

Body size and resource partitioning in ladybirds

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Introduction

Resource utilization is usually viewed in terms of food species size (Schoener, 1974) with each species in a predator guild adapted to exploit a particular sized species of prey. Large species of predator exploit large species of prey and *vice versa*. That is, each species in a guild is able to displace other species from a particular portion of the resource space by virtue of it being better adapted to exploit that particular species of prey in that resource space.

Ladybirds feed on a wide range of prey of different sizes. Generally the size of each species reflects the size of their prey, with those feeding on mites being small and those feeding on chrysomelid larvae large (Dixon & Hemptinne, 2001). Aphidophagous species, however, all exploit aphids as food but there appears to be no association between the size of aphidophagous predators and that of the species or age structure of the aphid colonies they exploit. Aphid colonies generally increase, peak and decline in abundance, and are exploited by a sequence of natural enemies, which is consistent from year to year (Dixon, 2000; Stewart et al., 1991). For example, they are often first attacked by a small and then a large species of ladybird (eg., Agarwala & Bardhanroy, 1999; Smith, 1966). The objective of this study was to use unpublished information and published results to determine the mechanisms underlying this temporal pattern and how several species of predators can coexist on the same resource.

The system

As indicated above aphid colonies are ephemeral, with the aphids in the colony only remaining abundant for a period of time similar in length to that taken by a ladybird to develop from egg to pupa. Therefore, ladybirds should lay their eggs early in the development of an aphid colony. This is referred to as the egg-window, is well supported by empirical data and the mechanisms by which it is achieved are well studied (Dixon, 2000). Interestingly, aphid colonies are often attacked by several species of natural enemies and in particular frequently by two, and more rarely, by three species of ladybird of different sizes. Although, there appears to be a clear advantage in ladybirds attacking aphid colonies early in their development nevertheless they do not all lay their eggs at the same time. There is a marked tendency for the smaller species to lay eggs before the larger species. This is well illustrated by *Adalia bipunctata* (L.) laying its eggs before *Coccinella septempunctata* L. in temperate regions and *Menochilus sexmaculatus* (Fab.) before *C. transversalis* Fab. in subtropical regions (e.g., Agarwala & Bardhanroy, 1999; Smith, 1966). In addition, these species are able to coexist. The mechanisms underlying the attack sequence and the coexistence of these ladybirds are first discussed from a theoretical point of view and then the predictions tested by comparing them with empirical data.

Theory

Food required for oviposition: If a ladybird is to develop and lay eggs it must consume more aphids per unit time than is required to meet its basic metabolic costs, which increase with increase in body size. Initially, work on warm-blooded animals led to the 'surface rule' and the extensive use of body surface as a base of reference for metabolic rate. However, it soon became evident that the need for heat dissipation cannot be the primary reason for the relationship between metabolic rate and body size as fish show the same relationship. The equation that describes these relationships is the familiar exponential equation:

$$y = b \cdot x^a \quad (1)$$

In the logarithmic form this equation gives a linear function:

$$\log y = a \cdot \log x + \log b \quad (2)$$

where a , the slope of the straight line, is the exponent in equation (1). When referring to metabolic curves in which log metabolic rate is related to log body weight this relationship is:

$$\log \text{metabolic rate} = a \cdot \log \text{body weight} + k \quad (3)$$

If the slope, a , is 0.67 then a simple surface relationship applies. Interspecific comparisons, however, usually give a value of 0.75, which is the value used in most theoretical studies. Suffice to say at this stage there are no theoretical grounds for favouring an exponent of 0.75, many studies consistently indicate larger values and it is difficult to prove these values are statistically different from 0.67 (Schmidt-Nielsen, 1972).

Energy obtained by ladybirds in excess of their metabolic costs can be converted into eggs. If one assumes that this is done with equal efficiency and the proportion of the body made up of gonads is the same in all ladybirds then it is possible to make a prediction. The minimum food intake per unit time required for egg laying should be proportional to weight raised to the power of 0.75 or greater.

Area Searched: Ladybirds mainly only respond to the presence of prey after physical contact (Dixon, 2000). Therefore, the area they can search per unit time depends on their speed of movement and range of perception. The former is likely to be determined by leg length and the latter the spread of the fore limbs. The speed and range of perception, therefore, are both likely to be directly proportional to leg length, which is equivalent to weight raised to the power of 0.33, i.e., $Wt^{0.33}$. Thus, the area searched per unit time should be proportional to:

$$Wt^{0.33} \times Wt^{0.33} = Wt^{0.66} \quad (4)$$

Assuming that both the minimum food required for oviposition and the search rate relative to body weight are as predicted then they can be used to determine the minimum amount of food per unit area required for oviposition by ladybirds of different weights.

