BioControl **47:** 537–543, 2002.

Does the satiation hypothesis account for the differences in efficacy of coccidophagous and aphidophagous ladybird beetles in biological control? A test with *Adalia bipunctata* and *Cryptolaemus montrouzieri*

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Received 15 January 2001; accepted in revised form 10 August 2001

Abstract. Mills (1982) formulated the satiation hypothesis in order to explain why ladybirds are generally more effective in the biological control of coccids than of aphids: aphidophagous ladybirds are supposedly less efficient because they become more rapidly satiated than coccidophagous ladybirds. If this is true, the former should spend less time eating than the latter. This hypothesis is tested in this study using the coccidophagous *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) and the aphidophagous *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae). Contrary to Mills' (1982) prediction the coccidophagous ladybird did not feed continuously and even spent less time feeding than the aphidophagous ladybird. Furthermore, the gut capacity of *C. montrouzieri* is smaller than that of *A. bipunctata*.

Key words: *Adalia bipunctata*, biological control, Coccinellidae, Coleoptera, *Cryptolaemus montrouzieri*, feeding behaviour, satiation hypothesis

Introduction

Although ladybird beetles (Coleoptera: Coccinellidae) are often used as a symbol of good biological control practice they are not very effective biocontrol agents. Worldwide there have been 155 attempts to control aphids by introducing ladybirds, with only one substantially successful case, while 613 introductions to control coccids had an outcome of 53 complete or substantial successes (Dixon, 2000). Striking differences in efficacy among natural enemies of coccids and aphids always raised questions and several explanations were proposed as early as the nineteen thirties (Thorpe, 1930; Hodek, 1973; Dixon *et al*., 1995, Hodek and Honek, 1996; Dixon, 2000). Among the proposed explanations there is the satiation hypothesis (Mills, 1982):

> "the coccidophagous coccinellids feed on an immobile prey and may reduce the proportion of each prey item eaten to that which is most readily extracted, easily assimilated and rapidly digested. A reduction in digestion time would allow more continuous feeding, while a reduction in the proportion of each prey item eaten would increase the potential impact on the prey population".

Therefore, in our opinion, the satiation hypothesis implies that the developmental rate of coccidophagous ladybirds should be greater than those of aphidophagous species because the former process their food more efficiently than the latter, but this is not confirmed in the literature. On the contrary, Dixon *et al*. (1997) showed that ladybird predators of aphids develop rather faster than those feeding on coccids.

In this paper we present and discuss the results of three experiments designed to test the satiation hypothesis, using two similar-sized species of ladybird beetles, one of which is aphidophagous, *Adalia bipunctata* (L.), and the other coccidophagous, *Cryptolaemus montrouzieri* Mulsant. The first experiment was set up to determine whether both species are selective feeders, preferring a particular part of their prey. The second experiment aimed to determine which species spend more time feeding and finally, in the third experiment the gut capacity of *C. montrouzieri* was estimated and compared with that of *A. bipunctata*.

Materials and methods

C. montrouzieri, fed on *Planococcus citri* Risso (Homoptera: Pseudococcidae), and *A. bipunctata*, fed on *Acyrthosiphon pisum* Harris (Homoptera: Aphididae), were both reared individually in Petri dishes (5.5 cm diameter). An excess of fresh food was supplied daily to the stock cultures. *A. pisum* were collected from their host-plant and introduced into the rearing dishes of *A. bipunctata*. A section of stem of broad bean (*Vicia faba* L.) was also put in each Petri dish to provide a source of humidity and to keep the aphids alive for as long as possible. For *C. montrouzieri*, potato sprouts infested with *P. citri* were separated from their tuber and introduced into the rearing dishes.

Is C. montrouzieri *a selective feeder?*

The satiation hypothesis suggests that coccidophagous coccinellids may selectively feed on the more readily extracted, more digestible parts of the prey. To test this idea we recorded the body part attacked.

