NOTES AND COMMENTS

Special feature: predatory ladybirds: individuals, populations, and interactions

Body size and resource partitioning in ladybirds

A. F. G. Dixon

Abstract Aphidophagous insects all exploit aphids as food, but there appears to be no association between the size of the aphidophagous predator and that of the species or the age structure of the aphid colonies they exploit. Aphid colonies generally increase, peak and decline in abundance, and are exploited by a sequence of predators, which is consistent from year to year. The objective of this study was to determine the rules underlying this temporal pattern. For example, in the field, aphid colonies are often first attacked by a small and then a larger species of ladybird. Theory based on the geometry and physiology of ladybirds predicts that the quantity of food required for oviposition and the area searched per unit time should scale with body weight, with exponents of 1 and 0.66, respectively. An analysis of empirical data supports these predictions. Thus, in relative terms a 35 mg ladybird requires 1.5 times more aphids per unit area for oviposition than a 10 mg ladybird. That is, the temporal pattern in oviposition is possibly mainly determined by geometrical and physiological constraints associated with body size, with small species of ladybird able to lay eggs at lower aphid population densities than large species. Cannibalism is thought to be the mechanism by which these predators are able to coexist.

Keywords Coccinellidae · Aphidophagous guilds · Body size · Coexistence · Intraguild predation

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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 size of prey species. 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 its prey, with those feeding on mites being small and those feeding on chrysomelid larvae large (Dixon and 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 the 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 (Stewart et al. 1991; Dixon 2000). For example, they are often first attacked by a small and then a large species of ladybird (e.g. Smith 1966; Agarwala and Bardhanroy 1999). The object 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, it 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 or more rarely by three species of ladybird of different sizes. Although there appears to be a clear advantage of ladybirds attacking aphid colonies early in their development, 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 *Coccinella transversalis* Fab. in subtropical regions (e.g. Smith 1966; Agarwala and Bardhanroy 1999). 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 are 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 are required to meet its basic metabolic costs, which increase with increasing body size. Initially, work on warm-blooded animals led to the "surface rule" and the extensive use of body surface area 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:

$$y = bx^a. \qquad (1)$$

In the logarithmic form this equation gives a linear function:

$$\log y = a \log x + \log b, \qquad (2)$$

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

$$\log metabolic\ rate = a\ \log body\ weight + k. \qquad (3)$$

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 that 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 the weight raised to the power of 0.75 or greater.

Area searched

Ladybirds usually 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 by 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:

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

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 reg-

ulated below the carrying capacity by the activity of their natural enemies, or if each ladybird regulated its own abundance. Intraguild predation (IGP) is currently seen as a major factor structuring predator guilds (Polis and 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 by large species of ladybirds in aphid colonies has been recorded (e.g. Smith 1966; Agarwala and Bardhanroy 1999), the mechanism resulting in this phenomenon has not been addressed. I used a mainly physiologically based theoretical approach to the problem above to obtain certain predictions, which need to be checked against empirical data.

The metabolic rates (ml O_2 h^{-1}) of different-sized ladybirds have been studied (e.g. Mills 1979; Tanaka and Itô 1982), but I only know of one interspecific study. It was done on three species, *Adalia bipunctata, C. septempunctata* and *Propylea quatordecimpunctata* (L.), which ranged in weight from 8 to 48 mg (Stewart 1988). The relationship obtained was:

$$\log metabolic\ rate = 0.961 \log body\ weight - 0.562,$$
$$(n = 93, r = 0.92, P < 0.001). \quad (5)$$

This indicates that metabolic rate in ladybirds increases in direct proportion to body weight (exponent = 1). The energy that ladybirds harvest in excess of that needed to fuel their metabolic rate can be utilized to produce eggs. However, the minimum energy required for laying eggs 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:

$$\log gonad\ size = 1.19 \log weight + 1.62, \quad (6)$$

where 1.19 is not significantly different from 1 (J.-L. Hemptinne et al., unpublished data). This also indicates that the minimum energy required for laying eggs is likely to increase in direct proportion to body weight.

There are very few studies that record, or that 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 h and then whether they laid eggs or not, and how many, is 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 of 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 (B. K. Agarwala, unpublished data), *A. bipunctata* and *C. septempunctata* (J. S. Rana, unpublished data) and *Cycloneda sanguinea* (L.) and *Scymnus levaillanti* Mulsant (Isikber 1999)—indicate that the minimum amount of food (mg) required for oviposition increases relative to body weight with an exponent of 1.26 (A. F. G. Dixon, unpublished data). 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 *Coccinella 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.) (B. K. Agarwala, unpublished data) 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:

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

That is, a large ladybird like *C. septempunctata* (35 mg) requires a minimum population density of aphids per unit area which is 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 which is 1.2 times greater than that required by the smaller species. Thus the mechanism that determines the stage of development at which an aphid colony 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 and Holt 1992). There is some experimental evidence that indicates that *H. axyridis* could be a top predator (Dixon 2000: S. Sato, R. Jimbo, H. Yasuda, A. F. G. Dixon, unpublished data). 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 at 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 the species this can result in their death or it can adversely affect their development (Agarwala and 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 and 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, it is advantageous for ladybirds to avoid eating other species of ladybird.

Thus, the problem of how two or more predators coexist—in particular *A. bipunctata* and *C. septempunctata* and *M. sexmaculatus* and *C. transversalis*—remains to be resolved. Theory also predicts that cannibalism, which is widely reported in aphidophagous ladybirds (Hodek and 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 predictions of IGP theory, different ladybirds appear to have very little effect on one another's abundance. This appears mainly to be 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 prompted the evolution of the very effective chemical and other defences against predators seen in ladybirds. 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 more numerous very large aphid colonies because they

can lay more eggs per unit time than can 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 and Majerus 1996). However it needs to be shown that this is not just due to the fact that the size and behaviour of *C. septempunctata* makes 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 and 27 °C than ladybirds do, whose LDT is 10 °C. As a consequence, early in the 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). The question of 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, throws doubt on 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 paying closer attention to the patterns and processes determining or associated with predatory guilds and experimentally testing 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 interactions occurring at the level of aphid colonies should be reviewed. The factors that determine the structuring of aphidophagous guilds might be more attributable to selection operating at greater spatial scales and, or, may be due to events that occurred in the evolutionary past of the natural enemies of aphids.

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