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Predators use volatiles to avoid prey patches with conspecifics

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Summary

1. Simple models of optimal foraging, such as ideal free distribution models, are based on the assumption that foragers are omniscient with respect to the quality of all patches in the environment; they know how much food and how many competitors are present in each patch.

2. In contrast, simple population dynamic models treat predator–prey distributions in a phenomenological way, and do not take fitness consequences for individual foragers into account. Yet, the precise way in which these distributions come into being is what really matters to population dynamics. It is therefore necessary to study the behavioural mechanisms underlying the distributions of foragers over patches.

3. We studied the behaviour of a predatory mite, *Phytoseiulus persimilis*, in response to prey patches occupied by conspecifics. It is well known that high predator densities in prey patches promote dispersal of these predatory mites. Our question was to what extent predators can assess the presence of conspecifics from a distance.

4. Experiments with a Y-tube olfactometer showed that predatory mites avoid patches occupied by conspecifics.

5. This avoidance cannot be attributed to odours of conspecific predators, or of prey damaged by predation, as these odour sources both appear to be attractive.

6. Separating the prey patch from the conspecific predators in the odour source led to the avoidance response only when the predators in the odour source were positioned upwind from the prey patch, and not when they were positioned downwind. This suggests that predators release an odour that elicits the production of yet another odour by the prey. This was supported by the observation that removal of adult prey led to a quick disappearance of the avoidance response.

7. We argue that distant discrimination between patches with and without competing conspecifics may be quite common among predators and parasitoids, and that the use of odours instead of physical inspection of patches allows predators to instantaneously integrate information on the distribution of food and competitors.

8. This behavioural mechanism may bring predators and parasitoids closer to behaving as ideal free foragers than was previously thought possible.

Key-words: foraging behaviour, olfactory searching, Phytoseiidae, predator distributions, semiochemicals.

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Introduction

The distribution of foraging animals over patchily distributed resources is of paramount importance in evolutionary ecology. For example, in the theory of sex allocation, the optimal sex ratio produced by insect parasitoids and predators depends on the number of females present in a patch (Hamilton 1967; Charnov 1982; Nagelkerke 1993). Distribution of for-

aging animals over food patches is also the focus of attention in another body of theory, that of the ideal free and ideal despotic distributions (IFD and IDD, respectively; Fretwell & Lucas 1970; reviewed by Milinski & Parker 1991; Kacelnik, Krebs & Bernstein 1992). Both the theory of sex allocation and the IFD theory are based on the assumption that, on an evolutionary time scale, selection on behaviour of individuals has led to the highest possible fitness of the

foraging individual, or to maximization of some currency that is assumed to be positively correlated to fitness (Stephens & Krebs 1986). For this to be achieved, individual foragers should be omniscient with respect to their environment (each individual should know how many prey and/or competitors are present in each patch), or they should be able to learn from previous foraging experiences (Bernstein, Kacelnik & Krebs 1988, 1991).

The distribution of predators and parasitoids over prey (or host) patches is also of great importance in the population dynamics of arthropod predator–prey and parasitoid–host systems. In particular, the role of aggregation of predators in certain prey patches in stabilizing predator–prey dynamics has been the subject of much debate (Hassell & May 1973, 1974; Chesson & Murdoch 1986; Murdoch & Stewart-Oaten 1989; Godfray & Pacala 1992; Taylor 1993a; reviewed by Taylor 1993b). The behavioural submodels of most of these studies are notoriously rigid. Predators are often assumed to choose one prey patch for their entire lifetime (but see Murdoch & Stewart-Oaten 1989 and Godfray & Pacala 1992 for counterexamples). Moreover, they are assumed to choose prey patches independent of the distribution of other predators. This leads to aggregation of risk of parasitism or predation, resulting in a decreased per capita prey-capture rate (Taylor 1993b). Recently, van Baalen (1994) and van Baalen & Sabelis (1993) have relaxed this latter assumption. In a combination of the classic Nicholson–Bailey model and a game theoretical model, they allowed parasitoids and hosts to distribute themselves among patches in an evolutionarily stable manner. This resulted in a decrease of the parameter space in which the model has a stable equilibrium.

