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Dispersal and functional response of *Uscana lariophaga* in two different habitats: stored cowpea pods and seeds

Frans A. N. VAN ALEBEEK[1,2], Kwaku Kyei ANTWI[1,3], Arnold VAN HUIS[1], Joop C. VAN LENTEREN[1]
[1]*Laboratory of Entomology, Wageningen University, The Netherlands*
[2]Present address: *Applied Plant Research (PPO), Wageningen University and Research, Lelystad, The Netherlands*
[3]Present address: *Plant Protection and Regulatory Services Department, Ministry of Food and Agriculture, Accra, Ghana*

Abstract

The effect of two different habitats, stored cowpea [*Vigna unguiculata* (L.) Walpers] pods and seeds, on the dispersal and functional response of *Uscana lariophaga* Steffan (Hymenoptera Trichogrammatidae) was investigated, with *Callosobruchus maculatus* (F.) (Coleoptera Bruchidae) eggs as hosts. In the presence of directional light from the top, parasitoids moved faster through columns filled with pods than through columns (either filled with pods or seeds) in darkness. The different habitats, seed or pods, did not have a significant effect on dispersal. The maximal dispersal rate of colonising *U. lariophaga* females may be up to several meter per day, and median net displacement rates are around 0.5 - 0.8 m per 24 h. The functional response of *U. lariophaga* could be described by Rogers (1972) random parasitoid equation as a Holling Type II curve and resembles the ones found in earlier experiments. At host densities below 40 eggs per cluster, *U. lariophaga* was more efficient at finding host eggs in a seed habitat than in a pod habitat, probably due to area restricted searching behaviour after oviposition. At higher host densities, *U. lariophaga* becomes egg limited, and neither walking behaviour nor the habitat structure significantly influence her foraging success.

Key words: *Callosobruchus maculatus*, *Vigna unguiculata*, West Africa, biological control, egg parasitism, foraging behaviour.

Introduction

Much of the agricultural activity in West Africa is devoted to subsistence farming. An important crop for such farmers is cowpea, *Vigna unguiculata* (L.) Walpers. Most cowpea is grown in West Africa, which is probably also the region where it was first cultivated (Padulosi and Ng, 1997). Cowpea is relatively tolerant to drought, and it can produce relatively well under nitrogen-poor conditions due to nitrogen binding, symbiotic nodule bacteria that occur in the roots (Summerfield *et al.*, 1974; Turk *et al.*, 1980). Apart from the seeds, young pods and leaves are eaten, and leaves and stems are used as animal feed and green manure (Duke, 1990). Unfortunately, cowpea is often infested by two or three species of bruchid beetles (Coleoptera Bruchidae) (Singh *et al.*, 1990). These beetles oviposit on the ripening pods in the field. Hatching larvae penetrate the pod wall and enter a seed, where they develop up to pupation. The adult emerges through a "window" in the seed. One of these bruchids, *Callosobruchus maculatus* (F.) (Coleoptera Bruchidae), is well adapted to storage. Emerging females from stored pods taken from the field continue to oviposit on pods or seeds during storage in the granary. *C. maculatus* is the only serious storage pest of cowpea, but it is generally very destructive and can result in complete loss of cowpea in individual granaries (Caswell, 1981). At the end of the storage season it is hard to find undamaged cowpea at local markets, while the few compea stocks that are then still not so seriously infested may have been treated with potentially unsafe pesticides.

Many traditional methods have been aimed at prevention or control of *C. maculatus*, but their reported efficacy often seems to be limited (Stolk, 2002), though extracts of African plants may offer an acceptable degree of protection (Boeke *et al.*, 2001; 2004). Another promising option might be biological control of this pest. In West Africa, *C. maculatus* is attacked by a number of natural enemies both in the field and in storage (van Huis, 1991 and van Huis *et al.*, 2002). These naturally occurring parasitoids are responsible for substantial mortality of *C. maculatus*. The indigenous egg parasitoid *Uscana lariophaga* Steffan (Hymenoptera Trichogrammatidae) has been identified as the most important mortality factor for *C. maculatus* eggs in the field (Sagnia, 1994). In addition, during a survey in Niger, egg parasitism by *U. lariophaga* was found in 69% of all granaries, with parasitism percentages of up to 73% (van Alebeek, 1996). These findings resulted in the idea to develop a conservation strategy of biological control with this egg parasitoid.

