Entomol. exp. appl. **56**: 209–217, 1990.

The role of kairomones in prey finding by *Diomus* sp. and *Exochomus* sp., two coccinellid predators of the cassava mealybug, *Phenacoccus manihoti*

R. A. F. van den Meiracker,[1]* W. N. O. Hammond[2] & J. J. M. van Alphen[1]
[1] *Department of Population Biology, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands* [2] *Africa-wide Biological Control Programme, I.I.T.A., International Institute of Tropical Agriculture Oyo Road, PMB 5320, Ibadan, Nigeria* * *Present address: Research Institute For Plant Protection, P.O. Box 9060, 6700 GW Wageningen, The Netherlands*

Accepted: January 4, 1990

Key words: Diomus sp., *Exochomus* sp., *Phenacoccus manihoti,* prey finding, kairomone, kairomone preference, cassava

Abstract

We studied searching behaviour of *Diomus* sp., a coccinellid predator introduced into Africa as a natural enemy of the cassava mealybug, when searching on cassava leaves, and compared its behaviour with the searching behaviour of *Exochomus* sp., an African predator of mealybugs (MB's). Female adults of *Diomus* and *Exochomus* spent more time searching on cassava leaves previously infested with cassava MB than on clean cassava leaves, in response to substances produced by MB's (wax and/or honeydew) still present on these leaves as kairomones after removal of the MB's. Both species were also arrested by wax and/or honeydew of the citrus mealybug, *Planococcus citri.* When offered a choice between kairomones of both MB species only experienced *Diomus* (reared on cassava MB) showed a clear preference for kairomone of cassava MB. Separate influences of wax and honeydew were tested. Wax from cassava MB was an arrestment stimulus for both coccinellid species. Honeydew produced by cassava MB arrested *Exochomus* and inexperienced *Diomus.*

Introduction

The cassava mealybug, *Phenacoccus manihoti*, accidentally introduced from South America and discovered in Congo and Zaire in 1973, spread rapidly through about 70% of the African cassava belt and became the major pest on cassava, *Manihot esculenta* (Herren *et al.*, 1987). The South American parasitoid *Epidinocarsis lopezi* was released against this pest and is now established in at least 18 countries (Herren *et al.*, 1987, Neuenschwander & Herren, 1988). It persists through the wet season (when MB populations collapse due to heavy rainfall) and keeps MB numbers low during the dry season (Hammond *et al.*, 1987). Another introduced natural enemy was *Diomus* sp., a South American coccinellid predator of the cassava MB. *Diomus* was released in Nigeria together with *E. lopezi* early in the dry season and brought cassava MB population density even below the rainy season level (Herren & Lema, 1982). In contrast to *E. lopezi*, *Diomus* was not recovered next dry season (Hammond *et al.*, 1987).

To elucidate the factors determining this lack of success, prey searching behaviour of *Diomus* was studied. Hagen *et al.* (1976) divided the processes leading an adult predator to prey into four steps: 1. habitat selection, 2. prey finding, 3. prey acceptance and 4. prey suitability. Hammond, van den Meiracker and van Alphen (unpubl.) investigated whether the coccinellid uses olfactory cues in habitat selection. In this paper we report a study of the possible role of contact kairomones in prey location. Brown *et al.* (1970) defined kairomones as transspecific chemical messengers of adaptive benefit to the receiver rather than the emitter. After a predator has reached the proper habitat it may enhance the prey finding chance by intensifying search upon contact with chemicals produced by its prey or related with its presence. These chemicals are called arrestants if they slow or stop movements of the predator (Dethier *et al.*, 1960). Waage (1978) characterized the different arrestment responses kairomones elicit in parasitoids (or predators): a decrease in walking speed (orthokinetic response) or an increase in turning rate, which may be random in orientation (klinokinetic response) or directed (klinotactic response).

