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Abundance and spatial distribution of aphids and scales select for different life histories in their ladybird beetle predators

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Abstract: Life history parameters tend to differ between aphidophagous and coccidophagous ladybird beetles. It seems that the nature of prey, in particular the abundance, number and size of the colonies and their spatial distribution, may have been selected for the evolution of the life histories in these two groups of coccinellids, leading the aphidophagous ladybird beetles to develop at a fast pace and the coccidophagous beetles at a slower pace. To study the abundance, number and size of the colonies and the spatial distribution of aphid and coccid species, 100 sampling plots regularly spaced along four parallel transects were surveyed in the summer of 2004. At each sampling plot, species abundance, and the number and size of colonies of aphid and coccid species were recorded. Iwao's patchiness regression was used to assess the spatial distribution of aphids and coccids. From this study, it was found that coccids are much rarer than aphids but formed more colonies. Whereas aphids display a stonger tendency to crowding, aphid colonies are randomly distributed in space while coccid groups are aggregated. So, it seems that the abundance and spatial distribution of prey distribution may be factors selecting for the evolution of different life histories among aphidophagous and coccidophagous ladybird beetles.

Key words: abundance, aphids, coccids, colony, Iwao's patchiness regression, spatial distribution

1 Introduction

The first case of successful biological control was the introduction, in the USA, of the Australian coccidophagous ladybird *Rodolia cardinalis* Mulsant to control the coccid *Icerya purchasi* Maskell. Dixon (2000) refers to 155 worldwide attempts to control aphids and 613 to control coccids. Only one of the attempts to control aphids was substantially successful, whereas 53 of the attempts to control coccids were completely or substantially successful. So aphidophagous ladybirds have not proven to be as effective as the coccidophagous species in introduction biological control programmes.

Dixon (2000) compiled the bibliography on aphidophagous and coccidophagous ladybirds in order to analyse divergence in life-history parameters between these two different groups of predators and argued that their size and rate of development are very dependent on the nature of their prey. It seems that coccidophagous ladybirds present life-history parameters consistent with a slow pace of life, whereas aphidophagous ladybirds experience a fast pace of life.

As coccidophagous and aphidophagous coccinellids belong to different genera of the same family, Coccinellidae, it seems that it is the nature of the prey rather than phylogeny that determines the rate of development in ladybirds (Dixon 2000). Prey, being more or less abundant in the habitat and more or less contagiously distributed in space, would appear to have influenced the evolution of the life histories of ladybird beetles. However, no field data have yet been collected to correlate abundance and spatial distribution of aphids and coccids with the life history parameters of predaceous ladybirds.

The aim of this work was to test the hypothesis, that the scarcity of coccids in the habitat favours a slow pace of life for their predators. If so, then a slow pace of life and a greater longevity would be advantageous, allowing the predators more time to search for prey. Thus we predict that, in general, aphid populations will contain a larger number of individuals and colonies in contrast to coccid populations that will have fewer individuals and colonies. We also expect to find the spatial distribution of aphids to be more aggregated than that of coccids.

2 Materials and Methods

2.1 Study area, experimental design and sampling method

To assess species richness, abundance and spatial distribution of aphids and coccids, 2.25 ha of natural woodland located at Mata dos Cavacos (Central part of São Miguel Island,

Azores) were sampled during the first fortnight of July in the summer of 2004. The sampling design consisted on 100 sampling plots equally distributed over four parallel transects. Transects were 10 m apart from each other. Circular 5-m diameter plots were located every 10 m along each of the transects. Each plot was searched for 30 min; during that period of time shoots were randomly selected. Individual Aphid individuals were collected for further accurate identification. The number of aphids per colony and the number of colonies per plots were counted (see section 2.2 for a working definition of colony). It was not possible to count coccids in the field because larval instars are minute and often translucid. Therefore, randomly selected shoots were cut off plants, put in plastic bags and brought back to the laboratory. They were then examined under a binocular stereomicroscope for 30 min in order to maintain coccid sampling as similar to aphid sampling as possible.