In order to evaluate the suitability of the egg parasitoid *U. lariophaga* for conservation biological control of bruchid pests in stored cowpea in West Africa (Stolk *et al.*, 2001; van Huis *et al.*, 1990; 1992; 1998; van Huis, 1991) we investigated the functional response of *U. lariophaga* to different densities of its host, *C. maculatus* in cowpea stock (van Alebeek *et al.*, 1996a). This functional response could satisfactory be described by Rogers (1972) random parasitoid equations as a Holling Type II functional response. The parasitoid *U. lariophaga* appeared egg-limited in the maximum number of hosts she could parasitise in a given amount of time, and demonstrated a strong aggregative response (van Alebeek *et al.*, 1996a). Subsequently, we investigated the effect of different *C. maculatus* egg distributions within host clusters on the functional response of *U. lariophaga* females. *U. lariophaga* females found significantly fewer eggs in low density clusters with a random egg distribution than in clusters with an even or clumped host distribution (van Alebeek *et al.*, 1996b). The egg parasitoid searches predominantly by walking (van Huis *et al.*, 1994). Analysis of *U. lariophaga* walking behaviour on cowpea seeds revealed that female wasps demonstrated area restricted search just after parasitisation (van Alebeek and van Huis, 1997). This may reflect adaptation to bruchid egg distribution patterns under field conditions, which is clustered at the plant and pod level (Huignard *et al.*, 1985; Germain *et al.*, 1987).

In West Africa, traditional cowpea storage in granaries is either as pods or, after threshing, as loose seeds in bags. Cowpea storage in pods provides some protection against bruchids, because the pod wall acts as a physical and chemical barrier to the first instar bruchid larva drilling in from the egg (Caswell, 1973; 1984; Kitch *et al.*, 1991). The storage habitat is a special kind of environment with discrete units (pods or seeds). The spatial structure of cowpea stored as pods is different from that of cowpea stored as seeds. In pods, there are fewer contact points between units and air spaces are relatively large compared with storage as seeds. Habitat structure and variation within habitats is known to have significant effects on pest populations (Margolies, 1993). Leaf morphology and structure (e.g. hairiness) are known to affect the effectiveness of natural enemies (Dicke, 1998). However, relatively little research has been undertaken to compare the effects of different habitat structures on the foraging behaviour and success of natural enemies, although significant effects have been found in some parasitoids (e.g. Thorpe, 1985; Casas, 1991).

In this article we report on the effect of different storage habitat structures (i.e. cowpea stock as pods and as seeds) on *U. lariophaga* foraging behaviour, measured as her dispersal abilities and her functional response to different host densities.

Materials and methods

General

Details on the rearing and origin of *C. maculatus* and *U. lariophaga* are given in van Alebeek *et al.* (1996a). All wasps used in the experiments were 0-16 h old, mated and fed with honey. One hour before the experiment, individual females were given an oviposition experience on a fresh *C. maculatus* egg. All experiments were carried out at 30 ± 1 °C.

Cowpea seeds were of the Black-eye variety from California. Cowpea pods were of variety TVx 3236, and obtained from Niger. Pods with eggs from host clusters in the functional response experiments were intact; the surrounding mass of pods to fill up the containers contained a fraction of broken and split pods.

Dispersal studies

Opaque PVC cylinders of 5 l (diameter 22 cm, height 20 cm) were filled with either cowpea pods or cowpea seeds. Our observations indicate that *U. lariophaga* females are negatively geotactic and tend to move upwards (van Alebeek *et al.*, 1996a). Furthermore, wasps are attracted and arrested by volatile cues from *C. maculatus* eggs (Van Huis *et al.*, 1994; Ormel *et al.*, 1995). Therefore, wasps were released at the bottom of a column, and their arrival at an odour bait on top of the column was monitored. At the bottom of each column, a small glass tube was placed with 10 *U. lariophaga* females. This tube was closed with a cork which could be pulled from outside by means of a thread, at the start of an experiment. The top of each cylinder was closed with a glass plate, with a central hole (diameter 2 cm). Over the hole in the glass plate, an odour bait was placed to attract the wasps. This bait consisted of approximately 60 *C. maculatus* eggs (20 h old) on 10 cowpea seeds in a small polyamine gauze bag. The bag was covered by a petri dish lid. The underside of the glass plate was covered by a layer of insect-glue (Soveurode Aérosol, Sovilo, Siegfried, Switzerland). Glass plates were changed every hour after wasp release, and the wasps trapped in the glue were counted.