Wax and/or honeydew produced by the cassava MB might be used by *Diomus* as a kairomone. MB infested leaves are contaminated with wax and possibly with honeydew. We compared search times of the coccinellid on clean and on previously infested leaves and tried to separate responses elicited by wax and honeydew. To test the prey specifity of *Diomus*, we also studied whether it was arrested by wax and honeydew of the citrus mealybug *Planococcus citri*. For comparison with *Diomus* most of the experiments were replicated with *Exochomus* sp., an indigenous African polyphagous predator, member of the *E. flavipes* group. *Exochomus* is often the most important predator of cassava MB, and is common on cassava MB populations late in the dry season (Neuenschwander *et al.*, 1987).

Materials and methods

Cultures

Cassava: For cultures and experiments potted cassava plants were used. See for culturing details Nadel & van Alphen (1987).

Potatoes: Potatoes were potted and grown at 27 °C (24–29), 60% RH (45–80). When the shoots had reached a height of 15 cm, potatoes were harvested and washed. Roots and leaves were removed to prevent shoots from drying up.

Mealybugs: Cassava MB's were reared on potted cassava plants in perspex cages (70 x 70 x 50 cm) at 25 °C (22–27), 65% RH (55–75), 16L:8D (fluorescent lamps). The cultures were started in 1985 with egg masses acquired from the Commonwealth Institute of Biological Control laboratory in England. Plants were infested with egg masses, or crawlers were allowed to settle on them. When enough egg mass producing adults were present (4–5 weeks after infestation) plants were used for beetle cultures. Citrus MB's were collected in the botanical garden at the University of Leiden, and were reared on potato shoots in small plastic boxes (16 x 11 x 6 cm) at 26 °C (24–27) 38% RH (34–42), 14L:10D (fluorescent lamps).

Coccinellids: *Diomus* was acquired from mass rearing cultures at I.I.T.A., Ibadan, Nigeria, originating from a stock from South America. *Exochomus* was collected in experimental fields at I.I.T.A., Ibadan. Both species were reared on cassava MB's on potted cassava plants in small cages (40 x 30 x 30 cm) and on citrus MB's on potato shoots in small plastic boxes (16 x 11 x 16 cm) at 27 °C (24–29), 60% RH (45–80), 16L:8D (fluorescent lamps). *Exochomus* was able to reproduce on the aphid *Myzus persicae*, but beetles reared on this prey were not used in experiments. Experienced beetles were kept with MB's for at least 5 days. Inexperienced beetles were isolated as pupae and fed on honey when emerged. Before using them in experiments single beetles were starved for 24 h in empty 50 mm petri dishes. Only female beetles were used. Experiments were done at 25 °C.

Experiments

Series 1. Search times on clean cassava leaves and on leaves contaminated with cassava MB wax and/or honeydew. Infested leaves with MB's of all stages (including ovipositing adults) were taken from the cassava MB culture. Petioles were removed. MB's, egg masses and exuviae were removed with a wet brush, resulting in leaves with a thin layer of wax and some honeydew spread over the lower surface of the leaf. Clean leaves were taken from uninfested cassava plants. Single leaves were placed on the bottom of a 140 mm petridish with the lower surface facing upward.

At the start of each experiment a beetle was placed at the inside of the lid of the petri dish. Beetles not arriving at the edge of a leaf within 20 min were discarded. An experiment lasted 20 minutes after the first leaf contact. In this series search time was defined as the total time a beetle was present on a leaf (moving or not). After an experiment on one leaf type the beetle was placed in an empty 50 mm petri dish for 1 h and then used in an experiment with a leaf of the other type. Both leaves were always comparable in size and had the same number of leaflets. Equal numbers of beetles started on clean and contaminated leaves.

Series 2. Search times on clean cassava leaves and on leaves contaminated with citrus MB wax and/or honeydew. A slightly different set up was used in the second series of experiments. Circular patches of 29 mm diameter were punched out of clean cassava leaves, main veins dividing patches into equal parts (clean leaf patches). Leaves contaminated with a thin layer of citrus MB wax and honeydew were obtained by carefully rubbing MB's, egg masses and exuviae over the patches with a wet brush. Patches were placed in 50 mm petri dishes with the lower surface facing upward. At the start of an experiment a beetle was placed on a leaf patch. Experiments lasted 10 min. In this and the following series search time was defined as time spent walking on a leaf.

