

The functional response of *Uscana lariophaga* Steffan (Hym.: Trichogrammatidae) under different egg distributions of its host *Callosobruchus maculatus* L. (Col.: Bruchidae)

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Abstract

Callosobruchus maculatus is an important pest of stored cowpea (*Vigna unguiculata* Walp.) in West Africa. The egg parasitoid *Uscana lariophaga* is under investigation as a potential biological control agent.

The parasitoid's functional response was tested under random, even and clumped distributions of *C. maculatus* eggs in a three-dimensional cowpea stock. At different host densities, *U. lariophaga* showed a functional response resembling a Holling Type II, or III curve. The decrease in the percentage parasitisation at higher host densities is due to egg limitation of the parasitoid, and not an effect of increased total handling time.

The chance of a patch being found by an *Uscana* female was positively correlated with the number of host eggs within a patch. Apparently, *U. lariophaga* females are able to assess egg odour concentration differences.

Within a host patch, *Uscana* females showed a strong arrestment response, and continued to search until (almost) all eggs had been parasitised or until their egg load was depleted.

These results imply that *U. lariophaga* can have a strong impact on its host populations.

Introduction

Cowpea (*Vigna unguiculata* Walp.) is an important protein source for small-scale farmers and their families in West Africa. The seed beetles *Bruchidius atrolineatus* (Pic.) and *Callosobruchus maculatus* (Fab.) (Coleoptera: Bruchidae) infest cowpea pods in the field and subsequently cause serious losses in storage (Jackai and Daoust 1986). Surveys of cowpea in markets and in village stores in West Africa have demonstrated that heavy losses due to bruchids (up to 100% of the beans attacked) are common (Caswell 1970, 1974).

The bruchid larvae develop inside the seeds, protected against most control measures. A number of traditional protective measures for stored cowpea are being used (e.g. Sagnia and Schütte 1992), but their effectiveness remains to be proven. Chemical control of these pests does not seem feasible for farmers in the Sahel region, because of a lack of necessary resources, and a poorly developed infrastructure. Other methods, such as biological control, seem more appropriate (van Huis 1991).

In West Africa, the egg parasitoid *Uscana lariophaga* Steffan (Hymenoptera: Trichogrammatidae) parasitises on fresh bruchid eggs, both in cowpea fields and stores. Egg parasitism of *C. maculatus* eggs by *Uscana* spp. in cowpea fields

ranged from 25% to 60% (Lammers and van Huis 1989; Huignard et al. 1985). In experimental cowpea granaries in Niger, Lammers and van Huis (1989) reported 60% of all bruchid eggs parasitised; Monge et al. (1991) reported 58% for *C. maculatus* eggs.

The conservation strategy for biological control of bruchids with *U. lariophaga* (van Huis et al. 1990) aims at increasing the impact of the indigenous natural enemies on the development of bruchid populations. This may be achieved by manipulation of abiotic factors (van Huis et al. 1994) or feeding the parasitoid with honey (van Huis et al. 1992).

In this context, we focused on the foraging behaviour of the parasitoid. Within the constraints of a longevity of a few days only, and a size of less than 1 mm, *U. lariophaga* females have to find suitable habitats and hosts therein. In addition, the parasitoids have to cope with completely different situations during the year: in the rainy season, open, green cowpea fields are colonised with relatively low host densities, and during the dry season, foraging in a closed, dark storage structure with dry beans or frayed pods with sometimes very high host densities.

How do *U. lariophaga* females respond to different host densities, and how are they able to find their hosts? The parasitoid's behaviour under different host egg densities and distributions (functional response) will be reported here. The role of host and host-plant related odours in the foraging behaviour of the parasitoid has also been investigated (see van Huis, these proceedings).

Functional response

The functional response is the number of hosts parasitised per female wasp as a function of host density. Holling (1959, 1966) defined three types of functional response curves. In a Type I response, parasitoids parasitise a constant proportion of the hosts present, until their egg load becomes limiting. This results in a linear curve which suddenly arrives at a horizontal plateau. In a Type II response, Holling (1959, 1966) introduced the concept of handling time (T_h), which increases at increasing host densities, thus reducing the total time left for searching. This results in a number of hosts parasitised which increases with host density at a decreasing rate, until a plateau is reached. This response, commonly found among invertebrate predators and insect parasitoids, was mathematically described by Holling (1959, 1966) with the so-called disc-equation. The Type III response occurs if handling time or the searching efficiency of a parasitoid is not constant, but a function of host density. This is a sigmoid function, in which the parasitisation rate initially increases with increasing host density, and subsequently decreases again when a plateau in the number of hosts parasitised is being reached. This response has also been found in parasitoids, and requires special attention for the experimental conditions (van Lenteren and Bakker 1976). The Type I and II responses demonstrate density-independent and reverse density-dependent parasitism, and such parasitoids do not regulate host popula-

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tions, unless they compensate with a numerical response or aggregation response (Hassell and May 1974).

