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Biological control of the bulb mite, *Rhizoglyphus robini*, by the predatory mite, *Hypoaspis aculeifer*, on lilies: predator–prey interactions at various spatial scales

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Summary

1. Experiments in closed jars with lily bulbs showed that the predator, *Hypoaspis aculeifer*, can suppress populations of its prey, the bulb mite *Rhizoglyphus robini*, to very low levels. When the bulbs were decomposed into scales, the prey was suppressed earlier, supposedly because of increased accessibility to the sites where bulb mites reside.

2. Repeating the experiment in open jars also led to strong suppression of the prey population: the predators did not leave the jars until almost all prey was eaten.

3. To assess the possibility for biological control of bulb mites in lilies at a larger spatial scale, experiments were carried out in closed plastic bags filled with lily bulb scales and vermiculite, as is common practice in lily bulb propagation. The results showed that *H. aculeifer* was able to suppress its prey to very low densities, but probably due to a more complex spatial structure (i.e. vermiculite), prey suppression took longer.

4. The results of these small- and large-scale population experiments suggest that local predator–prey interactions are very unstable despite the presence of refuges and spatial complexity. At which spatial scale complexity becomes large enough to cause spatial decoupling of the predator–prey interactions and thereby promote predator–prey persistence rather than prey extinction, will be the subject of future investigations.

Key-words: Acaridae, Laelapidae, *Lilium*, biological control, population dynamics, spatial heterogeneity.

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Introduction

Cultivated lilies (*Lilium speciosum*, *L. longiflorum*) are frequently infested by the bulb mite *Rhizoglyphus robini* Claparède (Acari: Acaridae) (Latta 1939; Jeppson *et al.* 1975). To find natural enemies for biological control of the bulb mite, lily bulbs were sampled at various locations in three countries (Holland, Taiwan, Japan). This resulted in the collection of a large number of mesostigmatic predators on lily bulbs that were infested by *R. robini* (Lesna *et al.* 1995). Among these predators *Hypoaspis aculeifer* (Canestrini) (Acari: Laelapidae) was the most abundant. Under laboratory conditions this predator showed high prey consumption and oviposition on *Rhizoglyphus* spp., in agreement with Ragusa & Zedan (1988). Hence, it was worthwhile to test *H. aculeifer* as a biological control agent of the bulb mite.

Bulb mites are not an easy target for a predator as they hide between bulb scales and inside roots and sprouts. Therefore, predators capable of reaching the hidden sites of bulb mite colonies are needed. If predator size is taken as a measure of reaching the hidden target, then there are good prospects for *H. aculeifer* since predator and prey females are of approximately equal size (somal lengths of *c.* 700 µm). Clearly, not only size is important, but also the predator's ability to find infested bulbs and to detect the prey mites within them.

Although *R. robini* infests lily in all phases of cultivation (propagation, growth in the greenhouse and in the field, cold storage), the most severe damage is done during propagation. This phase lasts 6–8 weeks and enables the bulb mites to produce a number of overlapping generations and to build up a large population. Bulb mite outbreaks are promoted directly by

(i) the microclimatic conditions (22–23 °C; 90–95% RH), (ii) the vulnerable state of plant material, and indirectly through (iii) the absence of predators. The population growth rate of bulb mites depends on temperature and is therefore higher during bulb propagation where temperature is kept at 22–23 °C, than during any other phase of cultivation. In addition, bulbs are more vulnerable during the propagation phase when the scales are separated from the basal plate, which causes a wound, thereby creating access for mite invasion. Also, the natural enemies of the bulb mites are eliminated by the treatments preceding the propagation phase. These treatments are intended to control various pests; for example, plant pathogenic fungi are controlled by dipping bulbs in solutions of a mixture of fungicides, such as prochloraz, captan and carbendazim, nematodes as well as bulb mites are controlled by submerging the bulbs in 'hot' water (*c.* 39–41 °C for 1–2 h) and additionally (or alternatively) bulb mites are controlled by dipping the bulbs in a pesticide (pirimifos-methyl) solution. However, these treatments do not eradicate all bulb mites, whereas they do lead to the complete elimination of predatory mites (C. Conijn & I. Lesna, personal observation). This differential mortality arises because, compared to bulb mites, predatory mites are much more sensitive to submersion and they tend to frequent the outer parts of the bulb causing them to be more exposed to the control measures than the bulb mites. For these reasons priority was given to the development of biological control in the propagation phase.

