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Searching behaviour and mate recognition by males of the two-spot ladybird beetle, *Adalia bipunctata*

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Abstract. 1. Adult males of the two-spot ladybird beetle, *Adalia bipunctata*, did not show a functional response to increase in aphid abundance and consumed markedly fewer aphids than do the females.

2. At high densities of prey, females spent more time in area-restricted search than when prey was scarce. Males were always less active than females and they did not respond to an increase in prey abundance by a change in searching behaviour.

3. After a brief encounter with a female, a male showed area-restricted searching behaviour. This behaviour occurred in response to encountering a female's elytra and in particular to a chloroform-soluble component (sex pheromone) present on or in the elytra.

4. Males needed to encounter a female in order to respond to her presence, which indicated the pheromone is a contact pheromone.

5. The searching behaviour of males appeared to be mainly directed towards locating females; that of females towards locating aphids. This difference between the sexes should be taken into account when quantifying the predatory response of ladybirds to aphid abundance in the field.

Key words. *Adalia bipunctata*, coccinellids, contact sex pheromone, ladybirds, mate recognition, searching behaviour.

Introduction

Adult ladybirds show a marked numerical response to aphid density (Wright & Laing, 1980) and both larvae and adults are regarded as important predators of aphids (Ives *et al.*, 1993; Kauffman & Swalbe, 1991; Hodek, 1973; Ferran *et al.*, 1986; Brown, 1972). Studies on the searching behaviour of adult ladybirds either ignore (Brown, 1972; Karner & Manglitz, 1985; Kareiva & Sahakian, 1990; Grevstad & Kepletka, 1992) the fact that there are approximately equal numbers of females and males (cf. Hurst *et al.*, 1992) or assume that males have a similar searching behaviour to that of females (Gutierez *et al.*, 1981, 1990). There is one exception: Honek (1985) indicates that males are more frequently observed flying and walking between plants, and less often seen eating aphids than are females. He concluded that males spent more time searching for females than for aphids. Although there is evidence that female *Adalia bipunctata* (L.) in some populations prefer to mate with melanic males (Majerus *et al.*, 1982; O'Donald & Majerus, 1988; but see Kearns *et al.*, 1990, 1992) nothing is known of the cues used by ladybirds in mate recognition. However, it has been suggested that the secretion of the coxal glands that open on the coxites of the female genitalia might be used for this purpose (Hemptinne *et al.*, 1991).

In this paper we quantify the functional response and change in activity of the two-spot laydbird in response to an increase in aphid abundance and the reaction of males when they encounter females, and present evidence that a contact pheromone is used in mate recognition.

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Materials and Methods

Two-spot ladybirds, *A.bipunctata*, were reared at 20 ± 1°C and a photoperiod of 16 h light and 8 h darkness. Groups of approximately twenty males and twenty females were kept in 5 litre plastic boxes, which also contained a piece of corrugated filter paper and wet paper tissue to increase the surface area and provide a source of drinking water. Every other day the ladybirds were fed an excess of the pea aphid, *Acyrthosiphon pisum* (Harris). Once a week they were transferred to clean containers to stimulate egg laying. The adults were sexed by examining the shape of the tip of the last abdominal sternite, which is hemispherical in females and notched posteriorly in males (Hodek, 1973).

Functional response. 1-month-old males from the stock

culture were isolated in 9 cm diameter Petri dishes lined with damp filter paper. In order to eliminate the effects of previous food consumption, they were fed one, two, five, ten or twenty adult aphids per day (mean weight of an adult aphid: 3.44 mg, SD 1.12 mg) for 2 days. Food availability is expressed as the number of aphids supplied each day per 150 cm^2, the later figure being the area of the internal surface of a 9 cm Petri dish. Each day each beetle was transferred to a clean Petri dish. On the third day their food consumption was recorded between 08.30 and 20.30 hours. There were eight replicates of each feeding regime.

The same method was used to measure the food consumption of females but in this case there were 10 replicates of each feeding regime.

