be the best choice for a female. The issue depends on the merits of rejecting a known quantity in search of a better alternative (to paraphrase the old saying, is an aphid at hand better than two in the bush?). Thus, a female may be best off remaining where she is if she has a low chance of locating another aphid colony in a more appropriate stage of development (factors such as the female's age [e.g., see Dixon & Agarwala, 2002] and the time of the season come into play here). To understand the issue more clearly, we certainly need a better understanding as to how (and how readily) ladybirds locate patches of their prey. Relatively little work has been completed on this important topic for ladybirds (in contrast in particular to lacewings [Duelli, 2001]), and it is currently a matter of great mystery. As Hodek (1993) points out, it has most often been supposed that such long-distance searching behavior is largely random. Visual and olfactory cues, however, may assist adult ladybirds in finding their prey from long distance (e.g., Lorenzetti et al., 1997) as well as from shorter distances (e.g., Obata, 1986; Mondor & Roitberg, 2000; Acar et al., 2001). Such cues may contribute to the often impressive ability of ladybirds to reduce aphid numbers in natural settings (e.g., Frazer et al., 1981; Kring et al., 1985).

Finally, the concept of bet-hedging (i.e., spreading the risk) provides another perspective for why females may disperse from a local patch of aphids even before it begins to collapse. Thus, as has been suggested for other entomophagous insects (e.g., Duelli 1980, 2001; Evans, 1982; Antolin & Strong, 1987), females may be selected to spread their eggs widely among prey patches to insure against random collapse of favorable conditions in any one patch. With this in mind, it is intriguing to consider whether adult ladybirds have an innate tendency to disperse throughout their lives (Frazer & Raworth, 1985; Frazer, 1988), similar to that of lacewings that exploit field crops and similar herbaceous habitats (Duelli, 2001). In reflecting on the mark-recapture results of his student Ives (1981a) and other observations in related studies of ladybirds in field crops, Frazer (1988) was impressed by the relatively weak degree to which local aphid density could account for levels of observed rates of emigration from areas on the order of 30 × 40 m. Similarly, but at a finer scale, Ives et al. (1993) found that aphid density on individual stems of fireweed accounted for only 11% and 4% of the variation in the length of time that adults (both sexes combined) of *C. septempunctata* and *H. variegata* remained on a stem upon release there as single individuals (note, however, that a greater amount of such variation for females than for males was accounted for by aphid density). Frazer (1988, p. 238) concluded that local areas "are constantly receiving and losing coccinellids regardless of the density of aphids", and he attributed this to an innate tendency to disperse even in appetitive flight (such innate dispersal is well-recognized for migratory flight; e.g., see discussion in Hodek et al., 1993). Frazer considered that some of the apparent innate tendency likely can be explained as artifact, reflecting the stochastic nature of prey encounter and capture (i.e., even though average prey density may be relatively high in a local area, some fraction of the predator population may fail to encounter and capture sufficient prey per unit time of search, and may respond by dispersing). Nevertheless, Frazer & Raworth (1985) suggest that an innate tendency to disperse exists in addition to that which can be accounted for by stochastic artifact associated with the variable rates of prey encounter and capture experienced by individual ladybirds.

CONCLUDING COMMENTS

This review highlights both that much has been learned and that much remains to be learned about the decisions individual female ladybirds make concerning dispersal and reproduction. It is especially intriguing to compare the results from studies such as those of Honěk (1978, 1980, 1985) that females settle into local areas as aphid density rises and lay eggs in large numbers, with the results from others' studies (e.g., Ives, 1981a; Hemptinne et al., 1992) that females move frequently even from patches of high prey density, and consequently spread their eggs widely through the environment. In the laboratory, females quickly shift back and forth between producing many or no eggs, depending on their diet (e.g., Evans et al., 1999). Such shifts throughout the life of a female may well occur frequently in nature also, with active dispersal punctuating sedentary interludes of high reproductive activity. It will be especially interesting to learn more as to how much females actively determine the rhythms of such shifts. Do they choose in sophisticated fashion both how much to consume and how much to reproduce at individual sites? Or do they settle more passively into patches of high aphid density, essentially becoming trapped there until the local aphid prey population collapses and they are thereby forced to move on? The answers may well vary with species of ladybirds, as these differ in their feeding and dispersal habits and strategies (e.g., Ewert & Chiang, 1966; Sloggett & Majerus, 2000). Arboreal ladybirds, for example, may be especially well-adapted in their reproductive habits to the ephemeral nature of their aphid prey, which migrate at predictable seasons to secondary hosts (e.g., Hemptinne et al., 1992). Devising incisive experiments to address these issues further may not be easy. But certainly the effort will be rewarding and enlightening, and it should enhance the effective use of these predators for biological control (Obrycki & Kring, 1998; Coderre, 1999).

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