We assessed the functional response of *U. lariophaga*, as part of the evaluation of its potential as a biological control agent. In addition, information on the functional response is an essential element of population models simulating the parasitoid's impact on the bruchid populations. Much information can be obtained from functional response experiments in which the behaviour of individual parasitoids is recorded, e.g. host discrimination, handling times, and patch time allocation (e.g. van Lenteren and Bakker 1978). However, we doubt that observations of female behaviour on horizontal surfaces can realistically predict functional responses in a three dimensional cowpea stock. Therefore, the functional response was tested in containers filled with beans, thereby losing the ability of direct behavioural observations. Most *C. maculatus* strains distribute their eggs in an even way over the available beans. However, as strains have rather divergent egg laying strategies (Messina and Mitchell 1989), we also tested the effect of different *C. maculatus* egg distributions on the functional response of *U. lariophaga*.

Materials and Methods

Rearings

The rearing of *C. maculatus* was started in December 1990 with material originating from the Niamey region in Niger. Beetles have been maintained in petri dishes on cowpea (*Vigna unguiculata* Walp.), variety California black eyes, at densities of 2–4 larvae per bean. The rearing was held at a 12L:12D photoperiod, with temperatures $35\pm 1^\circ\text{C}$ during daytime and $25\pm 1^\circ\text{C}$ at night.

Uscana lariophaga was obtained at the same time from the same location. Parasitoids were reared on *C. maculatus* eggs (0–48 hours old) on cowpea seeds in glass tubes, and fed with honey. Temperature was $30\pm 1^\circ\text{C}$, and photoperiod 12L:12D.

All wasps used in the experiments were 0–16 hours old, mated and fed. Within 1 hour before the experiment, individual females were given one oviposition experience on a fresh *C. maculatus* egg.

Experimental units

All experiments were carried out at $30\pm 1^\circ\text{C}$. Plastic containers of 1 L ($\phi = 9$ cm, height 20 cm), filled with clean cowpea seeds and placed in total darkness, were used as experimental units. A gelatine capsule containing one *U. lariophaga* female was placed in the centre of a container. The capsule could be opened from outside, in order to release the wasp in the bean stock, by pulling threads attached to this capsule through small holes in the sides of the container. Because earlier observations indicated that, in the absence of host odours, *U. lariophaga* females are negative geotactic, a single host patch was situated 5 cm above the release site in the bean stock. Wasps were allowed to search and parasitise for 4 hours after which the host patches were recovered. This period was chosen because earlier experiments (van Alebeek, in preparation) in larger containers with multiple host patches demonstrated that in 4 hour only one patch was visited. Returning to the previously exploited patch was therefore unlikely and prevented an over-estimation of the level of exploitation in these patches.

Host patches

In each container, one host patch was offered to the parasitoid. Host patches consisted of small polyamine gauze bags,

filled with cowpea beans carrying fresh *C. maculatus* eggs (20 hours old). Three series of egg distributions were tested simultaneously:

A. fixed egg density, i.e. always 1 egg per bean. Thus, within a patch there is an even egg distribution. Egg densities aimed at were 2, 4, 8, 32 and 64 eggs per patch.

B. fixed patch size, i.e. each patch consists of 8 cowpea beans, and the eggs are distributed over those 8 beans. At the higher densities, a clumped egg distribution was obtained. Egg densities aimed at were 4, 8, 16, 32 and 64 eggs per patch.

C. fixed egg density and patch size, i.e. there is always a maximum of 1 egg per bean, and there are always 64 beans in a patch. Egg distributions were random at low densities, gradually becoming even at high densities. Egg densities aimed at were 2, 4, 8, 32 and 64 eggs per patch.

Density 8 in series A and B, and density 64 in series A and C are identical, and the same datasets of these densities were used in the analysis of the different series. The exact number of eggs per patch was variable, and was determined at the end of the experiment. Upon recovery from the experimental units, host patches were incubated in glass tubes until, 4–5 days later, parasitised eggs coloured black and were counted. One full combination of egg distribution and density was observed every day, until 35–38 replicates for each series were obtained.