Adult activity. The activity of males and females of *A.bipunctata* was measured at 08.30 and 20.30 hours. Individual beetles were fed one or twenty adult aphids per day (mean weight of aphid: 3.44 mg, SD 1.12 mg) and their level of activity was scored every 5 min over a period of 1 h 40 min. Therefore there were twenty records of activity for each beetle, which was scored as stationary, or displaying either area-restricted search or extensive search (cf. Ferran & Dixon, 1993). Twenty females at both prey densities, nineteen males at the density of 1 aphid/day and twenty males at the density of 20 aphids/day were observed. The percentages of time devoted to the three types of activity were calculated and arcsine transformed prior to analysis of variance. In order to eliminate the effect of previous food consumption on their behaviour the beetles were acclimatized to the experimental conditions for 48 h and tested on the third day.

Response of males to females. (i) *Do males recognize females?* Prior to each test, 1-month-old males were kept in groups separated from females for at least 24 h in the standard culture conditions. Subsequently these males were isolated in 9 cm diameter Petri dishes lined with damp filter paper and left to settle for 15 min before either being left on their own, presented with a conspecific female or male attached by its abdominal sternites to a wire loop by a drop of paraffin wax, or a female of *Propylea quatuordecimpunctata* (L.) or *Coccinella septempunctata* L. similarly attached to a wire loop. The males were allowed to touch with their maxillary palps and antennae the elytra of the ladybird presented, and then the stimulus was quickly removed and the male's subsequent movements recorded for 2 min by tracing them with a pen on the lid of the Petri dish. All observations were made at 20 ± 1°C between 11.00 and 15.00 hours. The length of the track was measured with an ipsometer and the number of changes of direction determined by drawing tangents to the track at regular intervals as described in Kareiva & Shigesada (1983). As the tracing of the males' tracks was not very accurate because of the thickness of the pen and possible parallax errors, changes of direction involving angles of less than 10° were not counted. Males that walked around the edges of the Petri dishes were considered as moving in a straight line. The number of changes of direction per cm was calculated. These results were analysed by means of ANOVA and pairwise mean comparisons following the method of Tukey (Wilkinson *et al.*, 1992). Each male was tested only once.

(ii) *What part of a female's body triggers recognition?* The experimental procedure, the recording and analysis of data were similar to that in the above experiment. To determine the part of the body of a female that triggers the sexual behaviour of males they were presented with the following parts of the body of a female two-spot beetle: elytron, pronotum, abdominal tergites or coxal glands.

(iii) *What feature of a female's elytra triggers recognition?* The experimental procedure was as in the above experiment but the males were presented with the following stimuli: an elytron removed from a female two-spot beetle or female of *Coccinella undecimpunctata* L. prior to the start of the experiment; an elytron of a female two-spot beetle that had been washed in chloroform; a similarly washed elytron but to which 5 ml of a chloroform extract of elytra had been added, or a washed elytron to which 5 ml of chloroform had been added. The elytral extract was obtained by immersing twenty elytra (14.79 mg) in 0.50 ml of chloroform for 15 s and then in two lots of 0.25 ml of chloroform, each for 15 s. The three chloroform extracts (1 ml of chloroform) were pooled and then evaporated. The residue was redissolved in 50 ml of chloroform; 5 ml of this extract contained the solute from two elytra. The elytra so treated and those to which the extract was applied were placed in a current of nitrogen for at least 20 min and subsequently dried at 30°C to evaporate the solvent before they were presented to the males.

(iv) *Do males respond to females at a distance?* Males were isolated in 9 cm Petri dishes lined with damp filter paper for at least 15 min before they were introduced into the olfactometer. Each male was presented with a current of air that had come equally from the two arms of the olfactometer, one of which was empty (control) and the other contained the odour source. A test was terminated when the male reached one of the two arms. In the first test, a female was randomly assigned to one of the arms of the olfactometer and randomly reassigned after testing five males. This was repeated twenty-nine times. In the second test, which was repeated forty-one times, filter paper with 5 ml of the chloroform extract of female elytra (see the above experiment) was used as the odour source instead of a female. In the third test, both arms of the olfactometer were empty and this treatment was repeated thirty times. For each of the treatments the proportions of males in both arms of the olfactometer were compared by mean of a binomial test (Siegel, 1956). In all these experiments the flow rate was 7 l/h. Each male was tested once.