The central role of predator distributions in evolutionary ecology and theory of population dynamics makes it essential to understand the foraging behaviour of predators that leads to these distributions. It is, for example, still unclear how exactly predators and parasitoids determine the number of conspecifics present in a prey patch. It is conceivable that predators, upon arrival in a patch, can estimate the number of conspecifics either through encountering them, or by encountering signals associated with their presence, such as substances used for patch marking or the remnants of attacked prey (parasitized hosts in the case of parasitoids). However, this would involve visiting and sampling patches, and it would be an obvious advantage to predators if they were able to estimate quickly the presence of conspecifics (or other predators) in a patch from a distance, for instance by using odours associated with the presence of conspecifics. Odours are important stimuli for arthropods, and many arthropod predators are known to use odours in detecting prey patches, i.e. in an early phase of the searching process. Surprisingly, there is not much known about the response of predators and parasitoids towards odours emanating from prey/host

patches with conspecifics. In this study we show that the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) is indeed able to perceive odours associated with the presence of conspecifics in prey patches.

THE PREDATOR–PREY SYSTEM

The prey species used here, *Tetranychus urticae* Koch (Acari: Tetranychidae), is an important pest in many agricultural crops (Helle & Sabelis 1985). It attacks plants by piercing leaf parenchyma cells with its stylets, and it subsequently sucks out the contents. The predator *P. persimilis* is often released to control *T. urticae* in agricultural systems (Helle & Sabelis 1985).

Many studies have been devoted to the foraging behaviour of predatory mites (including *P. persimilis*) in a patch with conspecifics. Kuchlein (1966), Eveleigh & Chant (1982a) and Yao & Chant (1990) found a decrease in rate of reproduction, in the number of prey killed, and in feeding rate (expressed as a reduction in body weight) with an increase in density of *P. persimilis* females under conditions where food was not limited, suggesting the occurrence of interference at high predator densities, and the existence of costs associated with aggregation of predators. It may therefore pay individual females to avoid aggregations of conspecifics and settle in patches with lower predator density. Many studies show that patch residence time of predatory mites decreases in the presence of conspecifics (Kuchlein 1966; Fernando & Hassell 1980; Sabelis 1981; Hislop & Prokopy 1981; Eveleigh & Chant 1982b; Bernstein 1984; Ryoo 1986; reviewed by Sabelis 1985), suggesting that predators indeed prefer to move away from patches with aggregations of conspecifics.

Although it is known that *P. persimilis* uses odours when searching for prey patches (Sabelis & van de Baan 1983; Sabelis, Afman & Slim 1984a; Sabelis, Vermaat & Groeneveld 1984b; Sabelis & Dicke 1985; Dicke & Sabelis 1988; Dicke *et al.* 1990a,b; Sabelis & van der Weel 1993; Dicke, Bruin & Sabelis 1993; Sabelis & Afman 1994), there is no published report of the response of this predator to odours emanating from prey patches invaded by conspecific predatory mites. In this study, we first describe the response of *P. persimilis* to such odours. Subsequently, we present results of a series of experiments that were carried out to elucidate the exact source of the odours emanating from predator-invaded prey patches.

Materials and methods

Bean plants (*Phaseolus lunatus*, Lima bean) were reared in a climate room at 25°C (light:dark = 16:8). Only young primary leaves were used for experiments. Spider mite prey (*T. urticae*) were reared on bean plants in a separate climate room (25°C; light:

dark = 16:8). Predators were cultured at 25°C on detached bean leaves infested with prey on a gauze platform in a water-containing tray.

GENERAL METHODS

A Y-tube olfactometer was used to study the response of adult female predators (Sabelis & van de Baan 1983). It consists of a glass tube in the form of a Y, with a black Y-shaped metal wire in the middle to railroad the mites. The base of the tube was connected to an air pump that produced an air flow from the arms of the tube to the base. Containers consisting of a partitioned plastic box (Fig. 1) were connected to both arms of the tube. Bean leaves with prey and/or predators were put on water-saturated tissue in a layer of water (*c.* 5 mm deep) at the bottom of the containers. In this way leaves stayed fresh for several days, and prey and predators refrained from escaping, because the water served as a barrier.

A flow meter with needle valves was connected to the air inlet of the containers, and was used to calibrate the speed of incoming air in each arm of the olfactometer. When wind speeds in both arms are equal, the odour plumes form two neatly separated fields in the base of the Y-tube, with the interface coinciding with the metal wire (Sabelis & van de Baan 1983).