While propagation conditions are favourable for pest outbreaks, they also seem advantageous for pest control by predatory mites. The impact of predatory mites partly depends on the predation rate, but especially when initial predator-to-prey ratios are low, it also depends crucially on the predator's population growth rate (Sabelis & van der Meer 1986; Sabelis 1992; Janssen & Sabelis 1992). The relatively high temperatures during the 6–8 weeks of the propagation phase enables the predatory mites to produce at least 3–4 generations. In addition to the favourable climatic conditions, biological control has good prospects of success because the bulb scales are contained in 40 litre plastic bags with only a few very small openings for ventilation; thus, the bags form a more or less *closed* system. If successful, biological control will be a matter of introducing predators into the plastic bags at the start of the propagation phase.

In the experiments described in this paper, we investigate whether biological control can be achieved by the introduction of predators after the treatments which precede the propagation phase of lily bulbs. These experiments are part of a more comprehensive study in which the ultimate aim is to achieve control at various spatial scales, i.e. not only in the propagation phase, but also in the other phases of cultivation. At each of these spatial scales different types of refuges will be available to the bulb mites and these may all

have their own effect on the predator–prey interactions. Therefore, we decided to investigate in a step-by-step fashion the effects of various types of refuges. In addition (moving from the propagation phase to cultivation in the field), the environment in which biological control takes place changes from a closed plastic bag to an open field, where predators may move in and out at will. Therefore, we decided to investigate how the predator–prey interaction is affected by whether the environment is open or closed. In this way we hope to analyse how spatial scale affects predator–prey interactions in an attempt to experimentally test current predator–prey theories (Murdoch *et al.* 1985; Taylor 1991; Kareiva 1989).

The experiments described here were designed to answer the following questions. (i) Can predatory mites control bulb mites despite low accessibility of the feeding sites in the lily bulb? (ii) How does accessibility change by breaking the bulbs into separate scales (decomposing the bulb) and how does this affect the predator–prey interaction? (iii) How do predator–prey dynamics change when the interaction takes place in an open rather than closed environment? (iv) How is the predator–prey interaction affected by increasing spatial scale and complexity?

Materials and methods

LIFE HISTORY OF PREY AND PREDATOR

Based on data obtained at 27 °C using garlic cloves as food (Gerson *et al.* 1983), the life history of the bulb mite *R. robini* can be described as follows. The female develops from egg to adult in 12.6 days. After mating, the female starts to produce eggs within *c.* 1 day; egg production reaches a peak of 20 eggs per day after *c.* 10 days and then gradually declines to zero at day 42 (since maturation). The average rate of oviposition is *c.* 10 eggs per day. In total a female produces *c.* 400 eggs with the sexes (both diploid) in equal proportions. Survival is very high during the oviposition period. It starts decreasing from day 15 (since maturation), reaching 50% at day 35 and 0% at day 42. A post-oviposition period is absent.

At 22 °C egg–adult development on garlic cloves is much slower (19.2 days) and on a diet of peanuts the rate of oviposition is drastically increased; on this diet a peak ovipositional rate of 40 eggs per day is reached at day 7 (since maturation) and a female produces on average a total of 690 eggs (Gerson *et al.* 1983).

Based on data obtained at 26 °C using nymphs of *Rhizoglyphus echinopus* (Fum. & Rob.) as prey (Ragusa *et al.* 1986; Ragusa & Zedan 1988; Zedan 1988), the life history of the predatory mite, *H. aculeifer*, has the following features. Development from egg to adult takes 11.5 days for the female and 0.5 day less for the male. After moulting into the adult stage the female starts producing eggs after 2 days, reaches a peak of 6 eggs per day after *c.* 5 days and

maintains peak production of eggs for *c.* 15 days, after which oviposition steeply declines. The average rate of oviposition is equal to 4.4 eggs per day. In total 99–115 eggs are produced per female. The mean oviposition period is 24–26 days, followed by a mean post-oviposition period of 10–12 days. Survival is very high during the oviposition period. It starts decreasing from day 36 (since birth), reaching 50% at day 80 and 0% a few days before day 100.