Series 3. Search times on cassava leaves contaminated with citrus MB wax and/or honeydew and on leaves contaminated with cassava MB wax and/or honeydew: choice experiment. In this series two leaf types were offered in a single experiment. Two adjacent half circular leaf patches were placed within 1.5 mm (experiments with *Diomus*) or 3 mm (for *Exochomus*) distance in a 50 mm petri dish, both halves forming a circular patch of 29 mm diameter. Originally cassava MB patches were prepared as in series 1 (removing MB's from infested leaves). Later cassava MB patches were prepared as in series 2 (rubbing MB's over patches). Citrus MB patches were always prepared as in series 2. Experiments lasted 10 min. Equal numbers of beetles started on either leaf type. These experiments were done between 20 and 30 times. If the beetle did not reach the second leaf patch, the experiment was discarded afterwards.

Series 4. Response in search time to cassava MB honeydew. The experimental set-up was similar to that of series 3 with a clean half circular leaf patch next to one treated with honeydew. Honeydew droplets were collected from the cassava MB cultures and dissolved in demineralized water. This solution was filtered and put on leaf patches, which were placed under a fan, allowing the water to evaporate.

Series 5. Response in search time to cassava MB wax. To test the response of the coccinellids to cassava MB wax alone, exuviae of cassava MB's (collected from the cultures) were rubbed over cassava leaf patches with a wet brush. Clean and wax contaminated patches were compared as in series 3.

Results

Series 1. Search times on clean cassava leaves and on leaves contaminated with cassava MB wax and/or honeydew. Diomus (inexperienced and experienced) and *Exochomus* (inexperienced and experienced) spent significantly more time on contaminated cassava leaves than on clean leaves (Fig. 1). Individual experienced beetles (of both species) always spent most time on contaminated leaves. For inexperienced beetles 10 out of 14 *Diomus* and 13 out of 14 *Exochomus* spent most time on contaminated leaves.

To test whether these coccinellids use olfactory cues from wax or honeydew on the contaminated leaves in short distance prey location, we compared the time required to reach a clean or a contaminated leaf from the start of the experiment (on the lid of the petri dish). Table 1 shows the results; no differences were found.

Figure 2 shows relative search times on different parts of a cassava leaf. Most of the time was spent on the leaf by walking along leaf edges and to a lesser extent along the main veins. Together they account for 75–97% of search time on average. Little time was spent in the interveinal area.

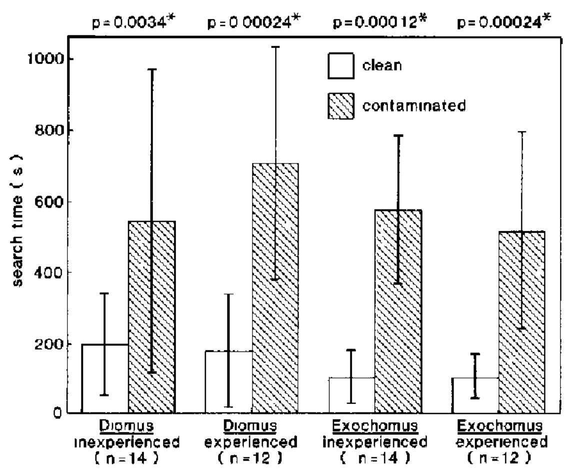

Fig. 1. Search times (s) on clean cassava leaves and on leaves contaminated with cassava MB wax and/or honeydew (series 1); p: one-tailed probabilities, Wilcoxon matched-pairs signed-ranks test; *: significantly different.

Series 2. Search times on clean cassava leaves and leaves contaminated with citrus MB wax and/or honeydew. Wax and/or honeydew of the citrus MB also arrested the coccinellids (Fig. 3). The mean search times show that experienced *Diomus* search longer on contaminated leaves than do inexperienced *Diomus*. Out of 20 experienced adult individuals of each species, 19 *Diomus* and 20 *Exochomus* spent most of their time on contaminated leaves as compared to 15 *Diomus* and 17 *Exochomus* out of 20 inexperienced individuals.