For introduction of an adult female predator, the pump was disconnected and a predator was put on the metal wire at the base of the Y-tube. After reconnecting the pump, the predator started moving upwind to the junction of the wire, where she had to choose for either of the two arms. Each individual was observed until she had reached the end of one of the arms, or for a maximum of 5 min, and was sub-

sequently removed. In this way, each predator was tested separately. Depending on the supply of predators, we tested about 20 predators per experiment. Numbers tested per experiment are presented in the Results section. Previous experiments have shown that there is no effect of possible predator residues deposited on the metal wire on behaviour of subsequent predators (Sabelis & van de Baan 1983). After a series of five mites, the odour sources were connected to the opposite arm of the olfactometer to correct for any unforeseen asymmetry in the experimental set-up. Predators were collected 1 h before an experiment and kept without food.

RESPONSE TO ODOURS FROM PREDATOR-INVADIED PREY PATCHES

The experimental procedure can be divided into four.

1. Two fresh bean leaves were put in each of two containers and infested with 100 adult prey each. Both primary leaves of two plants were divided between the two containers to make the odour sources as equal as possible.
2. The next day, attractiveness of the infested leaves was tested by connecting one of the containers to an arm of the Y-tube olfactometer, while no odour source was connected to the other arm. 10–20 predators were tested. In all cases, a preference for the infested leaves was found (two-tailed binomial test).
3. Subsequently, the other container, with similar leaves and an equal amount of prey, was connected to the other arm of the olfactometer, and about 20 predators was offered a choice between the two odour sources. Although usually one of the two attracted a few more predators than the other, the difference in

Fig. 1. Container used in olfactometer experiments. It consists of a transparent box (18 × 15 × 8 cm) with one partition in the middle and a lid with two partitions at one-quarter of the distance from the edge. An air inlet and outlet are fixed to the sides of the box. The air outlet is connected to the olfactometer. The inlets are closed with a fine mesh to prevent escape of mites from the box. Bean leaves were put on wet tissue on the bottom of the container. With the lid secured, air can only move as indicated by the arrows, causing an air flow over the surface of the bean leaves.

attractiveness of the two odour sources was never significant. In this way, each experiment had an internal control, against which the effect of a treatment (see below) could be seen.

4. The actual treatment consisted of adding 15–20 conspecific adult female predators to the leaves inside the container that had attracted most predators. This odour source then consisted of two bean leaves with adult female prey, prey eggs (deposited by the adult prey) and adult female predators. The next day, 20 predators was offered a choice between the two odour sources.

MIMICKING PREDATION

When predatory mites are present in a prey patch, they will feed mainly on prey eggs. They do this by inserting their stylet-shaped mouth parts into the eggs and sucking out the contents. In a series of experiments we tried to mimic this feeding activity. Odour sources were prepared as described above in steps 1–3, but instead of adding predators to the most attractive of the two, we used a fine needle to puncture a number of prey eggs equal to the average number of eggs fed upon by the predators in the first series of experiments. Subsequently, an olfactometer experiment was done with one container with prey-infested leaves with intact eggs and the other container with prey-infested leaves with a mixture of intact and punctured eggs.

SEPARATING PREDATORS FROM PREY IN THE ODOUR SOURCE

In another series of experiments, we again followed steps 1–3, but instead of putting predators in the odour source, they were separated from the bean leaves with prey in the containers by putting them on uninfested bean leaves placed on wet cotton wool in a glass tube (diameter 4 cm). This tube was then connected to the air inlet or outlet of the container. Mite-proof gauze prevented the predators from escaping from the glass tube. In this way the odours of predators and of prey-infested leaves were combined, while predators were unable to attack and kill prey.

PREY FEEDING ACTIVITY

The feeding behaviour of adult female prey was observed on bean leaves that were put on water-soaked cotton wool. The leaves were constantly illuminated with a cold-light source, and prey were observed with a binocular microscope (magnification 30 ×) suspended from a stand. Care was taken that the prey were not disturbed during observation. Two treatments with one bean leaf each (originating from the same plant) were done at the same time and under the same conditions. Forty prey were put on each leaf, and after a few hours five adult female predators were

put on one of the leaves. The mites were allowed to settle overnight. During the next day, the numbers of feeding prey were counted twice an hour. The feeding behaviour in treatments and controls was compared pair-wise using the Wilcoxon signed rank test. Four independent experiments were carried out in this way.