Coexistence: Frequently many more ladybird eggs are laid in an aphid colony than can develop to maturity. In such circumstances one would expect intense interspecific competition for resources. However, several species of ladybirds can coexist in an aphid colony, even though the smaller species would appear to be at an advantage in that it starts to exploit the resource before the large species. They could coexist if their numbers were regulated below the carrying capacity by the activity of their natural enemies or each ladybird regulates its own abundance. Intraguild predation (IGP) is currently seen as a major factor structuring predator guilds (Polis & Holt, 1992) and there are many papers implying such an interpretation for aphidophagous guilds. IGP is defined as the killing and eating of species that use similar resources and are thus potential competitors. It is distinguished from competition because one participant (the predator) obtains immediate energetic gains. It differs from classical predation because the act reduces potential competition. As the “top predator” in a guild has a greater effect on the abundance of the “intermediate predator” than on the aphid the two predators are able to coexist. Alternatively, cannibalism of the inactive by the active stages, which is very marked in aphidophagous ladybirds, could regulate their abundance.

Empirical Data

Food required for oviposition: Although the laying of eggs first by small and then large species of ladybirds in aphid colonies has been recorded (e.g., Agarwala & Bardhanroy, 1999; Smith, 1966) the mechanism resulting in this phenomenon has not been addressed. Above a mainly physiologically based theoretical approach to the problem led to certain predictions, which need to be checked against empirical data.

The metabolic rate ($\mu\text{l O}_2 \text{ hr}^{-1}$) of different sized ladybirds has been studied (e.g. Tanaka & Yosiaki, 1982; Mills, 1979) but I only know of one interspecific study. It was done on three species, *A. bipunctata*, *C. septempunctata* and *Propylea quatordecimpunctata* (L.), which ranged in weight from 8mg to 48mg (Stewart, 1988). The relationship obtained was:

$$\log \text{metabolic rate} = 0.961 \log \text{body weight} - 0.562 \quad (5)$$

(n=93, r = 0.92, P < 0.001)

This indicates that metabolic rate in ladybirds increases directly proportionally to body weight (exponent = 1). Energy ladybirds harvest in excess of that needed to fuel their metabolic rate can be utilised to produce eggs. However, the minimum energy required for egg laying is likely also to be determined by the relative investment in gonads. This has been determined for 22 species of ladybirds. The index of gonad size used was ovariole number multiplied by egg weight (Stewart et al., 1991). The relationship obtained was:

$$\log \text{gonad size} = 1.19 \log \text{weight} + 1.62 \quad (6)$$

(1.19 is not significantly different from 1, Hemptinne et al., unpublished)

This also indicates that the minimum energy required for laying eggs is likely to increase directly proportionally with body weight.

There are very few studies that record, or can be used to calculate, the minimum amount of food required per unit time for oviposition in ladybirds. What is required are studies in which ladybirds are fed fixed numbers of similar sized aphids every 24 hours and whether they laid eggs or not, and how many, recorded. Such studies indicate that large species require more aphids per day for oviposition than small species. Although the relationship between the number of eggs laid and aphids eaten per day for all the species studied first increases and then stabilizes at a particular level, large species can lay more eggs per unit time than small species. That is, although small species can begin laying eggs at a lower feeding rate their maximum rate of egg laying is less than that of a large species. The data available for seven species: *M. sexmaculatus*, *C. transversalis* and *Harmonia axyridis* Pallas (Agarwala, unpublished), *A. bipunctata* and *C. septempunctata* (Rana, unpublished) and *Cycloneda sanguinea* (L.) and *Scymnus levaillanti* Mulsant (Isikber, 1999), indicates that the minimum amount of food (mg) required for oviposition increases relative to body weight with an exponent of 1.26 (Dixon, unpublished). That is, the relationships between metabolic rate, investment in gonads and minimum amount of food required per unit time for oviposition and body weight all have exponents relative to body weight in the region of 1. Thus it is reasonable to assume that the energy required for oviposition by ladybirds of different sizes should scale relative to body weight with an exponent of around 1.

Area searched: There are few studies that record the area searched by ladybirds and even fewer that also record their weight. A study of *C. septempunctata* and *C. undecimpunctata* L. (McLean, 1980) indicates that the area traversed per unit time scales with body weight with an exponent of 0.77 and that of *Megalocaria dilatata* (Fab.) (Agarwala, unpublished) with an exponent of 0.6. That is there is good empirical evidence to support the prediction that the search rate scales relative to body weight with an exponent of 0.66.

Minimum amount of food per unit area required for oviposition: Theory and empirical data indicate that the minimum amount of food required by ladybirds for oviposition should scale with body weight with an exponent of around 1, and the search rate around 0.66. If this is the case then the minimum number of aphids per unit area required by ladybirds for oviposition can be derived as follows:

$$Wt^1 / Wt^{0.66} = Wt^{0.33} \quad (7)$$

That is, a large ladybird like *C. septempunctata* (35 mg) requires a minimum population density of aphids per unit area of 1.5 times greater than that required by a small ladybird like *A. bipunctata* (10 mg). In the case of *C. transversalis* (31 mg) and *M. sexmaculatus* (16 mg) the larger species requires a population density of aphids 1.2 times greater than that required by the smaller species. Thus, the mechanism that determines the stage in development of an aphid colony at which it is attacked by different species of ladybirds could be their size.