In *Diomus* 34 to 57% of search time was spent

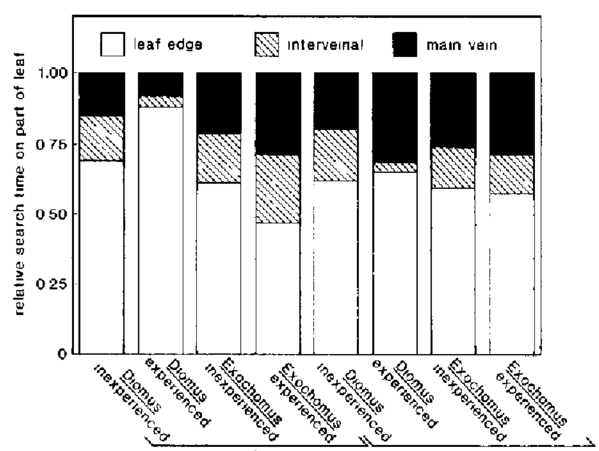

Fig. 2. Relative search times on different parts of a cassava leaf (series 1).

Table 1. Times (s) required to reach clean leaves and leaves contaminated with cassave MB wax and/or honeydew (series 1)

	N	Time required for clean leaves, mean (s.d.)	Time required for contaminated leaves, mean (s.d.)	P[1]
Diomus inexperienced	14	484.0 (399.6)	364.7 (328.2)	0.16
Diomus experienced	12	274.2 (225.5)	299.1 (263.9)	0.60
Exochomus inexperienced	14	211.1 (168.4)	305.3 (318.2)	0.71
Exochomus experienced	12	318.5 (300.0)	325.0 (290.0)	0.60

[1] One-tailed probabilities, Wilcoxon matched-pairs signed-ranks test.

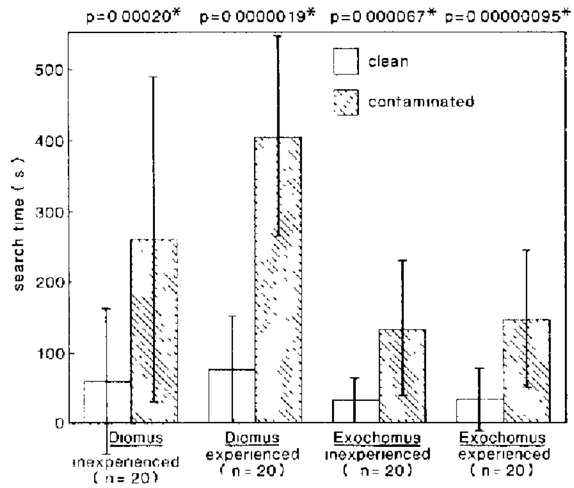

Fig. 3. Search times (s) on clean cassava leaves and on leaves contaminated with citrus MB wax and/or honeydew (series 2); p: one-tailed probabilities, Wilcoxon matched-pairs signed-ranks test; *, significantly different.

by walking along (artificial) leaf edges and the main veins on average (circular patches). In *Exochomus* this was 62 to 72%.

Series 3. Search times on cassava leaves contaminated with citrus MB wax and/or honeydew and on leaves contaminated with cassava MB wax and/or honeydew: choice experiment (Table 2). The first experiments were carried out with cassava MB infested leaves from the cultures and cassava leaves contaminated with citrus MB wax and/or honeydew just before the start of the experiments. Experienced *Diomus* reared on cassava MB spent more time on leaves with cassava MB wax and/or honeydew, thereby showing a preference for this prey. But inexperienced *Diomus* reared on cassava MB spent most time searching on leaves with citrus MB wax and/or honeydew. When leaves contaminated with cassava MB wax and/or honeydew were prepared in a similar way as leaves with citrus MB wax and/or honeydew no difference between both MB's was found.