A similar series of observations was obtained by placing bean leaves in two containers (Fig. 1), and adding 80 adult female prey (40 per leaf) to them as described above. A transparent lid was fitted to the containers to allow observation of prey behaviour, and a tube with 15–20 predators was connected upwind to one of the containers, as described in the previous section. An olfactometer experiment was done first to compare attractiveness of the container with only prey with the container with prey and upwind predators. After that, the behaviour of the prey was observed as in the previous series, with both containers connected to the olfactometer, so that prey in one container received odours from upwind predators. Only two replicates of this experiment were done because feeding behaviour in the presence or absence of predator odours clearly did not differ in these experiments.

MIMICKING REDUCED PREY FEEDING ACTIVITY

In the experiments described previously, it was found that the presence of predators in the patch caused a reduction in prey feeding time of 15% (see below). To test whether this reduction would lead to a change in attractiveness of an odour source, we mimicked it by reducing the number of adult prey by 15% in one of the odour sources. We offered predators a choice between prey patches with 200 and 170 adult prey, respectively.

REMOVAL OF ADULT PREY

As a final test to elucidate the effect of the presence of adult prey on attractiveness of an odour source, a series of experiments was done with predators present in one of the prey patches, following steps 1–4 of the first series of experiments (see above). Subsequently, all adult prey were removed from the prey patches, whereas prey eggs, prey webbing and predators were left undisturbed. Another series of olfactometer experiments was done with the same odour sources within 1.5 h after removal of the adult prey.

Results

RESPONSE TO ODOURS FROM PREDATOR-INVASED PATCHES

When predators were offered a choice between the odours of bean leaves infested with prey and bean leaves infested with prey and predators, significantly

more predators chose the odour source without conspecifics (Fig. 2), whereas both odour sources had been equally attractive before predators were added to one of them. Clearly, the difference in attractiveness was caused by addition of predators to one of the odour sources, and predators preferred the odours emanating from prey patches without conspecific predators. This effect would be easy to explain if predators on their own are repellent to conspecifics. However, when predators were offered a choice between uninfested bean leaves with and without predators, they were strongly attracted towards conspecifics (Fig. 3, upper bars).

MIMICKING PREDATION

The observed avoidance of predator-invaded prey patches may not be caused by the odours produced by the predators themselves, but rather by their feeding activity. It is possible that volatiles leak from prey eggs damaged by predators, and that these volatiles signal the presence of predators to downwind conspecifics. To test this, we mimicked predation by puncturing eggs with a needle (see the Materials and methods). In contrast to what was found after introduction of predators (Fig. 2), the puncturing of prey eggs resulted in a strong increase in attractiveness of the odour source with punctured eggs relative to the untreated one (Fig. 3, lower bars).

SEPARATING PREDATORS FROM PREY IN THE ODOUR SOURCE

When predators were positioned downwind from the container with prey, predators in the olfactometer significantly preferred the odours of a prey patch combined with predators to odours of a prey patch alone in two out of three experiments (Fig. 4a). This is in agreement with the finding that predators on their own are attractive (Fig. 3, upper bars). When predators were placed upwind from the container with prey, in four out of five replicates, predators in the olfactometer showed a preference for the odour source without conspecifics (Fig. 4b). This preference is comparable to (albeit slightly weaker than) that found when predators were present on the same leaves as the prey (Fig. 2). These experiments show that actual predation on prey or prey eggs is not necessary to make a prey patch less attractive to conspecific predators, but predators need to be positioned upwind from the prey patch. This suggests that either the presence of predators or predator odours cause a change in the behaviour of the spider mite prey, which in turn invokes a change in response in downwind predatory mites.

PREY FEEDING ACTIVITY

One could conceive that prey try to escape when predators (or their odours) are present. As actual escape

Fig. 2. The response of the predatory mite *P. persimilis* to the odours of prey patches with (right) and without (left) conspecific predators. Prey patches consisted of two bean leaves with 200 adult spider mites and their eggs. Shown are the results of four independent experiments. Numbers inside the bars represents the number of individual predators tested. Predators preferred the odours of prey patches without conspecifics in each experiment. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$, two-sided binomial test.