Handling time and egg laying capacity

Several factors might explain the shape of the functional response curve, e.g. searching efficiency, handling time, initial egg load, etc. Therefore, the handling time of a single unparasitised egg was estimated by detailed behavioural observations of individually parasitising females, using an event recorder with The Observer software (Noldus 1991) for time registration. Each female was allowed to forage on the surface of cowpea cotyledons carrying *C. maculatus* eggs 18–21 hours old. The sequence and duration of behaviour (van Huis et al. 1991) was recorded until she finished 10 ovipositions. Handling time was defined as the time from first contact with a host, until the female abandoned the host. Twenty replicates were recorded.

The egg laying capacity of *U. lariophaga* was determined by offering individual females a surplus (> 150) of fresh *C. maculatus* eggs on about 20 beans in a small glass tube ($\phi = 2$ cm, length 7 cm) during 4 hours. Females (0–16 hours old) had one oviposition experience, and had access to a drop of honey. The number of replicates was 35.

Percentage of patches found

How is *U. lariophaga* able to find host patches? There are indications that *U. lariophaga* females are able to perceive *C. maculatus* eggs odours, and are being attracted to the odour source (van Huis, these proceedings; Ormel et al. 1994). Would then the number of host eggs in a patch and/or the patch size (volume) influence this attraction?

Therefore, we tested the percentage of discovered patches for the different egg densities and distributions in functional response experiments. A discovered patch was defined as a patch in which one or more eggs were parasitised. It should be realised that, for a given number of eggs in a patch, the patch size between series A, B and C may differ markedly. For example, at 32 eggs per patch, the patch size is 32 beans in series A, 8 beans in series B, and 64 beans in series C. Patches were arranged in classes of different egg numbers (see Table 2), because the actual numbers of eggs sometimes varied between replicates.

Analysis

Results presented are in a preliminary form. Fitting Holling's 'disc equation' for a Type II functional response, or a Type III response with a hyperbolic relation between the attack rate *a* and host density *N* (Hassell 1978) is not realistic. Both methods assume a constant host density, in which parasitised hosts are replaced immediately with unparasitised hosts (Houck and Strauss 1985). In our setup, this was not feasible, and females foraged in patches that gradually became depleted in unparasitised hosts. More and more time is spent on encounters with parasitised hosts. For such cases, Rogers (1972) developed the 'random predator equation', which allows for host depletion over the time of the experiment. However, curves with a Rogers' Type II equation gave a poor fit to our data.

We fitted functions derived from photosynthesis efficiency curves described by Goudriaan (1979). The general equation for these curves is:

$$Y = a_0 * \{1 - \exp[1 - \exp(X/a_1)]\} \tag{1}$$

in which *Y* = no. of hosts parasitised; *a*₀ = the maximum level of parasitism (the plateau); *a*₁ = a constant for the slope of the initial part of the curve; and *X* = number of hosts offered.

There is no direct biological meaning for coefficients estimated. The curves were fitted with least squares regression, using Statgraphics software.

Results

Functional response experiments

Results of the functional response experiments are shown in Figures 1a, b and c. Patches without observed parasitism have been left out of this analysis, as it may be assumed that *U. lariophaga* did not find those patches. Thus, results on the functional response presented here refer to the response of the parasitoid *within* one host patch. The foraging behaviour leading to the detection of those patches is discussed later.

Initially, parasitism within low density patches was close to 100%, except in series C (random distribution). At higher host densities, the number of hosts parasitised levelled off. However, considerable variability in the number of hosts parasitised occurs at the higher densities. The curves drawn in Figure 1 are based on function (1). Parameters of the three functions are given in Table 1.

Mean percentages of parasitism were calculated for different host densities (visited patches only; Figure 2). The general trend in the curves is a decrease in percentage parasitisation with increasing host density, pointing towards a Type II functional response. For each egg density separately, differences between the three series were tested with a *G*-test in a *r x*

Table 1. Parameters for the fitted curves of the functional response data in Figures 1a, b and c. *r*² is the coefficient of determination.

