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DOI

[10.1046/j.1365-2311.2000.00240.x](https://doi.org/10.1046/j.1365-2311.2000.00240.x)

Publication date

2000

Document Version

Final published version

Published in

Ecological Entomology

[Link to publication](#)

Citation for published version (APA):

Faraji, F., Janssen, A., van Rijn, P. C. J., & Sabelis, M. W. (2000). Kin recognition by the predatory mite *Iphiseius degenerans*: discrimination among own, conspecific and heterospecific eggs. *Ecological Entomology*, 25(2), 147-155. <https://doi.org/10.1046/j.1365-2311.2000.00240.x>

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Kin recognition by the predatory mite *Iphiseius degenerans*: discrimination among own, conspecific, and heterospecific eggs

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Abstract. 1. Kin recognition is important in many social insects, but has also been found in several nonsocial insects such as parasitoids, where it plays an important role in oviposition behaviour. In nonparasitic arthropods, however, the fitness of ovipositing females also depends on the oviposition behaviour of related and unrelated females, especially when eggs are oviposited in clusters by several females.

2. In this paper, kin recognition in a predatory mite, *Iphiseius degenerans*, is studied. Mothers are capable of determining offspring sex ratio, and cannibalism on juvenile stages is a common phenomenon. Therefore, kin recognition is expected to occur in this predator.

3. Oviposition behaviour of this species is particularly interesting because it alternates foraging bouts in flowers with deposition of a single egg at a time on a leaf, where predation risk is lower. The eggs are not scattered but are deposited in clusters. After feeding in a flower, females therefore have to locate clusters of eggs.

4. Experiments on two-choice arenas showed that females prefer to oviposit close to conspecific eggs rather than close to heterospecific eggs. Females also showed a preference for ovipositing near closely related conspecific eggs rather than more distantly related eggs.

5. Females tended to displace eggs of heterospecifics more frequently than eggs of conspecifics.

6. These behavioural observations show that females can discriminate not only between conspecific and heterospecific eggs but also between eggs that vary in degree of relatedness. This enables females to oviposit in clusters containing related eggs and thus avoid cannibalism by non-kin and/or produce adaptive sex ratios despite the fact that the adults commute between flowers and leaves.

Key words. Cannibalism, clutch size, discrimination, kin recognition, oviposition decisions, sex allocation.

Introduction

It is generally acknowledged that kin recognition is important in many social insects, however there are many reasons for the potential adaptive benefits of kin recognition in nonsocial

arthropods. Fellowes (1998) listed six scenarios where kin recognition would be advantageous for nonsocial arthropods: (1) Resource exploitation strategies may depend on the presence or absence of related conspecifics. (2) Sex allocation strategies depend on relatedness. (3) Kin recognition may be used for avoidance of inbreeding. (4) It can be used to avoid cannibalism on kin. (5) Parasitoids can use kin recognition for deciding to superparasitise. (6) Arthropods may aggregate to reduce risk of predation, and aggregation with related individuals might confer extra fitness advantages.

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There is much argument in the literature over the terminology used for kin recognition (Grafen, 1990, 1991a,b; Barnard, 1991; Byers & Bekoff, 1991; Stuart, 1991). Actually, when the definition of kin recognition is used in its strictest sense, there are no foolproof examples of its occurrence (Barnard, 1991) and it has become a term without practical value. Therefore, the liberty is taken of using the term *kin recognition* to refer to changes in the response of an animal to conspecifics based on relatedness.

Most of the evidence for kin recognition in nonsocial insects comes from hymenopteran parasitoids. They stand out for the immobility of juveniles, who spend their entire juvenile period inside or on the body of one particular host individual. Hence, the ovipositing mother determines the environment in which her offspring will mature. The reproductive success of the mother depends not only on her own oviposition decisions, but also on those of other females and their relatedness to her. For example, to determine whether to superparasitise, it is advantageous for ovipositing females to distinguish their own offspring from other conspecific offspring. Another reason for the evolution of kin recognition in parasitoids is a consequence of the haplodiploid genetic system, where mothers can control the sex of each individual egg. Sex allocation theory predicts female-biased sex ratios when mating occurs frequently among sibs (Hamilton, 1967). Thus, females that can discriminate their own from conspecific offspring can use this information to manipulate the sex ratio in an adaptive manner.