The predatory mite reproduces by arrhenotokous parthenogenesis (De Jong *et al.* 1981; Usher & Davis 1983; Murphy & Sardar 1990). The overall proportion of females in the offspring is close to parity, but changes with the age of the mother (Lobbès & Schotten 1981; Ruf 1993; Murphy & Sardar 1990). The first eggs laid are probably males, but subsequently a steep increase in the production of females occurs, leading to sex ratios of *c.* 80%. In the last phase of the oviposition period most eggs develop into males.

POPULATION EXPERIMENTS

The population experiments were of two types, mainly differing in the spatial scale under consideration: small-scale experiments with a few lily bulbs (intact or decomposed into scales) in a plastic box and large-scale experiments in plastic bags with several hundreds of lily bulbs decomposed into scales, as is usual practice under conditions of lily bulb propagation.

Small-scale experiments

Small-scale population experiments were carried out from April to June 1991 in a climate room. Lily bulbs (*L. speciosum* var. Star Gazer) infested by *R. robini* were obtained from storage rooms at the Bulb Research Centre in Lisse (The Netherlands). The predatory mite, *H. aculeifer*, was collected from stored lily bulbs, harvested in December 1990 in Breezand (North-Holland). They were reared for 2 months under the laboratory conditions at 25 °C > 70% RH on *Tyrophagus putrescentiae* (Schrank) (Acari: Astigmata) as prey.

Experiments were done under two conditions of spatial heterogeneity; accessibility of the feeding sites of the bulb mites was increased by decomposing the lily bulbs to scales or the bulbs were kept intact so that the feeding sites in between scales were less accessible. Three bulbs (infested with *c.* 200 *R. robini* per bulb ranging between 158 and 245) or their scales (*c.* 14 scales obtained per bulb) were placed in one plastic jar (7 cm Ø, 7 cm height). Four predator females per bulb were released into the jars, to provide a predator–prey ratio of 1: 50. (Note that to express the densities the bulb is taken as a unit rather than the separate scales.) The jars were closed and kept in darkness at a constant temperature of 25 °C for a period of 4 weeks. Each treatment was replicated nine times and

nine jars, in which no predators were released, were used as the control.

The predator and prey mite densities were assessed after 2, 3 and 4 weeks. At each sampling date three jars were taken from each treatment. The bulbs and scales were transferred from the jars to Tullgren funnels, where they were kept for 4 days to extract the mobile stages of mites. The mites collected in the vial below the funnel were counted under a binocular microscope. The walls of the jars were also inspected for predators that had left the bulb scales.

A second series of experiments with open and closed jars was carried out in December 1992 to investigate how the predator–prey interaction was affected when predators could leave the system. The plastic jars (10 cm Ø, 12 cm height) were up to 60% filled with a mixture of moistened vermiculite and scales from 10 infested bulbs (*c.* 10 scales obtained per bulb). The bulbs (*L. speciosum* var. Tender) were collected in Breezand in December 1992 and infested with *c.* 120 *R. robini* per bulb, ranging between 105 and 152. Predatory mites were collected from lily fields in Breezand in September 1991 and reared under laboratory conditions for 15 months. Adult females of *H. aculeifer* were released into the jars to provide a predator–prey ratio of 1: 20 (6 predatory mites per bulb). The jars with the bulb scales were kept in two closed boxes (50 × 50 × 70 cm) in the dark, at 23 °C and > 95% RH (created by an air-filtered water bath to avoid desiccation of the scales). Each box contained three jars, that were either closed or open. In the experiment with open jars, predators leaving one could enter another jar in the same box, but were unlikely to escape from the box. Densities of mobile mites were assessed as before on three bulbs taken from each jar at each sampling date.