Three columns were used: one filled with seeds and standing in total darkness, and two columns filled with pods; one in total darkness and one standing in the light. This allows for comparison of two treatments: movement through pods and through seeds (both in the dark), and movement through pods in the light and in the dark. Since column walls were opaque, only light coming from above through the glass cover could penetrate the column filled with pods standing in the light. Light intensity at the pod column top level was 750 Lux; light intensity at 5 cm depth within the pod column was 6 Lux. Penetration of light in a column filled with seeds was very poor (0.2 Lux at 5 cm depth), and therefore this treatment was omitted.

Accumulated numbers of wasps trapped on top of each column (13 replicates for each type of column) were compared between treatments and, based on arrival times, maximum and median net displacement rates were calculated.

Functional response studies

Experimental units

Plastic containers of 5 l (diameter 24 cm, height 18 cm), filled with clean cowpea seeds or pods and placed in total darkness, were used as experimental units (van Alebeek *et al.*, 1996a). A gelatine capsule containing one *U. lariophaga* female was placed in the centre of a container. The capsule could be opened with threads from outside, to release the wasp in the stock. A single host cluster was situated directly above the release site in the stock. Wasps were allowed to search and parasitise for 4 h, after which the host clusters were recovered. This period was equal to earlier experiments and allows females to spent approximately their initial egg load, without over-exploitation of host clusters due to multiple visits (van Alebeek *et al.*, 1996a; 1996b).

Host clusters

In each container, one host cluster was offered to the parasitoid. For the comparison of two habitat types (pods and seeds), we aimed at host clusters with identical surface areas, i.e. the same number of eggs per square centimetre. The surface of cowpea seeds was approximated by considering them as a cylinder with a half sphere at both ends. The length, largest and smallest diameter of 50 California Black-eye seeds were carefully measured, giving a mean surface area of 2 ± 0.3 cm^2 per seed. Pods were considered as long cylinders with a cone at both ends. The length, largest and smallest diameter of 50 pods from Niger were measured, giving a mean surface of 25 ± 5 cm^2 per pod. Based on these measurements, a host cluster of 65 seeds has approximately the same surface area as a cluster of 5 pods.

In containers filled with seeds, host clusters consisted of small polyamine gauze bags, filled with 65 cowpea seeds carrying fresh *C. maculatus* eggs (20 h old). In containers filled with pods, host clusters consisted of 5 cowpea pods, marked with a felt tip pen at one end for easy recovery. The total volume of a seed cluster was estimated by wrapping 65 seeds into thin plastic foil and immersing them in a known volume of water. The measured volume includes the air spaces between seeds. The total volume of a 65 seed cluster was 20 cm^3. The average volume of a 5 pod cluster was 71 cm^3 (air spaces included), and was estimated by measuring the total volume of 300 pods in an experimental container.

The exact number of eggs per cluster was variable, and was determined at the end of the experiment. In each replicate, host densities aimed at were 4, 8, 16, 32, and 64 *C. maculatus* eggs per cluster, although in reality the whole range of 1-85 eggs per cluster was covered. Upon recovery from the experimental units, host clusters were incubated in glass tubes until, 4-5 days later, parasitised eggs coloured black and were counted. One full combination of treatments was carried out twice a week, until 40 replicates were obtained.

Because of the amount of cowpea seeds and pods involved, seeds and pods were re-used throughout the experiment. In between replicates, seeds and pods were kept in a clean oven at 45 °C for 48 h. As a result of this, we expect to have removed possible volatiles left by bruchid egg clusters or walking parasitoids. Due to frequent handling in the course of the experiment, the fraction of split and broken pods increased from about 5% to approximately 50%. Before each experiment, loose seeds were removed from containers filled with pods.