Series	Distribution	<i>a</i> ₀	<i>a</i> ₁	<i>r</i> ²	<i>n</i>
A	Variable patch size				
	Fixed egg density	17.62	34.35	0.60	99
	Even egg distribution				
B	Fixed patch size				
	Variable egg density	16.77	19.27	0.54	112
C	Clumped egg distribution				
	Fixed patch size				
	Fixed egg density	18.02	34.56	0.60	91
	Random egg distribution				

k table. At 4 eggs per patch, parasitism in series B (fixed patch size, even distribution) was significantly lower (0.01 < *p* < 0.05) than series A and C. At 8 eggs per patch, series C (both fixed, random distribution) showed a sharp drop in the percentage parasitism, significantly different (*p* < 0.01) from series A and B. At 32 eggs per patch, series B (fixed patch size, even distribution) demonstrated a significantly higher percentage parasitism (*p* < 0.01) than series A and C. Thus, it is evident that the distribution of hosts within a patch has an effect on the foraging behaviour of *U. lariophaga*. Both the clumped and the random distributions (series B and C respectively) show an initial increase and subsequent decrease in parasitisation rates. This suggests a Type III functional response, with a very short range of density dependent parasitism (below 4 eggs per patch). Further analysis is required to test this hypothesis (see discussion).

Arrestment

A strong arrestment of *U. lariophaga* females can be deduced from the high percentages of parasitism within patches at low host densities (Fig. 2). In such patches, *U. lariophaga* females apparently continue to search for unparasitised eggs, although they may have frequent encounters with already parasitised eggs. For patches of 1–2 eggs (in series A and B), 83% of the visited patches had all eggs parasitised. For patches of 3–5 eggs (in series A and B), this was 62%, and for patches of 6–9 eggs, only 30% of these patches was completely parasitised.

Results for series C (random distribution) are difficult to interpret. Apparently, the arrestment response was strong enough to find almost all eggs in patches with 3–5 eggs over 64 beans. However, in patches with 6–9 eggs over 64 beans,

Table 2. The percentage of patches found by *Uscana lariophaga* in the three series of functional response experiments (*n* = 35–38 per cell).

Distribution: # eggs/patch	Percentage of patches found by <i>U. lariophaga</i>		
	A (even) fixed egg density	B (clumped) fixed patch size	C (random) both fixed
1–2	27.0	–	36.8
3–5	55.6	44.4	30.6
6–9	44.4 ^a	44.4 ^a	47.2
13–18	–	58.3	–
24–34	66.7	75.0	58.3
48–64	82.9 ^b	91.4	82.9 ^b
mean	55.0	62.2	50.6

^{a b} The same data-set has been used in both series respectively.