Large-scale experiments

Large-scale experiments were carried out from February to June 1992 in storage rooms at the Bulb Research Centre in Lisse. The predatory mite, *H. aculeifer*, was collected from a lily field in Breezand in September 1991 and was reared for 6 months under laboratory conditions. Lily bulbs (var. Star Gazer) infested with *R. robini* were harvested from the same lily field in December 1991. Prior to the start of the experiment there were *c.* 140 *R. robini* per bulb (with *c.* 10 scales obtained per bulb) together with *H. aculeifer* and a variety of plant pathogenic and saprophytic organisms, such as nematodes (Maas *et al.* 1978; Westerdahl *et al.* 1993), other astigmatic mites (I. Lesna, personal observation; B. Czjakowska, personal communication) and springtails (I. Lesna, personal observation). A hot water treatment (HWT) of 39 °C for 2 h was applied to the bulbs prior to the experiments. As a result of HWT the bulb mite population was reduced to 6 individuals per bulb (ranging between 1 and 9), and all predatory mites and other

organisms were eliminated. Scales of 200 lily bulbs were mixed with vermiculite and placed in four plastic 40 litre bags (with scales of 50 bulbs per bag). In each of two bags 15 predators (all stages, except eggs, obtained from laboratory rearing) were released to provide a predator-prey ratio of 1:20. The other two bags were used as a control experiment to assess population growth of *R. robini* in absence of predators. This experiment was sampled weekly (except for the first week) over a period of 6 weeks by removing a number of scales equivalent to 10 bulbs from each of the bags and extracting mobile mites as previously described.

Results

SMALL-SCALE EXPERIMENT

Prey population growth in closed jars

The control treatment with *R. robini* in the absence of predatory mites showed linear, rather than exponential population growth (Fig. 1a). Such a linear trajectory of population growth occurs in the classic model of logistic growth when population size is close to half its value at carrying capacity. This suggests that food quality and/or quantity is in a declining (but not yet limiting) phase. It is reasonable to assume that the initial population has a stable age distribution as it was collected from a field where no predators were present. Assuming a stable age distribution in the initial phase of the experiment the ratio $N_t/N_{t=0}$ is equal to $M_t/M_{t=0}$, where N represents the total number of mites, M the number of mobile stages of mites and t the time expressed in days. Hence, the intrinsic rate of population growth can be estimated from $r_m = \ln(M_t/M_{t=0})/t$. For the experiment with bulbs decomposed in scales ($t = 14$, $M_t = 1112$, $M_0 = 200$) the intrinsic rate of increase, r_m , is estimated to be equal to 0.122 day^{-1} (r_m estimates per replicate: 0.121, 0.113, 0.132) and for the treatment with intact bulbs ($t = 14$, $M_t = 1280$, $M_0 = 200$) r_m is 0.133 day^{-1} (r_m estimates per replicate: 0.121, 0.145, 0.130), suggesting that bulb structure had little effect on population growth. As will be shown later, the two estimates are still lower than the r_m estimated for the large-scale, control experiments, which started from a much smaller initial population size per bulb (2–6 mites rather than 200) and showed initially exponential rather than linear population growth. This suggests that food quantity and/or quality reduced the capacity for population growth from the start of the small-scale experiments.

Predator-prey dynamics in closed jars

The treatments involving a 1:50 ratio of predator to prey resulted in exponential decline of the *R. robini* population and exponential increase of the *H. aculeifer*

Fig. 1. Average numbers (dots) and confidence intervals (vertical bars) of mobile stages of *R. robini* on bulbs decomposed in scales (black dots) and on intact bulbs (open dots) in the absence (a) and the presence (b) of predators, of *H. aculeifer* (triangles) (c). Data points (x) are first transformed according to $\log(x + 1)$ and then used to estimate mean and standard error (SE). The confidence intervals are calculated as $SE \cdot t_{n-1}(\alpha = 0.05)$ for $n = 3$ replicates. Bulb structure had a significant impact on the numbers of prey (b) and predators (c) in weeks 2, 3 and 4 (t -test at the 5% level).

leifer population (Fig. 1b, c), indicating that the predator could virtually eliminate the prey population within 2–4 weeks. Spatial heterogeneity, however, had some marked effects on the predator-prey dynamics. First, the suppression of the prey population occurred 1 week earlier on bulbs decomposed in scales than on intact bulbs (Fig. 1b) (probably because the predators had more direct access to the feeding sites of bulb mites on the scales); after 2 weeks only 2% of the prey population on scales of lily bulbs was left, compared to 18% on intact bulbs. Secondly, the predator population on intact bulbs reached higher numbers than

on bulbs decomposed in scales (Fig. 1c; note that it is risky to calculate r_m from these data as the initial population consisted of predator females only, thus violating the assumption of a stable age distribution).