Analysis

Percentages of hosts clusters found (i.e. with one or more egg(s) parasitised) were calculated over different host cluster sizes. Clusters without any parasitism can be considered as clusters that were not visited (not found) by a parasitoid. We analysed the functional response data for visited clusters only (i.e. clusters with at least one egg parasitised) (van Alebeek *et al.*, 1996a). Clusters without parasitism are presented in figure 1 and table 1,

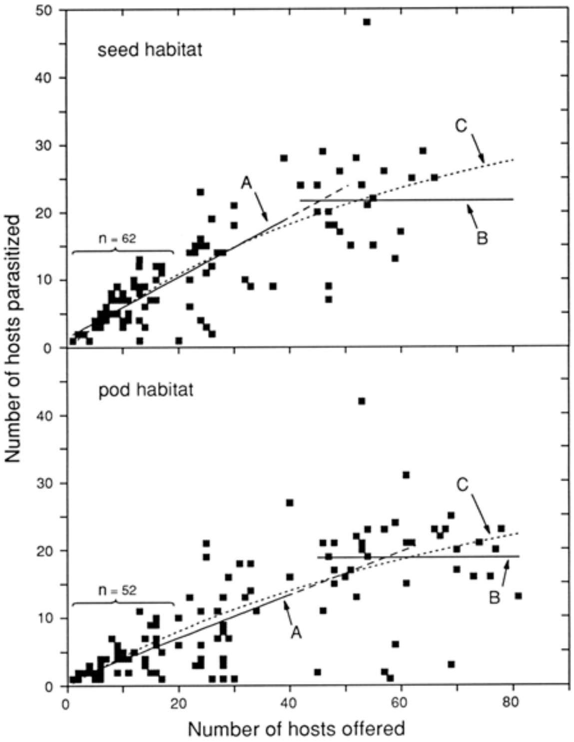

Figure 1. Functional response of *U. lariophaga* to different egg densities of *C. maculatus* in a seed habitat and in a pod habitat. Regression lines (A and B) assume a Type I functional response; curves C were fitted with Rogers (1972) random parasite equation (a Type II response). Details of regression lines, curves and parameters are given in table 1.

Table 1. Variables and correlation coefficients for the regression lines and Rogers (1972) random parasitoid equation curves fitted on the functional response data given in figure 1.

line	seed habitat	pod habitat	description of lines and curves
A	$y = 0.44 \times x + 1.50$ $R^2 = 55.4\%$ $p < 0.001$ $n = 86$ ($x < 40$)	$y = 0.32 \times x + 0.76$ $R^2 = 40.9\%$ $p < 0.001$ $n = 79$ ($x < 40$)	linear regression over low densities (Type I)
B	$y = 21.7$ (± 8.0) $n = 24$ ($x \geq 40$)	$y = 18.8$ (± 8.3) $n = 44$ ($x \geq 40$)	plateau level, mean over high densities (Type I)
C	$a = 0.27$ (± 0.06) $Th = 0.07$ h (± 0.02) $R^2 = 66.3\%$ $F = 357$, $df = 109$	$a = 0.16$ (± 0.04) $Th = 0.08$ h (± 0.03) $R^2 = 55.3\%$ $F = 254$, $df = 122$	Rogers random parasite equation (Type II), non-linear least squares regression
zero's	$n = 85$	$n = 77$	excluded from the analysis

y = number of hosts parasitised; x = number of hosts offered; R^2 = coefficient of determination; p = chance of regression coefficient being equal to 0; n = number of data points; a = attack rate in cm^2/s; Th = handling time in h; F = F-value from the ANOVA; df = degrees of freedom.

but have been ignored in the regressions. Linear and non-linear regression were applied, as models of a Holling Type I and Type II functional response respectively (van Alebeek *et al.*, 1996a). Rogers (1972) random parasitoid equation for host depletion over time was chosen as an appropriate model. The attack rate (*a*) and the handling time (*Th*) from Rogers random parasitoid equation were calculated by least squares non-linear regression using Statgraphics software (see also: van Alebeek *et al.*, 1996a). Equality of slopes of linear regression lines was tested with an ANOVA followed by comparison of regression coefficients, and plateau levels were compared with a GT2-test (Sokal and Rohlf, 1981).