Ten well-fed third instar larvae of *C. montrouzieri* from the stock culture were kept individually in Petri dishes (5.5 cm diameter) and starved for 18 hours, after which a mealybug (about 2 mm long) was placed in each dish. The part of each mealybug initially bitten by the larvae (i.e., the ventral or dorsal part of the head, thorax or abdomen) and whether the mealybug was alive or dead when released by the predator at the end of the meal were recorded. In order to determine whether the larvae and adults selectively eat a particular part of each prey the observations were subjected to a χ^2 test for goodness of fit (Sokal and Rohlf, 1995; Zar, 1996). Additional mealybugs were successively offered over a three hour period or until the larva refused to feed. The experiment was carried out at 25 °C.

How do C. montrouzieri *and* A. bipunctata *partition their time?*

Individual third instar larvae and adult females of both species from the stock culture were each observed for one hour in order to see how they partitioned their time between: walking, resting, subduing prey and feeding. The larvae and females were not starved prior to the experiment and the females were between 2 and 3 weeks old. The observation period of one hour always happened between 11 and 14 h, based on the few references available about periods of activity in ladybird beetles (Mack and Smilowitz, 1978; Miura and Nishimura, 1980; Nakamuta, 1987).

Ten individuals of each stage and species were tested. Each individual of *C. montrouzieri* was placed on a potato sprout well infested with all instars of *P. citri* or in case of *A. bipunctata* a broad bean plant well infested with all instars of *A. pisum*. Observations started 10 minutes later to allow the ladybirds to accommodate to the new situation. The observations were carried out at 25 °C for *C. montrouzieri* and 20 °C for *A. bipunctata*. There were few references to rely on for the selection of the experimental temperatures. It appears that *A. bipunctata* larvae achieve their best weight gain between 17.5 and 20 °C (Mills, 1979). *C. montrouzieri* grow best around 28 °C (Copland et al., 1985). In addition, *C. montrouzieri* at 25 °C and *A. bipunctata* at 20 °C behave similarly in terms of speed of movement (Magro, unpublished).

The proportion of time spent feeding by the larvae and the adults of both species were analysed by a Mann-Whitney test.

Gut capacity of C. montrouzieri

This experiment followed the methodology used by Mills (1982) for determining the gut capacity of *A. bipunctata.*

Six third instar larvae of *C. montrouzieri* were starved for 18 to 24 hours and then fed to satiation with excess prey. The relative gut capacity (RGC) of each individual was then calculated as follows:

$$RGC = (\frac{w_f - w_i}{w_i});$$

where w_f is the final weight, that is the weight after the meal was finished and w_i is the initial weight. The beetles were weighed to 0.1μg on a Sartorius Microbalance – SC2. These six values were compared with six values obtained from the results presented graphically by Mills (1982) for *A. bipunctata* larvae by means of a Mann-Whitney test.

Results

Is C. montrouzieri *a selective feeder?*

There is no evidence that *C. montrouzieri* is a selective feeder. Of the 22 bites observed, 7 occurred on the head, 8 on the thorax and 7 on the abdomen. The dorsal side of the coccids was bitten 14 times and the ventral side 8 times. These ratios are not significantly different from those expected if attacks to these areas of the body occurred at random (For the head: thorax: abdomen: $\chi^2 = 0.092$, 2 d. f., $P > 0.05$; from above opposed to from below: $\chi^2 = 0.834$, 1 d. f., $P > 0.05$).

How do C. montrouzieri *and* A. bipunctata *partition their time?*

The percentage of time larvae and adults of *C. montrouzieri* and *A. bipunctata* spent walking, resting or handling prey is given in Table 1. Both adults and larvae of *C. montrouzieri* spent significantly and considerably less time feeding than did *A. bipunctata.* The result was contrary to what Mills (1982) predicted. That is, larvae and adults of *C. montrouzieri* do not appear to feed more continuously than those of *A. bipunctata.*

Gut capacity of C. montrouzieri

The mean weight of prey eaten by starved *C. montrouzieri* larvae, weighing 3.4172 mg ± 1.8678 mg, was 0.6873 mg ± 0.3356 mg. That is, the relative

Table 1. Percentage of time spent walking, resting and handling prey by adult females and third-instar larvae (L3) of *C. montrouzieri* and *A. bipunctata*