Results

Functional response

The females displayed a strong increase in food intake with aphid densities up to 10 aphids/day/150 cm^2 after which their consumption did not increase (Fig. 1). The males showed a weaker response to increasing aphid availability than females (Fig. 1). When 1 or 2 aphids/day/150 cm^2 were provided, individuals of both sexes ate the same quantity. But at the higher densities (5, 10 and 20 aphids/day/150 cm^2) the males are less voracious than the females. The slope of the regression of food consumption at different aphid densities for males is significantly less than than the slope calculated for females ($b_{males} = 0.06$; $b_{females} = 0.80$; $t = 14.373$; 76 df; $P < 0.001$). It should be noted that in the case of the females, aphid consumption at a density of 20 aphids/day/150 cm^2 was not included in the analysis.

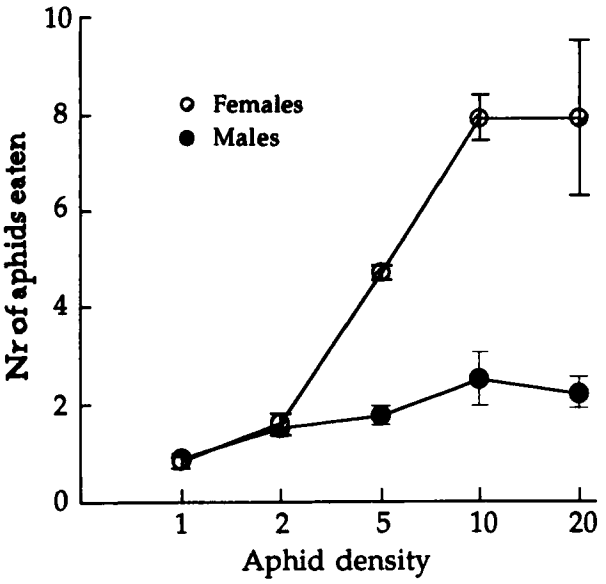

Fig. 1. The average number of aphids eaten daily by females and males of *Adalia bipunctata* at five prey densities (aphids/day/cm^2).

Table 1. The average percentage of time spent stationary or searching by females and males of *Adalia bipunctata* at two aphids densities (aphids/day/150 cm^2).

			Percentage of time		
				Searching	
Aphids/day	Sex	*n*	Stationary	Area-restricted search	Extensive search
1	♂	19	86.3	8.2	5.5
	♀	20	43.9	25.4	30.7
20	♂	20	71.4	17.0	11.6
	♀	20	51.4	31.8	16.8

Adult activity

As the levels of activity of females in the morning and evening were very similar, the two data sets were pooled. In the case of the males, the similarity in activity in the morning and the evening was not so obvious. Nevertheless, as the time of day did not affect significantly their level of activity ($F = 0.131$, 1 and 74 df, $P = 0.131$), the two data sets for males were also pooled.

Females were always more active than males as they spent less time stationary (Table 1: $F = 20.31$, 1 and 75 df, $P = 0.000$). But for both sexes an increase in food availability had no significant effect on the percentage of time spent walking ($F = 4.36$, 1 and 75 df, $P = 0.410$). The density of prey only modified the pattern of search. When fed 20 aphids/day the females spent more time in area-restricted search and less time in extensive search than when fed 1 aphid/day. Although the males also spent more time in area-restricted search at the highest density of prey, they did not show a reduction in the time spent in extensive search. An analysis of variance of these results reveals a significant interaction between sex of ladybird and density of prey ($F = 4.15$; 1 and 75 df; $P = 0.045$), which indicates that the sexes showed very different patterns of search at the two aphids densities (Table 1).

Response of males to females

Do males recognize females? Males that have been kept isolated for 24 h react in a very characteristic manner when they encounter a female. They immediately extrude their genitalia and attempt to mate. They also show a similar response to freshly killed females. In an attempt to quantify the sexual response of males, their locomotory behaviour following a brief encounter with a female was monitored and analysed. There was a very highly significant tendency for males presented with a female of their own species to subsequently walk more slowly and change direction more frequently than after encountering another male or female of another species of ladybird. That is, after encountering a conspecific female, males showed area-restricted searching behaviour in that the number of changes of direction per unit distance travelled was 3 times greater than

Table 2. Response of males of *Adalia bipunctata* in terms of distance travelled (1) and number of changes of direction (2) and the number of changes of direction per unit distance travelled (2/1) in the 2 min after encountering either a conspecific male, conspecific female or a female of either a fourteen-spot or seven-spot ladybird beetle.