Results

Dispersal studies

Wasps came out faster in the light than in the dark, from columns filled with pods (figure 2). In total darkness, up to 7 h after release, the number of wasps recovered was the same for columns filled with seeds and pods. Using accumulated numbers of wasps arriving (13 replicates), significant differences between columns were found (Kruskal-Wallis one-way ANOVA, KW = 19.3, df = 1, 231, $p < 0.001$). Significantly more wasps arrived from the column in the light filled with pods than from both columns in darkness filled with seeds and pods (Kruskal-Wallis multiple comparison, $\alpha < 0.05$). There was no significant difference in total arrivals between pods and seeds in darkness.

The maximum net displacement rate is the speed of the first wasps arriving on top of the 20 cm column. Displacement rates can only be (under)estimated based on the hourly observations. The first wasps were observed one hour after release, giving an estimated net displacement rate of 5.56×10^{-5} m/s, both for seed and pod columns. This is equivalent to 4.8 m/day or approximately 0.14 bodylength/s. Real distances covered will be larger because of the tortuous walking path within the cowpea stock, and actual walking speed within the seed and pod mass will also be higher. Based on 50% recovery of the wasps, we can calculate median net displacement rates also. With median arrival times of 6, 8 and 9 h in pods in light, pods in darkness and seeds in darkness respectively (figure 2), median net displacement rates are 0.93, 0.69 and 0.62×10^{-5} m/s respectively.

Functional response experiments

Host clusters with higher numbers of eggs tend to have a higher chance of being found by *U. lariophaga* females than smaller clusters (table 2). The overall percentage of clusters found was the same for the pod and seed habitat ($X^2 = 1.0$, $p > 0.25$). Although wasps were released directly under the host cluster, 41% of the host clusters did not show any trace of parasitism.

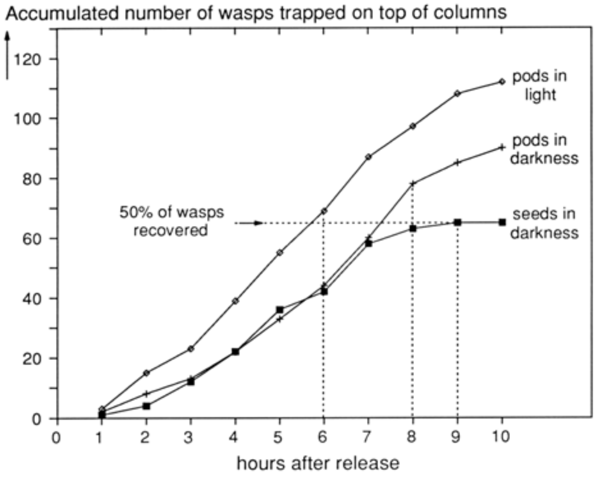

Figure 2. Cumulative number of *U. lariophaga* wasps arriving at top of a column filled with either cowpea seeds or pods (in light or in darkness) in the first 10 hours after release. Total of 13 replicates (130 wasps per treatment). Vertical lines indicate median arrival times.

Table 2. The percentage of host clusters showing egg parasitism by *U. lariophaga* in a seed and in a pod habitat, at various host egg densities per cluster.

No. host eggs	seed habitat		pod habitat	
per cluster	% paras.	n	% paras.	n
1 - 5	37.8	45	55.6	27
6 - 9	50.0	32	48.3	29
10 - 20	72.5	40	55.6	45
21 - 35	53.7	41	64.1	39
36 - 70	70.3	37	76.0	50
71 - 100	--	--	63.6	11
total	56.4 a	195	61.5 a	201

a: Overall percentages parasitism are not significantly different ($\chi^2=1.0$, $p>0.25$).

The functional response of *U. lariophaga* females in visited clusters can be described by a Type II Rogers' curve (figure 1, table 1, line C). Below 40 eggs per cluster, a Type I linear regression can also be fitted, as a tangent of the Rogers curve (figure 1, line A). The regression coefficient of this line is the average level of parasitism in clusters of less than 40 host eggs (table 1, line A). The parasitisation level over this range is significantly higher in seed clusters (44%) than that in pod clusters (32%) (ANOVA, F =1 2.8, df = 1, 160, $p < 0.001$).

Based on *U. lariophaga* limited egg load (Van Alebeek *et al.*, 1996a), a plateau level was calculated over host densities above 40 eggs per cluster (line B, figure 1 and table 1). Plateau levels were the same in the seed and pod habitat (table 1). At densities above 40 eggs per cluster, the Rogers curves continue to increase, which is not realistic in view of *U. lariophaga* limited egg supply.

