Abundance and spatial pattern of aphids (Homoptera: Aphidoidea) and coccids (Homoptera: Coccoidea): contribution to the knowledge of demographic strategies of aphidophagous and coccidophagous ladybird beetles (Coleoptera: Coccinellidae)

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INTRODUCTION

The first case of successful biological control was the introduction in the United States of America of the Australian coccidophagous ladybird *Rodolia cardinalis* Mulsant to control the coccid *Icerya purchasi* Maskell. However aphidophagous species of ladybirds have generally proved less effective biocontrol agents (Dixon *et al*., 1997).

This difference in efficiency mirrors the profound differences in these two predator-prey systems. Aphids generally develop at a much higher rate than coccids. Aphidophagous ladybirds are also much faster than coccidophagous species but still much slower than their prey. As a consequence, they are unable to track the variations of abundance of aphids. Their reproductive strategy did not evolved to develop a strong numerical response to aphid number but to cope with the diminishing number of prey available when their larvae complete their development. On the contrary, the success of coccidophagous ladybird lies in their quicker developmental rate than their prey.

A literature survey (Dixon, 2000) showed that the two kinds of ladybird beetles do not only differ in their speed of development. Following the values of all measured life history parameters, it seems that aphidophagous ladybirds live at a faster pace than coccidophagous species. Why are there two contrasted life style in this family of Coleoptera ? One hypothesis is that coccidophagous ladybirds might need more time to encounter enough coccids in order to lay all their eggs. This might be so because coccids are rarer and more difficult to meet than aphids.

The aim of this work is to test this hypothesis

2. Material & Methods

2.1. Study area, experimental design and sampling method

To assess species richness, abundance, colony number and spatial pattern of aphids and coccids, 2.25 hectares of natural habitat were systematically sampled at 100 plots regularly spaced along 4 parallel transects. Each plot was a circular area of 5 m of diameter (approximately 20 m^2).

For aphids, species richness, abundance, colony number and spatial pattern were assessed by observing the vegetation in each plot for 30 minutes. To evaluate the same parameters for coccids, several shoots per shrub and tree species were collected and brought back to the laboratory for coccid identification. In the laboratory, the sampling effort was the same as for the aphids, *i.e.*, 30 minutes of observation. For each type of prey, the number of colonies was counted and the size of the colonies estimated.

2.2. Data analysis

2.2.1. Abundance and colony number of aphids and coccids

The following population parameters were estimated: population density, species abundance, species relative abundance, total relative abundance, colony density, total number of colonies, colonies relative abundance and total relative abundance of colonies. We also registered the number and size of aphid and coccid colonies. We classified the colonies in three size categories: small (10 to 99 individuals), medium (100 to 499 individuals) and large ($\geq$ 500 individuals). The colonies with less than 10 individuals were excluded because we assumed they are too small for ladybird beetle reproduction. The proportions of colony size of aphids and coccids were compared using a χ^2 test (Zar, 1996).

2.2.2. Measure of spatial pattern of aphids and coccids

To assess the spatial pattern of distribution of aphids and coccids, the abundances of aphid and coccid species were respectively 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 ($\bar{x}$) is obtained according to the equation:

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

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

$$x^* = \bar{x} + \left(\frac{s^2}{\bar{x}} - 1 \right)$$

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 to crowding. β is the "density contagiousness coefficient" (Iwao, 1968) that describes the pattern in which the organism utilizes its habitat. It expresses the extent to which the colonies are contagious at high density (Southwood & Henderson, 2000).

In order to determine if the mean density and mean crowding of aphids and coccids followed a normal distribution we performed the Kolmogorov-Smirnov test. The mean density and mean crowding were Ln transformed. The significance of the regressions models was evaluated by ANOVA and the variance explained by the model was expressed by the coefficient of determination (Zar, 1996). All the statistical procedures were performed using the statistical package SPSS 12.0 for Windows (2001).

3. Results

3.1. Species richness, population and colony parameters

We observed 9 aphid species and 6 coccid species (Table I). These 15 species represent a total of 35 584 individuals, 67.98% of which were aphids and 32.02% were coccids (Table II). A total of 1 012 colonies were registered, of which 25.89% were aphids and 74.11% were coccids (Table III).

Table I. Aphid and coccid species found in the sampling 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 II. The population density (mean ± SE), species abundance (*n*), species relative abundance (%) and total relative abundance of aphids and coccids (% total).

	Species	Mean ± SE	(*n*)	(%)	(% total)
Aphid species	*Aphis sp*	10.37 ± 9.44	1037	2.914	67.98
	A. gossypii	24.17 ± 11.82	2417	6.791	
	A. hederae	16.46 ± 16.46	1646	4.625	
	A. ruborum	37.59 ± 13.80	3759	10.564	
	A. spiraecola	98.86 ± 21.85	9886	27.776	
	A. solani	2.75 ± 1.06	275	0.773	
	N. circumflexus	0.01 ± 0.01	1	0.003	
	T. aurantii	51.67 ± 15.04	5167	14.517	
	U. sonchi	0.03 ± 0.03	3	0.008	
Coccid species	*A. nerii*	9.99 ± 1.33	999	2.807	32.02
	I. purchasi	2.51 ± 0.92	251	0.705	
	P. pyriformis	92.53 ± 11.97	9253	25.997	
	P. longispinus	0.74 ± 0.55	74	0.208	
	P. viburni	0.97 ± 0.75	97	0.273	
	S. coffeae	7.19 ± 1.40	719	2.020	

Table III. The colony density (mean ± SE), total number of colonies (*n*), colonies relative abundance (%) and total relative abundance of aphid and coccid colonies (% total).