		Distance travelled (1)		No. of changes of direction (2)		Ratio (2/1)	
Stimulus	*n*	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)
None	28	53.7	(5.5)	23.4	(2.1)	0.5	(0.05) a
Conspecific ♂	25	52.1	(5.6)	29.2	(3.9)	0.6	(0.05) a
Conspecific ♀	23	34.4	(4.9)	42.3	(4.2)	1.5	(0.12) b
Fourteen spot ♀	25	61.4	(5.8)	29.4	(3.0)	0.6	(0.07) a
Seven spot ♀	25	54.3	(5.8)	16.2	(1.9)	0.4	(0.05) a
F-ratio						37.63***	

Stimulus as described in text. *** $P < 0.001$. For the ratio (2/1), means followed by different letters differ significantly ($P = 0.00$).

Table 3. Response of males of *Adalia bipunctata* in terms of distance travelled (1), the number of changes of direction (2) and the number of changes in direction per unit distance travelled (2/1) in the 2 min after encountering either the coxal glands, pronotum, abdomen or an elytron of a conspecific female.

		Distance travelled (1)		No. of changes of direction (2)		Ratio (2/1)	
Stimulus	*n*	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}^*$	(SE)
Coxal glands	20	39.7	(3.9)	21.0	(1.9)	0.6	(0.07) a
Pronotum ♂	20	38.1	(3.4)	24.0	(2.7)	0.7	(0.07) a
Abdomen ♀	20	37.0	(5.0)	27.3	(3.9)	0.8	(0.07) a
Elytron ♀	20	16.4	(2.2)	27.2	(4.4)	1.7	(0.15) a
F-ratio						26.77***	

Stimulus as described in text. *** $P < 0.001$. For the ratio (2/1), means followed by different letters differ significantly ($P = 0.00$).

after encountering a conspecific male or a female of another species (Table 2 and Fig. 2). Thus males appear to need only a brief encounter to recognize the presence of a conspecific female.

What part of a female's body triggers recognition? To determine where the mate recognition cue might be located on the body of a female, males were presented with either the coxal glands, pronotum, abdomen or an elytron of a conspecific female (Table 3).

After encountering an elytron of a conspecific female, males moved more slowly bud did not change direction more frequently than after encountering the coxal glands, pronotum or abdominal tergites of a female. However, the net effect of encountering an elytron on the rate of change of direction per unit distance travelled by the males was significantly greater than after encountering other parts of females and comparable to that observed after encountering whole conspecific females (cf. Table 2).