Discussion

Dispersal rates

Vertical dispersion of natural enemies of stored product pests, in order to locate loci of infestations in bulk masses, is a prerequisite for successful biological control in storage systems. Movements of pest through stored wheat was investigated extensively by Surtees (e.g. 1964; 1965), and dispersal also was a topic in several aeration and modified atmosphere studies (e.g. Navarro *et al*., 1981; Armitage *et al*., 1983; Adler, 1992). However, if net displacement rates were measured in any of these studies, it usually was over relatively long time intervals.

The predatory bug *Xylocoris flavipes* Reuter (Hemiptera Anthocoridae) successfully penetrated a 2.6 m column with wheat within 2 months after release (Press *et al*., 1979). The larval parasitoids *Anisopteromalus calandrae* (Howard) and *Choetospila elegans* Westwood (Hymenoptera Pteromalidae) penetrated a 2.2 m column with wheat and located hosts within 7 days after release (Press, 1992). *A. calandrae* moved predominantly upwards and, if released on top, remained near the wheat surface (Press, 1988). The egg parasitoids *Trichogramma pretiosum* Riley and *Trichogramma evanescens* Westwood (Hymenoptera Trichogrammatidae), when released on top of a wheat mass, parasitised lepidopteran eggs up to 20 and 55 cm depth respectively in 6 days (Brower, 1990; Schöller *et al*., 1994). *Eupelmus vuilleti* (Crawford) (Hymenoptera Eupelmidae), a larval parasitoid of bruchids in stored cowpea, predominantly moved upwards in an uninfested cowpea column. This parasitoid located hosts over 77 cm within 48 h after release, and did so more efficiently in the upward direction than downwards (Cortesero, 1994).

The time intervals in the studies cited above do not allow for precise estimates of displacement rates through bulk masses. Based on the maximum displacement rates in our experiments (20 cm/h), colonising *U. lariophaga* could cover distances of several meters in one day. This is more than the internal diameter of traditional West African cowpea granaries.

Dispersal and habitat structure

Few studies investigated the effect of habitat structure on dispersal and foraging behaviour of insect pests and their natural enemies; some examples can be found in Boethel and Eikenbarry (1986). Many reports aim at a description of spatial patterns of parasitism in one type of habitat (Walde and Murdoch, 1988), but few compare different habitats and their effect on spatial distributions.

At the herbivore level, Jones (1977) demonstrated that the spatial pattern of host plants influenced the oviposition pattern of *Pieris rapae* (L.) butterflies. The patchiness of the habitat and the number of host plants in the habitat may have an effect on prey and predators dispersal behaviour, and so can strongly influence the outcome of predator - prey population interactions (e.g. Kareiva, 1987; Nachman, 1987). In habitats where plants are touching or connected, and prey and predators can more easily disperse, overall population interactions become more stable (Sabelis *et al*., 1983; Nachman, 1987). In *C. maculatus* and *Callosobruchus chinensis* (L.), the effect of body size and of legume seed size on the ability of the bruchids to penetrate a column of seeds was investigated (Watanabe, 1984; 1985; 1986). In columns with larger seeds (relative to bruchid body size) dispersion was more easy. Smaller bruchid individuals also dispersed more easily than large individuals (Watanabe, 1984; 1985; 1986).

For parasitoids, the spatial structure of the habitat also interacted with foraging behaviour in some studies. The height of host clusters within a habitat significantly influenced parasitisation rates of *Trichogramma minutum* Riley and *T. pretiosum*, and indications were found that habitat type (soybean fields versus natural vegetation) influenced parasitism by *T. minutum* (Thorpe, 1985). The spatial architecture of fruit trees appears to influence spatial patterns of parasitism in the leafminer parasitoid *Cirrospilus vittatus* Walker (Hymenoptera Eulophidae) (Casas, 1990; 1991).