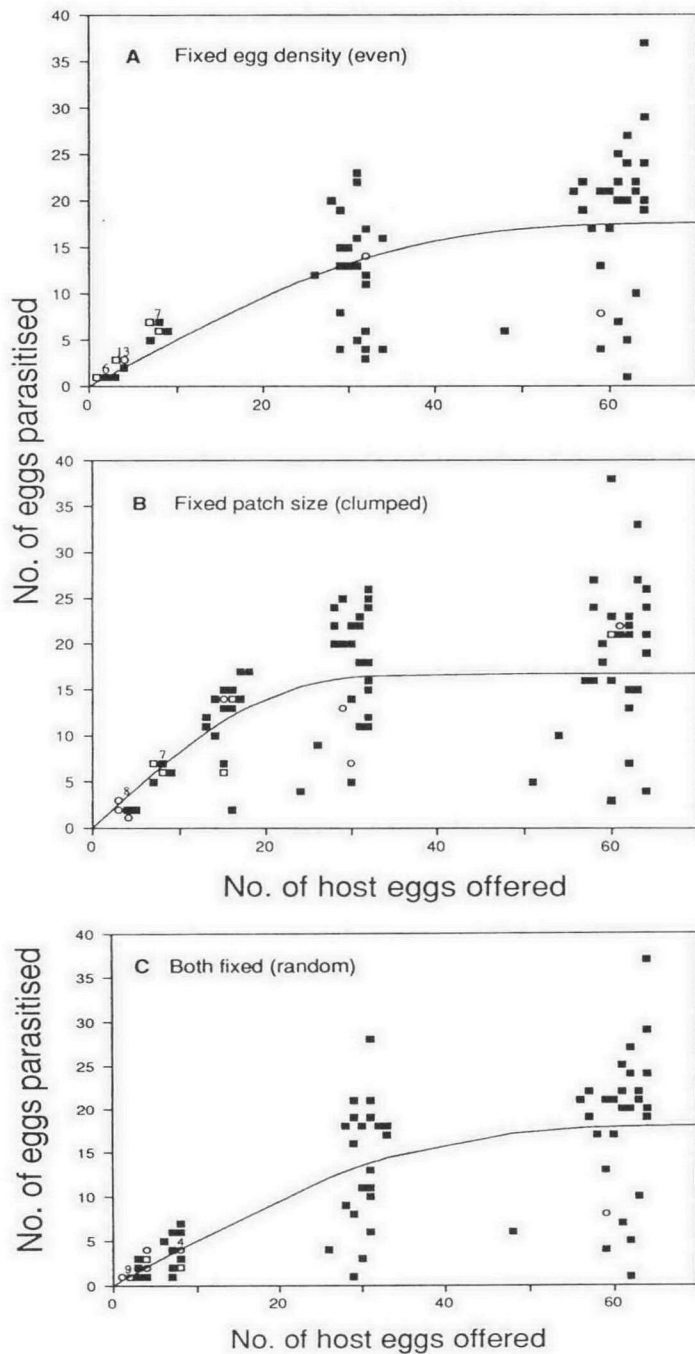


Fig. 1. The functional response of *Uscana lariophaga* under three different egg distributions of its host *Callosobruchus maculatus*. Experiments lasted 4 hours. Patches without traces of parasitism have been omitted. Symbols in the graphs as follows: ■=a single observation; ○=two overlapping observations; □=three observations. Numbers give other multiple observations. Details on the host distributions and on the fitted curves are given in the text.

the percentage parasitisation sharply declined. Either parasitoids gave up and left these patches, or searching times within the patch became so long that not all eggs could be found within 4 h.

Handling time and egg laying capacity

Mean handling time (\pm sd.), as estimated by direct observations, was 180.2 (\pm 28.1; $n=208$) seconds. Rejection of

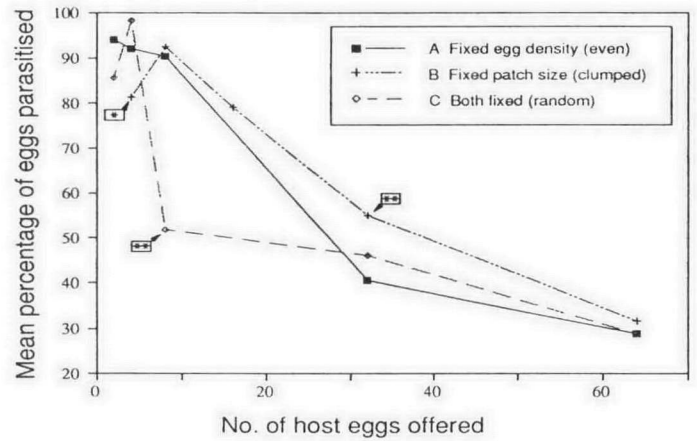


Fig. 2. The mean percentage of eggs parasitised by *Uscana lariophaga* at different patch size classes (no. of *Callosobruchus maculatus* eggs per patch), in three different host distributions. Percentages were calculated for visited patches only (see text). For each egg density, datapoint significantly different from other points have been indicated by * ($p < 0.05$) or ** ($p < 0.01$).

parasitised host eggs occurred mainly after the drumming phase, which on average took only 7.3 seconds.

The mean egg laying capacity of *U. lariophaga* females was 20.0 (\pm 4.90; $n=35$) eggs per female in 4 hours. The data from the functional response experiments for the highest patch density (64 eggs) resulted in 19.19 (\pm 9.39) and 17.59 (\pm 8.28) hosts parasitised per female, in series B (clumped) and A (=C, even) respectively. A Kruskal-Wallis Multiple Comparisons test showed no significant differences between these series and the egg laying capacity experiment.

Percentage of patches found

The percentage patches (of all replicates) found by *U. lariophaga* females at different egg densities and in the three series is given in Table 2. The percentage discovered patches increased with increasing numbers of eggs per patch in all series. It is evident from Table 2 that there are no significant differences between the three series of experiments. A linear regression was applied to the pooled data from Table 2, and yielded the line $Y = 38.337 + 0.840X$ ($n = 13$, $r^2 = 0.830$, $p < 0.05$), in which X is the patch size (number of eggs per patch) and Y is the percentage patches found. In other words, patches with more eggs have a significantly higher chance of being found by *U. lariophaga* females.

Discussion

Functional response has received considerable attention in the ecological literature. This interest arises from questions such as whether density dependent parasitism occurs, which would stabilise host-parasitoid interactions and which is thought to be an important criterion for the selection of parasitoids in biological control (e.g. van Lenteren and Bakker 1976). Furthermore, scientists working on simulation models for parasitism and resource competition have been interested in the estimation of parameters for their models, and in the effect of those parameters on stability (e.g. Hassell 1978).