Predator–prey dynamics in open vs. closed jars

The control treatment (Fig. 2a) showed that (i) there was little difference between prey population growth in the open and closed jars, (ii) population growth was close to being linear, suggesting that food quantity

Fig. 2. Average numbers (dots) and 95% confidence intervals (vertical bars) of mobile stages of *R. robini* in open jars (open dots) and closed jars (black dots) in the absence (a) and the presence (b) of predators, and of *H. aculeifer* (triangles) (c). Data points (x) are first transformed according to $\log(x + 1)$ and then used to estimate mean and standard error (SE). The confidence intervals are calculated as $SE\ t_{n-1}(\alpha = 0.05)$ for $n = 3$ replicates. Differences between treatments are not significant at the 5% level (t -test), except for the predators (c) in week 4.

and/or quality reduced potentials for population growth, and (iii) the r_m was lower ($0.063\ \text{day}^{-1}$ in the open jars and $0.059\ \text{day}^{-1}$ in the closed jars) than those estimated from the small-scale experiment ($0.122\ \text{day}^{-1}$), probably because the lily bulbs were of another variety (var. Tender) known to be more resistant to bulb mites (C. Conijn, personal communication).

Comparing the predator–prey dynamics in closed jars with those in open jars, it can be seen that: (i) the prey population initially declined faster (Fig. 2b); (ii) the predator population increased at a faster rate during the first 3 weeks (Fig. 2c); and (iii) in week 4 continued to increase, whereas the population found in the open jars decreased steeply (Fig. 2c). Probably, the latter difference was due to predator dispersal from the open jars after the prey was suppressed to very low densities. It is interesting to note that while the prey population in open jars was suppressed to less than 10% in the second week the populations of the predatory mites continued to increase up to the third week. This suggests that the predatory mites have a strong tendency to stay on infested bulbs and do not disperse until prey become scarce.

LARGE-SCALE EXPERIMENTS

Prey population growth

Two control treatments were applied, differing in the number of bulb mites that survived HWT prior to the start of the experiment and in the number of replicates: (i) one replicate with two *R. robini* per bulb, and (ii) two replicates with six *R. robini* per bulb. These initial densities were lower than those in the small-scale experiments. The results (Fig. 3a) show that during the first 3 weeks the populations grew exponentially with $r_m = \ln(100/2)/21 = 0.186\ \text{day}^{-1}$ and $r_m = \ln(321/6)/21 = 0.189\ \text{day}^{-1}$ (r_m estimates per replicate: 0.187, 0.191), whereas during the last 2 weeks populations grew much slower, i.e. with $r_m = \ln(698/221)/14 = 0.082\ \text{day}^{-1}$ and $r_m = \ln(2112/684)/14 = 0.0805\ \text{day}^{-1}$ (r_m estimates per replicate: 0.084, 0.077). Note that the two curves in Fig. 3a do not converge, as expected when density is the limiting factor. Instead, the two curves run parallel in the logarithmic plot. This indicates that bulb quality, rather than bulb mite density, is the limiting factor for population growth of *R. robini* mite.

Predator–prey dynamics

As in the small-scale experiments, release of predators ultimately lead to the almost complete elimination of the prey (Fig. 3b). However, the prey population was suppressed to 2% of its initial value after 4 weeks, which was later than in the small-scale experiments with bulbs decomposed in scales (i.e. 2% after 2 weeks). This is surprising since a higher initial predator–prey ratio was applied (but note that here pred-

Fig. 3. Average numbers (dots) and confidence intervals (vertical bars) of mobile stages of *R. robini* in the absence of predators (open dots) (a), and of *R. robini* (black dots) in interaction with *H. aculeifer* (open triangles) (b). Data points (x) are first transformed according to $\log(x + 1)$ and then used to estimate mean and standard error (SE). The confidence intervals are calculated as $SE \ t_{n-1}$ ($\alpha = 0.05$) for $n = 2$ replicates. In (a) one replicate of an additional control experiment is presented (black dots), which differed only in that the initial number of bulb mites was 2.1 per bulb (ranging between 1 and 5).

ators in all mobile stages were released, whereas in the small-scale experiments only adult females were introduced). One important factor causing the delayed suppression was probably the low density of prey, e.g. the initial density was 6 prey mites per bulb compared to 200 prey mites per bulb in the small-scale experiment.