2.2 Data analysis

2.2.1 Abundance and colony number

The following parameters were calculated from the field data: mean number of each species individuals per plot, mean number of each species colony per plot, relative abundance of each species colonies, relative abundance of aphid and coccid colonies, species relative abundance, total relative abundance of aphids and coccids. Throughout this study, a colony corresponds at a minimum to a group of 10 aphids or coccids living in contact with each other. We classified colonies in three size categories: small (10–99 individuals), medium (100–499 individuals) and large (≥500 individuals). Colonies with <10 individuals were excluded because we assumed that they are too small to support ladybird beetle reproduction. The proportions of colonies in different classes were compared between aphids and coccids using a chi-squared test (Zar 1996).

2.2.2 Measurement of spatial distribution

To assess the spatial distribution of aphids and coccids, the abundance of aphid and coccid species, respectively, in each sampling plot were pooled together. Then, we used the Iwao's patchiness regression (Iwao 1968). In this method, a regression of Lloyd's (1967) mean crowding index (x^*) and the mean density ($\bar{x}$) are obtained according to the equation:

$$x^* = \alpha + \beta\bar{x}$$

where x^* was calculated after Lloyd (1967) as:

$$x^* = \bar{x} + \frac{s^2}{\bar{x}} - 1$$

where $\bar{x}$ is the mean density and s^2 is the variance of the sample.

The α parameter is the 'index of basic contagion' (Iwao 1968) that gives a measure of the tendency for crowding. β is the 'density contagiousness coefficient' (Iwao 1968) that describes the pattern in which the organism inhabits the environment. It expresses the extent to which the colonies are contagious at high density (Southwood and Henderson 2000).

In order to determine if the mean density ($\bar{x}$) and mean crowding (x^*) of aphids and coccids followed a normal distribution, values of mean density and mean crowding were ln-transformed and then compared using the Kolmogorov–Smirnov test. Significance of the regressions models was evaluated by ANOVA and the variance explained by the model was expressed as the coefficient of determination (Zar 1996). All the statistical procedures were performed using the statistical package SPSS 12.0 for Windows (SPSS Inc. 2001).

3 Results

3.1 Species richness, population and colony parameters

We observed nine aphid species and six coccid species (table 1). These 15 species comprise a total of 35 584 individuals, 67.98% of which were aphids and 32.02% were coccids (table 2). A total of 1012 colonies were observed, of which 25.89% were aphids and 74.11% were coccids (table 3).

The majority of both aphid and coccid colonies were of small size. However, aphids tend to be found in larger colonies than coccids (table 4). The proportions of aphids and coccids in colonies of different size differ significantly, with aphids tending to occur in larger

Table 1. *Aphid and coccid species found in the study area*

Species
Aphid species
Aphis sp.
Aphis gossypii Glover
Aphis hederae Kaltenbach
Aphis ruborum (Börner)
Aphis spiraecola Patch
Aulacorthum solani (Kaltenbach)
Neomyzus circumflexus (Buckton)
Toxoptera aurantii (Boyer de Fonscolombe)
Uroleucon sonchi (L.)
Coccid species
Aspidiotus nerii Bouché
Icerya purchasi Maskell
Protopulvinaria pyriformis (Cockerell)
Pseudococcus longispinus (Targioni Tozzetti)
Pseudococcus viburni (Signoret)
Saissetia coffeae (Walker)

Table 2. *Mean number of individuals (mean ± SE), species relative abundance (%) and total relative abundance of aphid and coccid species (% total).*

Species	Mean ± SE	%
Aphid species		
Aphis sp.	10.37 ± 9.44	2.914
A. gossypii	24.17 ± 11.82	6.791
A. hederae	16.46 ± 16.46	4.625
A. ruborum	37.59 ± 13.80	10.564
A. spiraecola	98.86 ± 21.85	27.776
A. solani	2.75 ± 1.06	0.773
N. circumflexus	0.01 ± 0.01	0.003
T. aurantii	51.67 ± 15.04	14.517
U. sonchi	0.03 ± 0.03	0.008
% total		67.98
Coccid species		
A. nerii	9.99 ± 1.33	2.807
I. purchasi	2.51 ± 0.92	0.705
P. pyriformis	92.53 ± 11.97	25.997
P. longispinus	0.74 ± 0.55	0.208
P. viburni	0.97 ± 0.75	0.273
S. coffeae	7.19 ± 1.40	2.020
% total		32.02