Experienced *Exochomus* reared on cassava MB do not spend more time searching on leaves contaminated with cassava MB wax and/or honeydew than on leaves with citrus MB wax and/or honeydew However in 19 out of 27 replicates

Table 2. Search times (s) on cassava leaves contaminated with citrus MB wax and/or honeydew and on leaves with cassava MB wax and/or honeydew (series 3)

	N	Search time on leaves + ctr. MB wax/honeydew mean (s.d.)	Search time on leaves + csv. MB wax/honeydew mean (s.d.)	P[3]
Reared on cassava MB				
Diomus inexperienced[1]	18	254.8 (138.0)	125.6 (92.9)	0.0056*
Diomus inexperienced[2]	16	77.1 (64.4)	65.6 (45.7)	0.43
Diomus experienced[1]	16	142.1 (88.3)	194.4 (86.7)	0.018*
Exochomus experienced[2]	27	48.2 (36.2)	54.4 (36.2)	0.13
Reared on citrus MB				
Diomus inexperienced (fourth generation)[2]	17	118.8 (81.3)	120.1 (62.9)	0.93
Diomus experienced (first generation)[1]	16	108.4 (92.7)	103.0 (93.0)	0.90
Diomus experienced (fourth generation)[2]	21	106.0 (93.5)	97.3 (88.1)	0.84

[1] Leaf preparation: MB's removed from cassava MB infested leaf; citrus MB wax and/or honeydew put on clean cassava leaf.
[2] Leaf preparation: both cassava MB wax and/or honeydew and citrus MB wax and/or honeydew put on clean cassava leaves.
[3] Two-tailed probabilities, Wilcoxon matched-pairs signed-ranks test.
* Significantly different

Exochomus spent most time on leaves contaminated with cassava MB wax and/or honeydew (two-tailed probability = 0.052, sign test).

Results of experiments with *Diomus* reared on citrus MB are also presented in Table 2. Inexperienced and experienced *Diomus* (after 1 and 4 complete generations on citrus MB) showed no differences in search times between wax/honeydew of both species.

Series 4. Response in search time to cassava MB honeydew. Inexperienced *Diomus* reared on cassava MB were arrested by honeydew but experienced *Diomus* were not (Figure 4). Experienced *Exochomus* responded strongly to leaves treated with cassava MB honeydew.

Series 5. Response in search time to cassava MB wax. Experienced *Diomus* and *Exochomus* were arrested by cassava MB wax (Fig. 5).

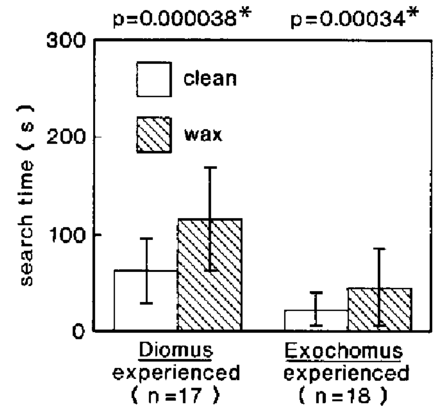

Fig. 5. Search times (s) on clean cassava leaves and on leaves with cassava MB wax (series 5); p: one-tailed probabilities, Wilcoxon matched-pairs signed-ranks test; *: significantly different.

Discussion

It is usually assumed that coccinellid larvae and adults are unable to detect their prey before actual physical contact (Hagen, 1962; Hodek, 1967). Coccinellid larvae often modify their searching behaviour after capturing prey, confining search to the immediate neighbourhood of discovery, thus increasing the chance finding another in a colony (Banks, 1957; Dixon, 1959; Marks, 1977). Evans (1976) found a similar switch in behaviour in adult anthocorids. Marks (1977) found that coccinellid larvae recognize plants previously searched unsuccessfully by detection of a chemical marker.