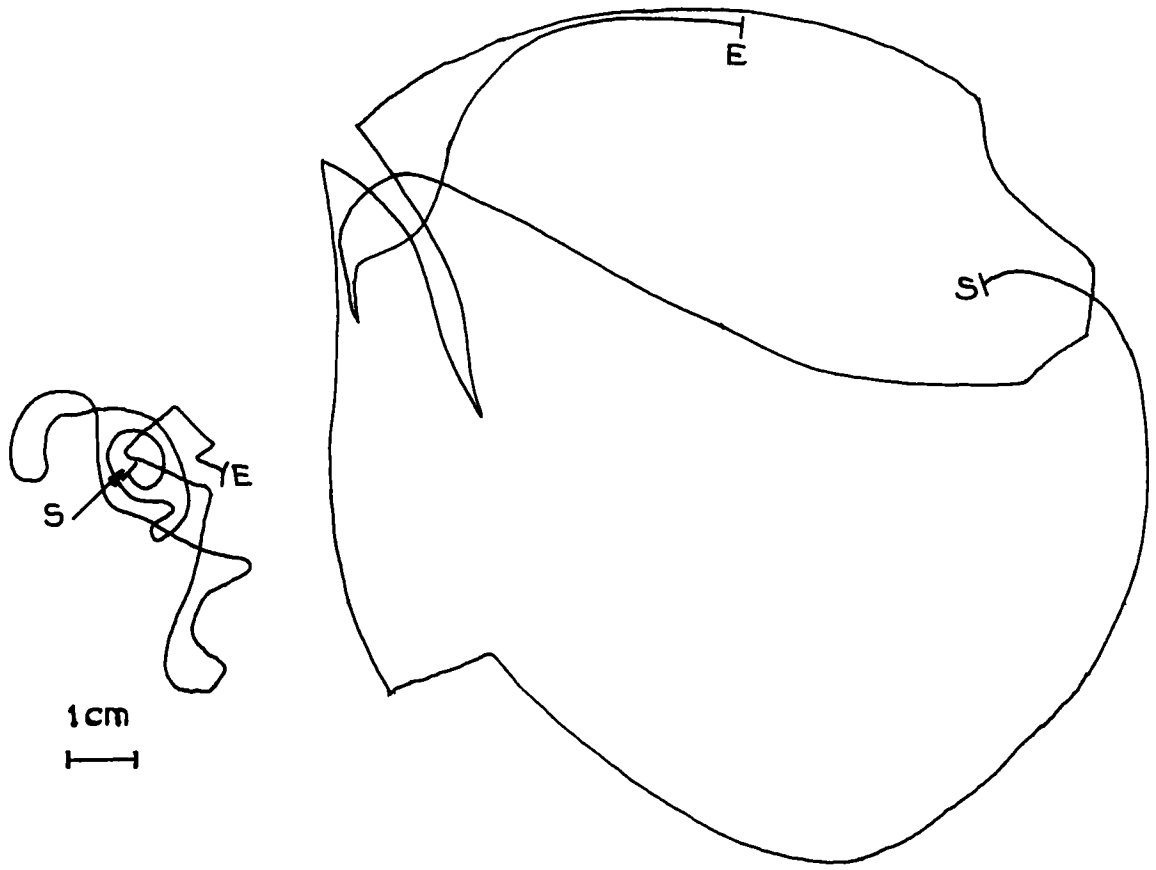

Fig. 2. Examples of the tracks followed by males of *Adalia bipunctata* after encountering a conspecific female (left) or male (right). S marks the beginning and E the end of the track.

Table 4. Response of males of *Adalia bipunctata* in terms of distance travelled (1), the number of changes in direction (2) and the number of changes in direction per unit travelled (2/1) in the 2 min after encountering either an elytron of a conspecific female, of a conspecific female washed in chloroform, chloroform washed elytron painted with the chloroform extract or an elytron of an eleven-spot ladybird beetle.

		Distance travelled (1)		No. of changes of direction (2)		Ratio (2/1)	
Stimulus	*n*	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)
Elytron of conspecific female							
Untreated	30	16.3	(1.7)	23.1	(3.0)	1.6	(0.14) a
Washed in chloroform	30	23.3	(2.7)	19.9	(3.3)	0.8	(0.07) b
Washed and painted with Chloroform extract	30	11.6	(1.9)	21.3	(3.2)	2.1	(0.26) a
Elytron of eleven-spot female	30	19.2	(2.6)	11.6	(1.5)	0.7	(0.08) b
None	30	14.3	(2.2)	9.2	(1.4)	0.9	(0.10) a
F-ratio						17.61***	

Stimulus as described in text. *** $P < 0.001$. For the ratio (2/1), means followed by different letters differ significantly ($P = 0.01$).

Thus, the mate recognition cue appears to be associated with the elytra.

What feature of a female's elytra triggers recognition? To determine whether the response shown by males to the elytra of females was triggered by the shape, colour or odour of the elytra, males were allowed to encounter an elytron of the females of other species, those of their own species and those of their own species that had been washed in chloroform (Table 4). They were also allowed to encounter an elytron of a conspecific female that had been washed in chloroform and subsequently painted with this extract.