	Species	Mean ± SE	(*n*)	(%)	(% total)
Aphid species	*Aphis sp*	0.03 ± 0.02	3	0.30	25.89
	A. gossypii	0.43 ± 0.08	43	4.25	
	A. hederae	0.02 ± 0.02	2	0.20	
	A. ruborum	0.33 ± 0.09	33	3.26	
	A. spiraecola	0.82 ± 0.12	82	8.10	
	A. solani	0.28 ± 0.06	28	2.77	
	N. circumflexus	0.01 ± 0.01	1	0.10	
	T. aurantii	0.69 ± 0.12	69	6.82	
	U. sonchi	0.01 ± 0.01	1	0.10	
Coccid species	*A. nerii*	2.19 ± 0.13	219	21.64	74.11
	I. purchasi	0.73 ± 0.11	73	7.21	
	P. pyriformis	2.68 ± 0.14	268	26.48	
	P. longispinus	0.18 ± 0.04	18	1.78	
	P. viburni	0.13 ± 0.04	13	1.28	
	S. coffeae	1.59 ± 0.11	159	15.71	

For both aphids and coccids the majority of the colonies were of small size. However, aphids tend to present larger colonies than coccids (Table IV). The proportions of colony size of aphids and coccids differ significantly, with aphids presenting larger colonies than coccids ($\chi^2 = 19.25$; df = 2; $P < 0.001$).

Table IV. Colony size of aphids and coccids in Summer 2004. The colonies were classified as small ([10; 100[individuals), medium ([100; 500[) and large ($\geq$ 500).

Colony size (number of individuals)	Aphids	Coccids
[10; 100[	101	153
[100; 500[	36	24
$\geq$ 500	9	0

3.2. Measure of spatial pattern of aphids and coccids

The Ln $\bar{x}$ and Ln x^* values were normally distributed for aphid (Kolmogorov-Smirnov; Z = 1.256; df = 58; $P = 0.085$; Kolmogorov-Smirnov; Z = 1.151; df = 58; $P = 0.141$ respectively) and coccid (Kolmogorov-Smirnov; Z = 0.695; df = 98; $P = 0.719$; Kolmogorov-Smirnov; Z = 0.850; df = 98; $P = 0.466$ respectively) data.

The Iwao's patchiness regressions described well the relationship between mean crowding and mean density both for aphids and coccids (Table V; Fig. 1).

Table V. Iwao's patchiness regression indices (α±SE, β±SE), ANOVA and coefficient of determination (R^2) for aphids and coccids.

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

For aphids the Iwao's α is significantly > 0 indicating a very strong tendency to crowding (T-test: t = 26.252; df = 58; $P \leq 0.001$). Although β is larger than 1, it is not significantly different than 1 (T-test: t = 1.96; df = 58; $P = 0.055$). Thus, it indicates that aphid colonies are randomly distributed in the sampling area.

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

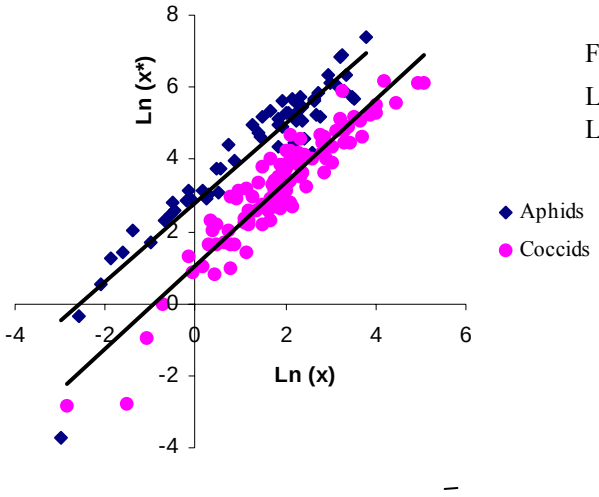

Figure 1. Iwao's patchiness regression between Ln $\bar{x}$ and Ln x^* (mean crowding index of Lloyd) for aphids and coccids.

4. DISCUSSION

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 coccids. That is, aphids display a neat tendency to crowding meaning they form less compact colonies than coccids. On the other hand, aphids colonies are randomly distributed in space while coccids groups are more aggregated. Moreover, their aggregation increase with density. Therefore, these two kind of herbivores do not utilize the habitat in a similar way.

This study has been set up in order to search for a correlation between the distribution of aphids and coccids in the vegetation and the life history parameters of predaceous ladybirds. Dixon (2000) indicated that coccidophagous ladybirds live at a slower pace and particularly for longer than species eating aphids. He went on suggesting that such a slow pace a life have 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 to lay all their eggs. Therefore, a long longevity is advantageous for these predators.

This field study add to the long list of facts suggesting that life history of predaceous ladybirds have been shaped by the life style of their prey (Dixon *et al.*, 1997). However, a detailed study of the foraging behaviour of coccidophagous and aphidophagous ladybirds is needed to demonstrate that the searching time of the former is greater than that of the later.

5. REFERENCES

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