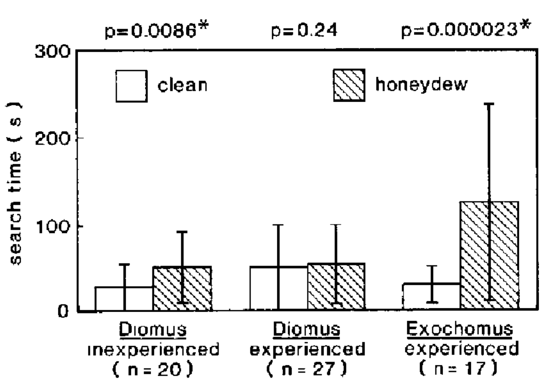

Fig. 4. Search times (s) on clean cassava leaves and on leaves with cassava MB honeydew (series 4); p: one-tailed probabilities, Wilcoxon matched-pairs signed-ranks test; *: significantly different.

However in some other studies it was shown that coccinellids larvae and adults use olfactory and visual cues in habitat selection and prey finding. Kesten (1969) found that adults of *Anatis ocellata* are attracted to aromatic substances of pine needles. *Stethorus punctum* is attracted to its prey *Panonychus ulmi* (Colburn & Asquith, 1970). Obata (1986) showed that *Harmonia axyridis* adults were visually attracted to the leaves of the host plants of its aphid prey, and were attracted to the odour of aphids, healthy leaves and especially aphid infested leaves. Adult *Diomus* are attracted to the odour of cassava MB infested leaves and only beetles with previous experience with MB's are attracted to the odour of MB's alone (Hammond, van den Meiracker & van Alphen, unpubl.). Stubbs (1980) made it plausible that adults of *Coccinella septempunctata* can detect aphids at short distance by sight. Their larvae detect crushed prey at short distance which might indicate olfactory detection. However Carter and Dixon (1984) considered this more likely to be the consequence of an arrestment response elicited by the haemolymph of the crushed prey. They found that *C. septempunctata* larvae spent more time searching in ears of wheat in the presence of honeydew than when no honeydew was present. This resulted in a better exploitation of their aphid prey.

In this study *Diomus* and *Exochomus* sp. were arrested on leaves by substances (wax and some honeydew) produced by cassava MB's previously present on these leaves. These substances were obviously used as kairomones. Both species were also arrested by substances produced by citrus MB's. The influences of wax and honeydew of cassava MB could be separated. Experienced *Diomus* was clearly arrested by wax alone, but arrestment by honeydew could not be demonstrated. This might increase searching efficiency, because wax and exuviae (carrying much wax) are found mostly on the lower surface of leaves where most of the MB's occur, while honeydew drops on the upper surface of leaves beneath. Inexperienced *Diomus* (fed on honey only, after emergence) spent more time searching on leaves with honeydew than on leaves without honeydew. It is difficult to tell whether they use honeydew as a cue for the presence of prey or if they search for honeydew to feed on (in the experiments only a very thin layer was present). *Exochomus* (experienced) responded to wax and responded strongly to honeydew. This response to honeydew might reflect a preference for aphids as assumed by Neuenschwander *et al.* (1987). Though it is unlikely that the honeydew used contained more than a small fraction of wax and vice versa, the way of collecting these substances does not exclude impurities.

Only when leaves with MB wax and/or honeydew of cassava MB and of citrus MB were offered to experienced *Diomus* (reared on cassava MB) a preference for cassava MB wax and/or honeydew was found. In the first choice series with inexperienced *Diomus* (reared on cassava MB) a preference for citrus MB wax/honeydew was found. A possible explanation of this unexpected result can be the way the leaves were contaminated with citrus MB wax and honeydew: MB's were taken from infested potato shoots on which, besides wax, probably a large amount of honeydew was present too. The lower surface of cassava leaves on the other hand is not likely to carry much honeydew. While inexperienced beetles have had no contact with MB's or their wax/honeydew, and were fed on honey, it is possible that the amount of honeydew on a leaf (of either species) plays a more important role than the kind of wax. Therefore leaves contaminated with cassava MB wax and/or honeydew were prepared in a similar way as leaves with citrus MB wax and/or honeydew in the second series to ensure that both leaf types contained wax and honeydew. In this series no difference was found. Neither *Diomus* reared on citrus MB, nor *Exochomus* did show, a clear preference. The results of this study do not support the assumption that *Diomus* is a specialist predator of the cassava MB. *Exochomus* probably feeds on a wide range of Homopterans, because it is also able to reproduce on the aphid *Myzus persicae*.