The predator population increased exponentially during the first 3 weeks. Since the predators released were selected randomly from a growing population in the laboratory cultures and therefore present in all stages, it is reasonable to assume a stable age distribution in the experimental system. The intrinsic rate of population growth appeared to be in the order of $c. 0.193 \text{ day}^{-1}$ during the first 3 weeks (r_m estimates per replicate: 0.191, 0.195), but declined thereafter. It is important to note that, albeit at a lower pace, the predator population continued to increase from week 3 to week 6, even though the prey population was almost completely wiped out.

Discussion

The experiments described show that the predatory soil mite, *H. aculeifer*, can control and almost eliminate populations of the bulb mite, *R. robini*, infesting lily bulbs and scales, despite the fact that this prey may hide on various sites in the bulb. Nevertheless, bulb structure may have an effect on the predator-prey interaction, as indicated by the small-scale experiments on intact bulbs and bulbs decomposed in scales. Suppression of prey numbers on intact bulbs occurred later than on decomposed bulbs; this may be due to the structural complexity reducing the likelihood of being found by the predators, thereby promoting opportunities for the prey to increase in future abundance by population growth. This larger supply of prey may also have given rise to the higher numbers of predators on intact bulbs. One explanation is that the more complex structure of intact bulbs promotes escape from cannibalism. However, predation on conspecific eggs does not occur and predation on juvenile stages takes place only under extreme conditions of hunger (Usher & Davis 1983). Another explanation is that the more complex structure decreases the effect of predator density on the predator's rate of oviposition. There is some evidence for this mechanism; Ruf (1991) noted that the oviposition rate decreased from two to one egg per day when predator density increased from one to five females in a small plastic box of 3.4 cm^3 .

Both *R. robini* and *H. aculeifer* can feed on various food types. For example, *R. robini* can feed and reproduce not only on bulbs and tubers, but also on nematodes, dead insect larvae, yeast and other fungi, groundnuts and their extracts (Gerson *et al.* 1991), while *H. aculeifer* feeds on other mites, springtails, sciarid and drosophilid fly larvae, *Tribolium* eggs, nematodes and even on pollen or fungi, such as yeast (Barker 1969; Inserra & Davis 1983; Usher & Davis 1983; Ragusa *et al.* 1986; Sardar & Murphy 1987; Murphy & Sardar 1990). Most of these food items were not present in our experiments, but *Fusarium* spp., *Penicillium* spp. were observed and yeasts may have been present; these foods might have influenced the potentials for survival, development and reproduction of both *R. robini* and *H. aculeifer*.

One way to detect dietary effects is to compare capacities for population increase in our population experiments with those calculated from life table studies on well specified diets. With respect to *R. robini* in the large-scale experiments we estimated maximum r_m -values of $0.174\text{--}0.186 \text{ day}^{-1}$ during the first 3 weeks of population growth in absence of predators. These values are lower than the r_m of 0.218 day^{-1} found by Gerson *et al.* (1983) on garlic at 27°C . Linear interpolation between the data of Gerson *et al.* (1983) at 16°C and 27°C on garlic gives r_m values of 0.162 day^{-1} for 23°C , the temperature used in our experiments. This r_m value is close to our estimates from the population growth curves, suggesting that in terms of food quality lily and garlic are similar.

The estimated r_m value of c. 0.193 day⁻¹ for *H. aculeifer* is higher than that estimated by Lobbes & Schotten (1980), who found 0.115 day⁻¹ on a diet of *T. putrescentiae* at 24.5°C. This suggests that either *R. robini* is a better food source than *T. putrescentiae* or there were alternative foods that promote the rate of population increase. Another estimate of r_m obtained from population growth experiments with *H. aculeifer* on an exclusive diet of bulb mites at 25°C (I. Lesna, unpublished) was 0.144 day⁻¹. This value is lower than those obtained from the large-scale experiments. This difference may well be due to the presence of alternative foods (fungi) in the large-scale experiments.