Experimental setups differ widely among different authors. For example, the size and 'artificialness' of the experimental arena, the actual densities tested (in relation to naturally occurring densities), the time duration of experiments, the distributions of hosts and patches, the possibility for searching

parasitoids to leave the experimental unit, and the number of parasitoids searching together (interference) vary between authors. It is often extremely difficult to replace parasitised hosts during the experiment without disturbing the searching female. Nevertheless, all these variables have their effect on the outcome of the experiments, and some variables put strong limitations on the type of models which are appropriate, and on the kind of statistical analysis which can be employed. Houck and Strauss (1985) discuss appropriate experimental designs. Our setup meets all criteria, if we use models with host depletion over time.

The selection of the appropriate model (Type II or Type III functional response) requires logistic regression of the proportion of hosts parasitised versus the number of hosts present (Trexler et al. 1988; Juliano 1993). Estimation and comparison of parameters is best done through nonlinear least squares regression techniques (Williams and Juliano 1985; Juliano and Williams 1987). Juliano (1993) describes appropriate non-linear curve fitting procedures for functional response experiments.

Preliminary curve fitting in this study was done with functions derived from Goudriaan (1979). Earlier experiments had shown good fits with this approach. However, the fit of the curves to the present data is poor (Table 1). Especially at lower densities, the curves predict lower parasitisation rates than actually observed. The data also suggest that the plateau level may be higher and/or may be attained at higher densities than the curves indicate (Figures 1a, b and c). Therefore, analysis will be continued, and new outcomes will be published elsewhere.

Handling time was estimated at 3 minutes per host, and discrimination of parasitised hosts took less than 10 seconds. Since the maximum number of eggs parasitised in the functional response experiments was 37, the total handling time in that case must have been near 2 hours. So, even at the highest host density and number of parasitisations in the functional response experiments, *U. lariophaga* females still had about 2 hours left for searching and re-encountering parasitised hosts. Thus, handling time cannot have been a limiting factor for the number of hosts parasitised in the functional response experiments.

The egg laying capacity of *U. lariophaga* in small glass tubes (with little searching time) closely agrees with the observed plateau level at the highest host densities in the functional response experiments. In other words, *U. lariophaga* females laid their maximum capacity of eggs in the functional response experiments at the highest densities. Thus, in the current experimental setup, *U. lariophaga* is egg-limited at the higher host densities, and this determines the plateau level in the functional response.

Delobel (1989) did functional response experiments with *Uscana caryedoni* Viggiani. The maximum number of eggs laid per female in the 24 hours functional response experiment was 49, which was even higher than the mean lifetime fecundity (41 eggs) of unfed females in a parallel test (Delobel 1989). Thus, as in our experiments, egg limitation will almost certainly have played a role in Delobel's experiments. However, his results may be difficult to interpret due to the methodology used. Delobel (1989) used different numbers of parasitoid females on a fixed number of host eggs, which allows for interference between females, and thus a reduction of parasitisation rates (Visser and Driessen 1991).

U. lariophaga females are being attracted to *C. maculatus* eggs odours, and are thus able to find host patches (van Huis, these proceedings; Ormel et al. 1994). The percentage of patches found in our experiments is positively correlated with the numbers of host eggs in a patch. Thus, it seems that *U. lariophaga* is able to make a quantitative assessment of the

numbers of host eggs per patch, probably through the detection of odour concentration differences. No differences were found between the three series with different egg distributions. This implies that the volume of the patch and the density or distribution of eggs within a patch do not significantly influence the chance that such a patch is found.

Conclusions

Uscana lariophaga seems to demonstrate a Type II functional response, although a Type III cannot yet completely be excluded. If a Type III response occurs, then density-dependent parasitism only occurs at host densities lower than 4 eggs per patch (Fig. 2).

Our parasitoid is egg-limited and not time-limited. All measures that increase her realised fecundity, e.g. the provision of honey (van Huis et al. 1992), will have a strong impact upon the biological control of bruchids with *Uscana*.

By using host egg odours, *U. lariophaga* is able to find host patches, and does so better when more host eggs are present. This aggregation response is an important factor in stabilising host-parasitoid interactions. In addition to this, *U. lariophaga* shows a strong arrestment response once she has arrived in a host patch. This allows her to parasitise as many eggs within a patch as her egg load permits.

All these characteristics make *U. lariophaga* a very interesting candidate for biological control of bruchids in West Africa.

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