Although an elytron of *C.undecimpunctata* is the same size and colour as that of *A.bipunctata*, it did not trigger the intense searching behaviour shown by males after encountering an elytron of a female of its own species. However, an elytron of a conspecific female that has been washed in chloroform did not induce intense searching behaviour. The application of the chloroform extract of elytra to a washed elytron made it once again attractive to males. The elytron painted with extract induced a rate of change of direction comparable to that shown by males after encountering live females or untreated elytra (Tables 2 and 4). This indicates that a chloroform-soluble pheromone associated with the elytra of females is used in mate recognition by males.

Do males respond to females at a distance? To determine whether the pheromone is volatile and can be sensed at a distance, males were exposed in an olfactometer to currents of air that had passed over whole females and an extract of the elytra of females. The males showed a positive anemotaxis but did not respond (Table 5) to the presence of a conspecific female or the pheromone. Thus males appear to recognize females by means of a contact pheromone present on their elytra.

Table 5. The numbers of males of *Adalia bipunctata* moving to the source of the odour of a conspecific female and the chloroform extract of two elytra of a conspecific female in an olfactometer.

	No. of males		
Odour source	To the source of odour	Tested	
None	15	30	NS
Conspecific female	10	29	NS
Extract of elytra	22	41	NS

Odour source as described in text. NS = not significant.

Discussion

Compared with females, the males of *A.bipunctata* consumed very few aphids, approximately half the number consumed by females when supplied with five aphids per day. More importantly, males only showed a very weak functional response to increase in aphid abundance. This is possibly because females have a greater energy requirement than males as they need to sustain egg production as well as locomotion. The relatively low energy demands of males may partly account for the weak numerical response shown by laydbirds in the field to aggregates of aphids (Karner & Manglitz, 1985; Ives *et al.*, 1993). It is likely that these studies would have revealed a more marked numerical response if the response of only the female ladybirds had been considered.

The females showed a change in their pattern of search when the density of prey was increased although the proportion of time spent searching remained the same. At the highest prey density females spent more time in area restricted search than at the lowest prey density. In contrast, males spent more time searching and their pattern of search did not change when prey was abundant. Thus the pattern of search of males was not affected by an increase in the density of prey. This coupled with their weak functional response indicates that the searching behaviour of males is little influenced by aphid abundance. Although males and females use the same cues to locate aphid colonies (Obata, 1986), it is unknown whether males rely initially on finding aphids to locate their mates. Male and female ladybirds seek different resources and this is reflected in their searching behaviour. For example, in the course of this study, males were often observed to perform shorts flights but not females. The flitting behaviour of males might account for Honek's (1985) observation that males are more conspicuous than females in the field.

After a brief encounter with a conspecific female, the males of *A.bipunctata* indulged in area-restricted search. As most of the dorsal surface of a ladybird consists of elytra, it is these structures that males are most likely to touch first on encountering a female. If a male remains in contact with a female, then after a short period spent palpating the elytral surface the male extrudes its genitalia and attempts to mate.

The experiments reported here indicate that males recognize conspecific females by means of a chloroform-soluble substance present on the elytra. Elytra that had been washed in chloroform were not attractive to males, but their attractiveness was restored when painted with the chloroform extract. Thus it appears that male *A.bipunctata* recognize females by means of a pheromone present on their elytra. However, males downwind from a female do not respond to their presence from a distance. This indicates that the pheromone is not volatile but acts as a contact pheromone.

The glands in the elytra of other Coleoptera are known to produce defensive chemicals (Deroe & Pasteels, 1977), and a preliminary study of the elytra of *A.bipunctata* has revealed that there are many secretory pores opening on to the outer surface of the elytra and an abundance of glandular cells under the cuticle (Hemptinne & Pasteels, unpublished results). Thus, it is possible that the sex pheromone of females is produced by glands opening onto the outer surface of the elytra and not by the coxal glands as previously suggested (Hemptinne *et al.*, 1991).

For an understanding of the mechanisms governing predator behaviour it is necessary to determine the types of behaviour that maximize fitness. In the case of male ladybirds, the location of females is important and to sustain this activity males need to capture and consume relatively few aphids compared to the energy requirements of females. Thus when studying the predatory behaviour of ladybirds it is important to take their sex into consideration. Males are more likely to respond to aggregates of females than aggregates of aphids.

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