Fig. 3. Top bars: predators (*P. persimilis*) was given a choice between odours emanating from clean bean leaves with (right) and without (left) conspecifics. Shown are the results of four independent experiments. Lower bars: predators could choose between odours from a prey patch with intact prey eggs (left) and a patch with a mixture of intact and artificially punctured eggs (right). Shown are the results of four independent experiments. See Fig. 2 for further explanation.

Fig. 4. The response of predators towards prey patches with and without conspecific predators. Conspecific predators were placed in a separate container positioned downwind (a) or upwind (b) from one of the patches. Shown are the results of three (a) and five (b) independent experiments. See Fig. 2 for further explanation.

in the set-up was prevented by a barrier of water (see the Materials and methods), this would not result in mites disappearing from the leaves, but it is possible that they walk around the leaf to find an exit. This could subsequently lead to less time spent feeding by the prey, and hence to a decrease in damage of the bean leaves. In turn, this is likely to cause a reduced production of volatiles by the leaves, resulting in

reduced attractiveness compared to leaves where prey feed undisturbed. It was indeed found that prey spent less time feeding in the presence than in absence of predators (Fig. 5a). In a subsequent series of experiments, we tested whether the same change in behaviour occurred when predatory mites were not present in the prey patch, but were positioned upwind from the prey, as in the previous section. Olfactometer

Fig. 5. The percentage of spider mite prey that were feeding on a bean leaf. (a) Predators were absent (left) or present (right) in the prey patches. Shown are averages (plus SD) of four independent replicates. The difference between treatments was significant in all four replicates ($P < 0.01$, paired comparison with Wilcoxon signed rank test). (b) Odour from clean bean leaves (left, upper compartment) or odour from bean leaves with predators (right, upper compartment) was led over the prey patches (lower compartments). Shown are averages (plus SD) of two independent replicates. Differences between replicates were not significant.

experiments that were done prior to the observation of prey feeding behaviour again showed that predators avoided prey patches with upwind conspecifics: 15 out of 20 predators chose for the odour source without predators in both experiments ($P < 0.05$, two-sided binomial test, cf. Fig 4b). However, observations on prey feeding behaviour in the odour sources showed no difference in feeding activity between prey that received the odour of predators and prey that did not (Fig. 5b). This shows that the observed change in feeding behaviour in the presence of predators by itself cannot explain the reduced attractiveness of prey patches with predators present.

MIMICKING REDUCED PREY FEEDING ACTIVITY

Further proof for this was obtained from another series of experiments. It can be seen that the presence

of predators in a prey patch caused a reduction in prey feeding time of 15% (Fig. 5a). We mimicked this reduction by reducing the number of adult females in one odour source by 15%. Three replicates of this experiment showed that 11, 8 and 10 out of 20 predators chose for the odour source with fewer prey (not significant, two-sided binomial test). This further corroborates the conclusion that the reduced feeding activity of the prey cannot explain the reduced attractiveness of prey patches with predators.

REMOVAL OF ADULT PREY

Although the reduction in number of prey feeding was not observed when predators were present upwind from the prey patch, it is still feasible that the change in preference of predators is caused by some response of the prey to the presence of (odours of) predators.

We therefore did a series of experiments where we again tested odour sources with and without predators, removed all adult prey, and retested the same odour sources (see the Materials and methods). We again found a preference for prey patches without predators (Fig. 6, upper bars), but this changed to no preference or a preference for prey patches with predators as a result of removal of the adult prey (Fig. 6, lower bars). Clearly, the reduced preference for predator-infested prey patches is associated with the actual presence of adult prey.

Discussion

Our results clearly show that *P. persimilis* females distinguish between odours emanating from prey patches with and without conspecifics. This is not due to the production of odours by predatory mites present in the prey patches; predators themselves probably do produce odours, but these odours are attractive to conspecifics (Fig. 3). We obtained strong evidence that the odour responsible for the decreased attractiveness of prey patches with predators is produced by adult prey: when separating prey from predators, we found avoidance only when predators were present upwind from the prey patch, and not when they were present downwind. In the first case, prey were able to smell predators, whereas in the last case they were not. This suggests that it was the adult prey that produced an odour that elicits avoidance in downwind predators. This was further confirmed by the finding that removal of adult prey resulted in a rapid disappearance of avoidance of predator-invaded prey patches.