On plants larvae tend to follow the edges and prominent veins of leaves, where their prey is mostly found (Banks, 1957; Dixon, 1959; Dixon, 1970; Wratten, 1973). Both species we examined showed the same tendency. Searching along veins is advantageous to them since most cassava MB's are found on main and secondary veins (Nwanze *et al.*, 1979). This does not apply to leaf edges, but walking along edges might be elicited by the way the experiments were done. The coccinellids had the legs of one side on the leaf edge and the legs of the other side on the glass of the petridish while walking. In a natural situation they might show a less pronounced tendency to walk along leaf edges.

The observations that *Diomus* reacts to kairomones produced by both cassava and citrus mealybug, that it can be reared successfully on both prey species, and that it is similar in these aspects to the polyphagous *Exochomus*, as well as the observation that prey preference in *Diomus* can be modified by experience, are all evidence that *Diomus* is not a monophagous predator of cassava mealybug.

Both field and laboratory studies showed that *Diomus* responds to olfactory cues emitting from its prey. The lack of permanent establishment after introduction in South West Nigeria is tentatively explained by Hammond, van den Meiracker and van Alphen (unpubl.) by the inability of *Diomus* to find low density mealybug infestations as these occur during the wet season.

The results presented here suggest however that *Diomus* could survive the wet season by switching to other prey species. However, other mealybug species show similar low densities during the wet season as observed for Cassava MB (J. Noyes, pers. comm.).

Acknowledgements

We thank Peter Neuenschwander for his stimulating discussions, the Botanical Garden of the Leiden University for rearing of cassava cuttings provided by the Africa-wide Biological Control Programme, (International Institute of Tropical Agriculture) and Paul Brakefield for bringing to our attention some of the relevant literature on coccinellid searching behaviour. W.N.O. Hammond thanks I.I.T.A. for financing his research at Leiden University. The research for this publication was in part financed by the Netherlands Minister for Development Cooperation, who also shares copyright.

Zusammenfassung

Die Rolle von Kairomonen beim Auffinden der Beute von Diomus *und* Exochomus *sp., zwei coccinellide Raüber der Cassaveschmierlaus*

Das Suchverhalten auf Cassaveblätter des coccinelliden Raübers *Diomus*, eines aus Süd Amerika importierten natürlichen Feindes der Cassaveschmierlaus wurde studiert und verglichen mit dem Suchverhalten eines afrikanischen Räubers von Schmierläusen, *Exochomus* sp.. Weiblichen Adulten von *Diomus* un *Exochomus* verwendeten mehr Zeit auf Cassaveblätter wenn diese Blätter vorher mit Cassaveschmierläuse infiziert waren als auf uninfizierte Blätter, und gebrauchten Substanzen (Wachs und/oder Honigtau) die von Schmierläuse produziert wurden und nach der Entfernung der Schmierläuse auf die Blätter zugeblieben waren als Kairomonen.

Beide Arten wurden auch von Wachs und/oder Honigtau der Citrusschmierlaus, *Planococcus citri*, auf den Blätter arretiert. Wenn die Tiere wahlen könnten zwischen Kairomone der beiden Schmierlausarten wurden die Kairomonen der Cassaveschmierlaus nur von erfahrenen *Diomus*-Individuen, die auf Cassaveschmierlaüse aufgezogen wurden, bevorzugt.

Die Einflüsse von Wachs und Honigtau wurden separat geprüft. Wachs von Exuvien der Cassaveschmierlaus ist ein Arretierungsstimulus für beide Räuberarten. Von Cassaveschmierläusen produzierten Honigtau arretierte *Exochomus*- und unerfahrene *Diomus*-Individuen.

References

Banks, C. J., 1957. The behaviour of individual coccinellid larvae on plants. Br. J. Anim. Behav. 5: 12–24.

Brown, W. L., Jr., T. Eisner & R. H. Whittaker, 1970. Allomones and kairomones: transspecific chemical messengers. Bioscience 20: 21–22.