	Walking m (sd)	Resting m (sd)	Handling prey Subduing m (sd)	Handling prey Feeding m (sd)
C. montrouzieri				
Adult[a]	36.1 (20.1)	56.6 (22.4)	0.6 (1.4)	1.7 (2.7)
L3	67.7 (23.8)	27.9 (21.9)	2.8 (7.9)	1.6 (4.6)
A. bipunctata				
Adult	38.8 (25.3)	49.9 (27.1)	0	11.3 (10.2)
L3	23.7 (19.9)	52 (16)	0	24.3 (16.5)

m = mean; sd = standard deviation.

[a] On average, the females spent 5% of their time in oviposition during the experiment.

Mann-Whitney U test statistic for feeding times: U test for adults = 81.0, P = 0.016; U test for larvae = 82.0, P < 0.001.

gut capacity in terms of weight of prey eaten was 22.3% of a larva's live weight (Table 2). This is significantly less than the 37.7% reported for *A. bipunctata* by Mills (1982) (Mann-Whitney U test statistic = 35.000; P = 0.006).

Discussion and conclusions

The results of the experiments reported here do not support Mills (1982) satiation hypothesis. The coccidophagous ladybird *C. montrouzieri* did not feed more continuously and even spent less time feeding than a similar sized aphidophagous ladybird, *A. bipunctata*. In terms of handling time (subduing plus feeding time) *C. montrouzieri* spent 6 fold less time in this activity than did *A. bipunctata*. There is also no evidence to support the suggestion that *C. montrouzieri* is a selective feeder but this point requires more experimentation. Due to the sample size of this study and the conditions in which *C. montrouzieri* were reared in the laboratory, some doubts remain on the feeding behaviour of this coccidophagous ladybird.

Finally the relative gut capacity of *C. montrouzieri* expressed as a proportion of total weight (22.3%) is less than that reported by Mills (1982) for *A. bipunctata* (37.7%). *C. montrouzieri* was satiated after eating a smaller quantity of prey. However, this cannot be entirely a consequence of gut capacity for if it were so, then the ratio of gut capacities (22.3/37.7) should

Table 2. The weight (mg) of 6 third instar larvae of *C. montrouzieri* that were firstly starved and then satiated, and their relative gut capacity; the weight of 6 starved third instar larvae of *A. bipunctata* and their relative gut capacity

	C. montrouzieri			*A. bipunctata*[a]	
	Starved (mg)	Satiated (mg)	RGC	Starved (mg)	RGC
1	0.9173	1.2015	0.3098	4.4	0.32
2	1.1857	1.4745	0.2436	3.9	0.54
3	3.9613	4.9451	0.2483	3.9	0.28
4	4.8577	5.8901	0.2125	2.9	0.42
5	4.6017	5.4740	0.1896	2.5	0.32
6	4.9796	5.6417	0.1330	1.8	0.39
$\bar{x}$			0.2228		0.38

[a] from Mills (1982); $\bar{x}$ = mean; RGC, relative gut capacity = (satiated weight – starved weight)/starved weight.

be the same as the ratio of feeding times (2/24). The fact that these two proportions are so different suggest that *A. bipunctata* processes its food more rapidly than *C. montrouzieri*. Therefore, the rate of food digestion might also partially explain the more rapid satiation of *C. montrouzieri*. That is, associated with their slower development (Dixon et al., 1997; Dixon, 2000) coccidophagous ladybirds also feed, and possibly digest, their prey more slowly than aphidophagous ladybirds.

This study of two similar-sized species of ladybird beetles needs to be confirmed by experimental evidence obtained from comparisons of other aphidophagous and coccidophagous coccinellids.

Acknowledgements

This paper was written while the first author was on a post-doctoral fellowship of the Fundação para a Ciência e Tecnologia – Portugal (Programme Praxis XXI – Sup-programa Ciência e Tecnologia do 2° Quadro Comunitário de Apoio). The authors warmly thank Nick Mills for his numerous valuable comments when reviewing this manuscript.

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