Table 3. *Mean number of colonies (mean ± SE), colonies relative abundance (%) and total relative abundance of aphid and coccid colonies (% total)*

Species	Mean ± SE	%
Aphid species		
Aphis sp.	0.03 ± 0.02	0.30
A. gossypii	0.43 ± 0.08	4.25
A. hederae	0.02 ± 0.02	0.20
A. ruborum	0.33 ± 0.09	3.26
A. spiraecola	0.82 ± 0.12	8.10
A. solani	0.28 ± 0.06	2.77
N. circumflexus	0.01 ± 0.01	0.10
T. aurantii	0.69 ± 0.12	6.82
U. sonchi	0.01 ± 0.01	0.10
% total		25.89
Coccid species		
A. nerii	2.19 ± 0.13	21.64
I. purchasi	0.73 ± 0.11	7.21
P. pyriformis	2.68 ± 0.14	26.48
P. longispinus	0.18 ± 0.04	1.78
P. viburni	0.13 ± 0.04	1.28
S. coffeae	1.59 ± 0.11	15.71
% total		74.11

Table 4. *Colony size of aphids and coccids*

Colony size	Aphids	Coccids
10–100	101	153
100–500	36	24
>500	9	0

colonies than coccids ($\chi^2 = 19.25$; d.f. = 2; $P < 0.001$).

3.2 Measurement of spatial distribution

The ln $\bar{x}$ and ln x^* values were normally distributed for the aphid (Kolmogorov–Smirnov: $Z = 1.256$; d.f. = 58; $P = 0.085$; and $Z = 1.151$; d.f. = 58; $P = 0.141$, respectively) and coccid (Kolmogorov–Smirnov: $Z = 0.695$; d.f. = 98; $P = 0.719$; $Z = 0.850$; d.f. = 98; $P = 0.466$, respectively) data. Iwao's patchiness regressions adequately described the relationship between mean crowding (x^*) and mean density ($\bar{x}$) for aphids and coccids (table 5; fig. 1). For aphids, Iwao's α is significantly greater than 0, indicating a very strong tendency to crowding (*t*-test: $t = 26.252$; d.f. = 58; $P < 0.001$). Although β is >1, it is not significantly different from 1 (*t*-test: $t = 1.96$; d.f. = 58; $P = 0.055$), indicating that aphid colonies are randomly distributed

Table 5. *Iwao's patchiness regression indices ($\alpha \pm SE$, $\beta \pm SE$), ANOVA and coefficient of determination (R^2) for aphids and coccids*

	$\alpha \pm$ SE	$\beta \pm$ SE	ANOVA	R^2
Aphids	2.821 ± 0.107	1.098 ± 0.050	$F_{(1,59)} = 474.481$, $P \leq 0.001$	0.893
Coccids	1.043 ± 0.099	1.154 ± 0.043	$F_{(1,99)} = 726.262$, $P \leq 0.001$	0.882

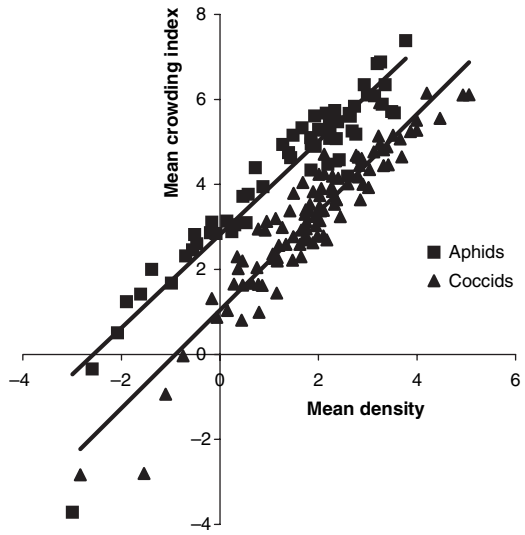

Fig. 1. *Regression analysis of Iwao's mean crowding index (x^*) on mean density ($\bar{x}$) for aphid ($x^* = 2.821 + 1.098\bar{x}$) and coccid ($x^* = 1.043 + 1.154\bar{x}$) populations*

in the sampling area. Iwao's α is also significantly >0 for coccids (*t*-test: $t = 10.508$; d.f. = 98; $P \leq 0.001$) but smaller than that for aphids. In this case, β is significantly >1 (*t*-test: $t = 3.581$; d.f. = 98; $P < 0.001$), indicating that coccid colonies tend to be aggregated, a tendency that increases with density.