In the present study, in total darkness, *U. lariophaga* movement in a pod habitat was not significantly different from movement in a seed habitat. Body size in *U. lariophaga* is so small (0.4 mm) relative to cowpea pod and seed size, that dispersal will not be hampered by body size constraints. In a pod habitat, the number of recovered wasps in the light was significantly higher than recovery in darkness. Thus, the effect of light on dispersal (positive phototaxis) is stronger than any possible effect of different habitat types. Probably, our number of replicates is insufficient to demonstrate significant differences in number of wasps arriving from pods and seeds in the dark. Arrival of wasps in darkness was the same for seed and pod columns until 7 h after release. From then onwards, it appears as if there is a difference between the two habitats (figure 2) (although numbers are too small to be significant). One can hypothesise that there are two groups of wasps with different behaviour. One group is not actively searching for hosts, and moves upwards to leave the column. This movement rate is apparently the same in a pod as in a seed habitat. A second group of wasps may be actively searching for hosts in the columns. They move more slowly, and arrive later at top of the column. For these wasps, foraging in seeds may be different from foraging in pods, as figure 2 suggests.

Habitat structure and functional response

The percentage of host clusters without parasitism (41%) is surprisingly high, in spite of the fact that wasps were released directly below the clusters. We have not been able to identify the causes for this result. The chance of clusters being parasitised appears to be related to the number of host eggs in a cluster, a result contrary to earlier findings (van Alebeek *et al*., 1996a). Possibly, such an effect is detectable only when foraging time is limited to 4 h, as in the current experiments, and is obscured when parasitoids can search for longer periods (e.g. 24 h, as in: van Alebeek *et al*., 1996a).

If clusters without parasitism are left out of the analysis and linear regression is applied over clusters of less than 40 eggs, a significant difference is found between seed and pod clusters. Seed clusters have higher rates of parasitism (44%) than pod clusters (32%) (table 1, line A). Rates of parasitism are substantial lower than results from earlier experiments (van Alebeek *et al*., 1996a; 1996b).

The fact that dispersal did not differ in a pod and a seed habitat but that parasitism within clusters with eggs does so, may result from area restricted search by *U. lariophaga* females after oviposition. In the dispersal studies, no hosts were present in the columns and parasitoids did not demonstrate area restricted search. In the functional response experiments, upon the first parasitisation of a host in a cluster, the walking track will show more turns over larger turning angles, and as a result wasps will remain longer on one unit (pod or seed) compared with parasitoid behaviour before first host contact (van Alebeek and van Huis, 1997). In the seed clusters, host eggs are on average more close together (seed cluster volume is smaller than pod cluster volume, for equal surface area), and seeds share many contact points facilitating walking from one seed to the next. Thus, the chance of finding a next host egg is relatively large. Contrary, in pods, eggs are more widely apart (larger cluster volume), and pods share relatively few contact points where wasps can change from one pod to the next pod. Thus, area restricted search may result in a lower chance to find eggs on other pods, and thus in wasps leaving a pod cluster early, when part of the available host eggs are still unexploited.

Conclusion

In summary, *U. lariophaga* can find host clusters equally well in a seed as in a pod habitat. Colonising females move at rates as high as 4.8 m per day. Since foraging *U. lariophaga* females are attracted to host clusters by volatile host odours from distances of at least 5-10 cm (van Huis *et al.*, 1994; Ormel *et al.*, 1995), *U. lariophaga* could well cover the volume of stored cowpea in traditional granaries, and locate host clusters therein.

Within host clusters, *U. lariophaga* appears more efficient at finding eggs in seeds than in pod clusters (over host densities below 40 eggs per cluster). This is probably due to area restricted searching behaviour after oviposition. Since median host densities in West African cowpea granaries are often well above 40 eggs per 100 seeds (van Alebeek, 1996), in practice a reduced searching efficiency in pods will be of limited importance. At higher host densities, *U. lariophaga* becomes egg limited, and neither walking behaviour nor the habitat structure will significantly influence her foraging success.

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Authors' addresses: Joop C. VAN LENTEREN (corresponding author, Joop.vanLenteren@wur.nl), Frans A. N. VAN ALEBEEK[1], Kwaku Kyei ANTWI[2], Arnold VAN HUIS, Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands.

[1] Present address: Applied Plant Research (PPO), Wageningen University and Research, P.O. Box 430, 8200 AK, Lelystad, The Netherlands.

[2] Present address: Plant Protection and Regulatory Services Department, Ministry of Food and Agriculture, P.O. Box M37, Accra, Ghana.

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