Coexistence: Two or more predators can exploit the same resource if the predatory guild consists of top as well as intermediate predators, and the top predators have a greater effect on the abundance of the intermediate predators than on that of the resource (Polis & Holt, 1992). There is some experimental evidence that indicates *H. axyridis* could be a top predator (Dixon, 2000, Sato et al., 2005). However, for this designation it needs to be established that *H. axyridis* has a greater effect on the abundance of intermediate predators than its aphid prey. The empirical evidence indicates that the presence of top predators in aphidophagous guilds appears to be rare, or non-existent, and the other natural enemies of ladybirds are ineffective in regulating their abundance. In addition, ladybirds are chemically defended against predation by other ladybirds. If very hungry then both larvae and adults of ladybirds will eat the immature stages of other species but depending on species this can result in their death or adversely affect their development (Agarwala & Dixon, 1992). That is, there is a cost associated with eating the immature stages of other species of ladybird. In particular, laboratory studies indicate that the adults of both *C. transversalis* and *M. sexmaculatus* readily eat their own eggs but are extremely reluctant to eat the eggs of the other species (Agarwala et al., 1998; Agarwala & Yasuda, 2001). Similarly, fourth instar larvae of *A. bipunctata* and *C. septempunctata* fed the eggs of the other species either survived very poorly – *A. bipunctata*, or died – *C. septempunctata* (Hemptinne et al., 2000). That is, there are advantages for ladybirds in avoiding eating other species of ladybird.

Thus the problem of how two or more predators, in particular *A. bipunctata* and *C. septempunctata*, and *M. sexmaculatus* and *C. transversalis*, coexist remains to be resolved. Theory also predicts that cannibalism, which is widely reported in aphidophagous ladybirds (Hodek & Honěk, 1996; Dixon, 2000), could be the mechanism resulting in coexistence. There is good support for this in that cannibalism acts as a strong density dependent regulating factor in the field (Mills, 1982; Osawa, 1993).

In summary, contrary to the prediction of IGP theory the different ladybirds appear to have very little effect on one another's abundance. This appears to be mainly attributable to the defences they have evolved against IGP. However, there is good empirical support for the idea that ladybird abundance is regulated by cannibalism.

Discussion

This study has revealed that the temporal attack sequence of ladybirds in aphidophagous guilds can be accounted for in terms of geometrical and physiological constraints associated with size. It is tempting to think that this structuring could be in response to competition and/or IGP. Certainly ladybird larvae of different species often compete with one another for prey and will eat one another.

It is likely that IGP resulted in the evolution in ladybirds of the very effective chemical and other defences against predators. Those species that attack aphid colonies early in their development would appear to be at an advantage. Therefore, it is not clear how IGP could account for the size differences and consequent temporal structuring of ladybird guilds. Accepting that the differences in size result in the temporal structuring one is left wondering whether there are any advantages in being small or large. Being small not only enables a ladybird to attack aphid colonies early in their development but may also enable them to exploit aphids even when they are generally relatively uncommon. Large species on the other hand could be at a disadvantage when aphids are generally uncommon but when abundant they can more effectively exploit the then more numerous very large aphid colonies because they can lay many more eggs per unit time than a small species of ladybird. If this is the case then small species should vary less in abundance and size from year to year than large species of ladybird. There is some empirical support for the first prediction as *C. septempunctata* is more frequently recorded in plague

numbers than the smaller *A. bipunctata* (Majerus & Majerus, 1996). However, it needs to be shown that this is not just a consequence of the size and behaviour of *C. septempunctata* making it more conspicuous.

The larvae of hoverflies (Syrphidae) generally occur in aphid colonies before ladybird larvae (e.g., Miñarro et al., 2005). In this case the temporal pattern in the attack sequence is associated with a difference in the lower developmental threshold (LDT) of these two groups of predators. The lower LDT of hoverflies (4°C) enables them to be active at lower temperatures and to develop faster between 10°C and 27°C than ladybirds, whose LDT is 10°C. As a consequence, early in a year, when temperatures are low but increasing, hoverflies appear before and complete their development more quickly than ladybirds, and in autumn, when temperatures are generally low and decreasing, only hoverfly larvae are likely to complete their development before the aphids disappear. Thus, the temporal patterning in this case is more a consequence of a phylogenetic constraint than a response to competition and/or IGP (Dixon et al., 2005). Why the members of these two groups of predators should all have similar LDTs, although interesting, will not be discussed further here.

Both the temporal patterns in the attack sequences shown by ladybirds and of hoverflies relative to ladybirds, and the marked incidence of cannibalism in these two groups of predators tend to question the supposed role of competition and/or IGP in the structuring of aphidophagous guilds. There is now a need to develop a more critical approach when studying the factors structuring aphidophagous guilds, especially the supposed role of IGP. This is most likely to come from a closer attention to the patterns and processes determining or associated with predatory guilds and the experimental testing of the assumptions of IGP theory. In addition, the tendency, for good pragmatic reasons, to view the evolution of ladybird life history strategies mainly in terms of the interactions occurring at the level of aphid colonies should be reviewed. The factors that determined the structuring of aphidophagous guilds might be more attributable to selection operating at greater spatial scales and/or a consequence of events that occurred in the evolutionary past of the natural enemies of aphids.

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