4 Discussion and conclusions

In this study, coccids are much rarer than aphids but form more colonies. Consequently, coccid colonies are significantly smaller than those of aphids. Iwao's regression shows that the distribution of aphid individuals more strongly depart from a Poisson distribution than do that of coccids. That is, aphids display a stronger tendency to crowding, meaning that they form more compact colonies than do coccids. On the other hand, aphids colonies are randomly distributed in space whereas coccids groups are more aggregated. Moreover, their aggregation increases with density. Therefore, these two herbivore groups are differentially distributed within their habitat.

This study has been conducted in order to seek a correlation between the spatial distribution of aphids and coccids in the vegetation and the life-history parameters of predaceous ladybirds. Dixon (2000) indicated that coccidophagous ladybirds develop at a slower pace and particularly have greater longevity than species eating aphids. He also suggested that a slow pace of life has been selected for because coccids might be rarer and more difficult to encounter in nature than aphids. As a consequence, coccidophagous ladybirds might need more time to encounter enough suitable prey patches on which to lay their eggs. Therefore, an extended longevity is advantageous for these predators.

Aphidophagous ladybirds are strongly constrained by the fact that aphid colonies only exist for short

periods of time (Kindlmann and Dixon 1993). The decision by ladybird females to lay eggs in or near a prey patch depends on their ability to assess the relative quality of patches in terms of their potential to sustain the development of their larvae. If they are to maximize their fitness, these predators should lay eggs in the early stages of a colony (Kindlmann and Dixon 1993). The life span of an aphid colony is often similar to the development time of the aphidophagous ladybird larvae (Kindlmann and Dixon 1999). If females oviposit too early, the aphid colony will not provide enough prey for larvae to complete development; if too late or if many females use the same patch, the prey colony will have collapsed before larval development is complete. Kindlmann and Dixon (1993) concluded that there should be strong selection pressure optimizing the number of larvae in each aphid colony and so that predator feeding pressure will thus not affect peak number substantially. Ladybird reproductive behaviour has evolved in order to maximize fitness rather than to reduce aphid abundance. After exploring an aphid colony, aphidophagous ladybirds are expected to quickly leave in search of another colony. If, as our results indicate, aphid colonies are not abundant and not unevenly distributed in space, having a faster pace of life would be advantageous.

Coccidophagous ladybirds have not experienced the same intense selective force for fast development because their prey develop an order of magnitude slower than that of aphids (Dixon et al. 1997). Coccidophagous ladybirds, in general, lay their eggs singly in or on the ovisac of the coccid prey that, in turn, provides a large food supply for their offspring. Moreover, coccid larvae can, in some cases, achieve an advanced development stage on one prey item (Dixon et al. 1997). In our experimental woodland, there are many small coccid colonies that were evenly distributed in space. The constraint for coccidophagous ladybirds is to find mature adult coccids with nearly filled ovisacs that can sustain the development of their larvae. For that, they might need to live longer, search more and travel greater distances than aphidophagous species.

We believe that not only abundance, but also the period of resource availability within patches may play a major role in the evolution of a fast pace of life. If aphids presented high abundances over longer periods, the selection pressure for a fast pace of development would not be as strong as in cases where the resource is available for shorter periods.

This field study adds to the list of facts suggesting that the life histories of predaceous ladybirds have been shaped by the life styles of their prey (Dixon et al. 1997). However, further supporting evidence could be provided by detailed studies of the foraging behaviour of coccidophagous and aphidophagous ladybirds to demonstrate that the former require longer searching times for prey patch location than do the latter.

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