The most convincing reason why alternative food may have played a role in the large-scale experiments is that the population of *H. aculeifer* continued to increase from week 3 to week 6 despite the virtual absence of its prey. As fungi seem to be the only possible alternative food source, there is a need for more detailed studies on fungivory in *H. aculeifer*.

The experiments in open and closed jars suggest that bulb mite control does not simply result from lack of opportunity to disperse and escape, but rather that the predators have a strong tendency to stay on infested bulbs until the prey population is virtually eliminated. This strong arrestment of the predators cannot be explained by a response to alternative foods, as these were virtually absent in the small-scale experiments. Hence, it must be due to a response to the presence of prey mites alone. These observations on arrestment until the prey is wiped out are reminiscent of the phenomena observed in interactions between local populations of plant-inhabiting predator and prey mites (Acari: Phytoseiidae, Tetranychidae); in predator-prey experiments on plants positioned at the windward side of a windtunnel, the predatory mites were allowed to disperse aerially during the population interaction on the plants, but apparently did not do so until after their prey was exterminated (Sabelis & Van der Meer, 1986). Thus, over-exploitation of the prey population seems to be the consequence of a strategy of individual predators in at least some acarine predator-prey systems.

These results shed new light on observations of over-exploitation in predator-prey interactions (Murdoch *et al.* 1985), such as in interactions between phytoseiid mites and spider mites (Huffaker 1958; Huffaker *et al.* 1963; Takafuji *et al.* 1983), between backswimmers and mosquito larvae (Chesson 1984) and between ladybeetles and cottony-cushion scales (Quezada 1969). In some of these examples (Huffaker 1958; Chesson 1984) interactions were studied in small and closed environments. Over-exploitation may then be considered to result from a strong numerical response of the predators and a lack of possibilities for the prey to escape. In others, over-exploitation was observed at a spatial scale that is much smaller than the space within which the population experi-

ment was carried out (Huffaker 1958; Huffaker *et al.* 1963; Takafuji *et al.* 1983) or at a small spatial scale in the field (Quezada 1969). In these studies the occurrence of over-exploitation was taken for granted and none of the authors proposed causal mechanisms or functional reasons that make over-exploitation a likely outcome of local predator-prey interactions. We suggest four reasons why it may be selectively advantageous for a predator to stay in a prey patch until the last prey has been eaten: (i) the high risks of death involved in dispersal and the low chances of finding prey after dispersal may not outweigh the benefits of staying, even when prey density in the current patch becomes low (the 'dispersal' hypothesis); (ii) the benefits of staying are greater because of the availability of other prey or food items (the 'alternative food' hypothesis) (compare to Holt (1977) who showed under which conditions adding a new prey may lead to the extermination of the originally present prey, even when the two prey species do not compete in a direct way); (iii) the probability of finding mates is higher in the current prey patch and will be drastically reduced after dispersal; and (iv) over-exploitation may be a strategy that is competitively superior to other less destructive exploitation strategies (the game theoretical or food competition hypothesis) (compare with Levin & Pimentel 1981, who analysed conditions for evolution of (a) virulence in pathogen-host systems). These hypotheses are not mutually exclusive; they may well act in concert. Further tests to discriminate between them are needed.

The ability to annihilate prey makes the predatory mite *H. aculeifer* a potential candidate for biological control of *R. robini* on lily bulbs during the propagation phase. While this predator is frequently found in association with lily bulbs infested by *R. robini* and probably contributes to suppress this pest under field conditions, its effectiveness is halted in the propagation phase due to the pretreatments (HWT), which eliminate virtually all predators. Reintroducing predatory mites at the start of the propagation phase after applying treatments to control other pests can prevent population explosions of the bulb mites. As *H. aculeifer* is easy to rear on *T. putrescentiae* and as it is a polyphagous predator shown to be a promising candidate for control of other pests, such as sciarid fly larvae (Gillespie & Quiring 1990) and thrips (Glockemann 1992), there are good perspectives for use of this predator to control a wider range of pests.

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