When adult prey do produce an odour in response to the presence of (the odours of) predators, it is still an open question what the function of this odour would be. It is possible that spider mite prey produce

an alarm pheromone to warn related conspecifics of the presence of predators. Since spider mite patches are founded by only one or a few adult females, many mites in a patch will be closely related. Identification of the volatiles by means of chemical analyses would facilitate the study of their possible functions.

There is only one other example of members of the third trophic level that respond to odours of competitors present in a patch. This concerns the larval endoparasitoid *Leptopilina heterotoma* (Thompson) (Hym., Eucoilidae). Adult females of this species refrain from visiting patches where another, closely related parasitoid species is present, even in absence of other patches (Janssen *et al.* 1995a,b). There is strong evidence that avoidance of patches with this competitor leads to dramatic changes in distribution of parasitoids over patches in the field (Janssen *et al.* 1995a). In the case of predatory mites, it is still unclear at what spatial scale predators will respond to these odours, and whether this response will lead to avoidance of plants with prey and conspecific predators when no plants with only prey are nearby (see Janssen *et al.* 1997 for a discussion).

It can be concluded that there are now two examples where natural enemies recognize odours associated with con- or heterospecifics from a distance, and that these odours affect the distribution of predators (or parasitoids) over prey patches. Given that odours are important stimuli for many foraging arthropods, we expect that this phenomenon is not restricted to the examples presented here. Instead of visiting patches to determine the presence of conspecific (or heterospecific) competitors, predators and parasitoids can use this mechanism to determine their presence from a distance, and decide whether to avoid or to visit this patch.

Avoidance behaviour in arthropod predators and parasitoids has important implications for ecological

Fig. 6. The response of predators towards prey patches with (right) and without (left) conspecific predators. The upper bars show the results of five experiments with predators present in the prey patch, as in Fig. 2. Again predators preferred odours of the prey patch without conspecifics. After these experiments, adult prey were removed from both odour sources, and the sources were tested again within 1.5 h. The lower five bars show the results of these experiments. The order of bars in the upper and lower half of the figure correspond. See Fig. 2 for further explanation.

theory. First, in studying sex allocation, one should bear in mind that simply confining animals together in an experimental arena to study resulting sex ratios among their offspring is too artificial a set-up. In doing this, a crucial step in the foraging behaviour, i.e. that of patch selection, is disregarded. That patch selection is crucial in sex ratio strategies was shown by Nagelkerke (1994) in a theoretical study of a combined sex-ratio and clutch-size model. He found that it may be an evolutionarily stable strategy for an ovipositing female to visit many patches when patches are nearby, and produce small clutches per patch, even without competition for food. Hence, sex-ratio games between females may provide a driving force for these females to disperse more frequently. Depending on the density of other females, it may either pay to visit patches already occupied by conspecifics, and add a few eggs with a male-biased sex ratio, or to select patches unoccupied by other females (Nagelkerke 1994). A crucial factor in Nagelkerke's (1994) models is the use of information about other predators, both on their presence and on the amount of eggs they produce. He suggested that female predatory mites may be able to recognize each other's eggs. This study shows that predatory mites can already obtain information on the presence of other females from a distance, and they possibly use this information in their sex-ratio and dispersal games.

A second implication of avoidance behaviour for evolutionary ecology is that predators and parasitoids that are able to distinguish between odours from food patches with and without competitors can save time and energy in determining which patches they should visit. Although it is generally agreed upon that parasitoids and predators can by no means be omniscient, the behavioural mechanism revealed in this study may bring them closer to behaving as ideal free foragers than was previously thought possible.

Refraining from visiting patches occupied by conspecifics prevents the formation of predator and parasitoid aggregations on prey patches, which has important consequences for the stability and dynamics of predator-prey and parasitoid-host interactions. As already mentioned in the introduction, van Baalen (1994) and van Baalen & Sabelis (1993) have shown that allowing parasitoids and hosts to distribute themselves in an evolutionarily stable manner leads to a reduction in the parameter space where the classic Nicholson-Bailey model is stable. We therefore expect that including behavioural mechanisms, like the one described here, in population models may have profound effects on model predictions. We hope that this paper not only stimulates such modelling efforts, but that it will also lead to the study of odour-mediated avoidance in other animals.

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