Carter, M. C. & A. F. G. Dixon, 1984. Honeydew: an arrestant stimulus for coccinellids. Ecol. Entomol. 9: 383–387

Colburn, R. & D. Asquith, 1970. A cage used to study the finding of a host by the ladybird beetle. *Stethorus punctum*. J. Econ. Entomol. 63: 1376–1377.

Dethier, V. G., L. B. Browne & C. N. Smith, 1960. The designation of chemicals in terms of the responses they elicit from insects. J. Econ. Entomol. 53: 134–136.

Dixon, A. F. G., 1959. An experimental study of the searching behaviour of the predatory beetle *Adalia decempunctata* (L.). J. Anim. Ecol. 28: 259–281.

Dixon, A. F. G., 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the sycamore aphid, *Drepanosiphum platanoides* (Schr.). J. Anim. Ecol. 39: 739–751.

Evans, H. F., 1976. The searching behaviour of *Anthocoris confusus* (Reuter) in relation to prey density and plant surface topography. Ecol. Entomol. 1: 163–169.

Hagen, K. S., 1962. Biology and ecology of predacious Coccinellidae. Ann. Rev. Ent. 7: 289–326

Hagen, K. S., S. Bombosch & J. A. McMurtry, 1976. The biology and impact of predators. In: C. B. Huffaker & P. S. Messenger (eds), pp. 93–142, Theory and Practice of Biological Control. Academic Press, New York.

Hammond, W. N. O., P. Neuenschwander & H. R. Herren, 1987. Impact of the exotic parasitoid *Epidinocarsis lopezi* on cassava mealybug (*Phenacoccus manihoti*) populations. Insect Sci. Applic. 8(4/5/6): 887–891.

Herren, H. R. & K. L. Lema, 1982. CMB – first successful releases. Commonw. Agric. Bur., Biocontrol News and Information 3: 1.

Herren, H. R , P Neuenschwander, R. D. Hennessey & W. N. O. Hammond, 1987. Introduction and dispersal of *Epidinocarsis lopezi* (Hym., Encyrtidae), an exotic parasitoid of the cassava mealybug, *Phenacoccus manihoti* (Hom., Pseudococcidae) in Africa. Agric. Ecosystems Envir. 19: 131–144.

Hodek, I., 1967. Bionomics and ecology of predaceous Coccinellidae. Ann. Rev. Ent. 12: 79–104.

Kesten, U., 1969. Zur Morphologie und Biologie von *Anatis ocellata* (L.) (Coleoptera: Coccinellidae). Z. Angew. Entomol. 63: 412–445.

Marks, R. J., 1977 laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae Bull. Ent. Res. 67: 235–241.

Nadel, H. & J. J. M. van Alphen, 1987. The role of host- and host-plant odours in the attraction of a parasitoid, *Epidinocarsis lopezi*, to the habitat of its host, the cassava mealybug, *Phenacoccus manihoti*. Entomol. exp. appl. 45: 181–186

Neuenschwander, P., R. D. Hennessey & H. R. Herren, 1987. Food web of insects associated with the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), and its introduced parasitoid, *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae), in Africa. Bull. Ent. Res. 77: 177–189.

Neuenschwander, P. & H. R. Herren, 1988. Biological control of the cassava mealybug, *Phenacoccus manihoti*, by the exotic parasitoid *Epidinocarsis lopezi* in Africa. Phil. Trans VR. Soc. Lond B 318: 319–333.

Nwanze, K. F., K. Leuschner & H. C. Ezumah, 1979. The cassava mealybug, *Phenacoccus* sp. in the Republic of Zaire Pans 25: 125–130.

Obata, S., 1986. Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Entomophaga 31: 303–311.

Stubbs, M , 1980. Another look at prey detection by coccinellids. Ecol Entomol. 5: 179–182.

Waage, J K., 1978. Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. Physiol. Entomol. 3: 135–146.

Wratten, S. D., 1973. The effectiveness of the coccinellid beetle *Adalia bipunctata* as a predator of the lime aphid, *Eucallipterus tiliae* L. J. Anim. Ecol. 42. 785–802.