Many parasitoids mark hosts with chemical substances during and/or after oviposition (van Lenteren, 1981; Godfray, 1994), and these marks may well serve to distinguish hosts containing kin from hosts of non-kin. Indeed, kin recognition has been demonstrated experimentally for several species of parasitoids (King, 1992; Godfray, 1994; Ueno, 1994; Ueno & Tanaka, 1996), although other studies show the absence of this discriminative ability (Hooker & Barrows, 1992; Godfray, 1994). In many cases, only conspecifics react to these marks (van Lenteren, 1981), but there are also examples of interspecific recognition of marking substances (Propp & Morgan, 1983; van Baaren *et al.*, 1994; Pijls *et al.*, 1995; see also Godfray, 1994).

Predatory mites (Acari: Phytoseiidae) form a group of arthropods where oviposition in clutches occurs (Nagelkerke *et al.*, 1996). They are small (adult females measure ≈ 1 mm) animals that can feed on phytophagous mites and thrips, as well as on pollen, and they are often used for biological control. As with parasitoids, juveniles from these clutches may compete for food and, upon reaching adulthood, males compete for mates. Despite the fact that males and females arise from fertilised eggs, females can manipulate sex ratio by inducing paternal genome loss during embryogenesis in sons and can thus play sex-ratio games (Sabelis & Nagelkerke, 1987; Nagelkerke *et al.*, 1996; Nagelkerke & Sabelis, 1998). It would therefore be advantageous for ovipositing females to distinguish kin from non-kin (Frank, 1986; Nagelkerke *et al.*, 1996). Cannibalism is a common phenomenon among predatory mites, and this offers another reason why kin

recognition may have evolved in these species. Hence, there are several evolutionary arguments for the occurrence of kin recognition in predatory mites.

There is only limited evidence that predatory mites use cues associated with the presence of conspecific or heterospecific competitors to determine where to feed and oviposit. It is known that patch residence time of predatory mites decreases in the presence of conspecifics (Kuchlein, 1966; Fernando & Hassell, 1980; Hislop & Prokopy, 1981; Sabelis, 1981; Eveleigh & Chant, 1982; Bernstein, 1984; Ryoo, 1986; see Sabelis, 1985 for a review). Moreover, one species of predatory mite, *Phytoseiulus persimilis* Athias-Henriot, was shown to produce fewer daughters when cues left by conspecific females were present in a patch (Sabelis & Nagelkerke, 1987). Recently, evidence was found that predatory and phytophagous mites, like parasitoids, can use volatiles to distinguish patches occupied by conspecific or heterospecific competitors from empty patches (Janssen *et al.*, 1997; Pallini *et al.*, 1997). There have been several studies on interactions between related and unrelated individuals in mites (Radwan, 1993; Saito, 1994; Roeder *et al.*, 1996), but only one study on phytophagous mites has demonstrated an increased female bias in sex ratio associated with increased relatedness among the ovipositing females, indicating kin recognition (Roeder *et al.*, 1996). There has been no study of kin recognition by predatory mites, although it would seem advantageous for ovipositing females to use information to decide where to oviposit and what offspring sex ratio to produce.

The ability of a predatory mite species *Iphiseius degenerans* (Berl.) to distinguish related from unrelated conspecific and heterospecific eggs is reported in this paper. The mite is used as a natural enemy for biological control of phytophagous thrips [*Frankliniella occidentalis* (Pergande)]. When released in a sweet pepper crop, the adults are found more frequently in flowers than on leaves (van Houten & van Stratum, 1995). This is not surprising because the flowers contain foods such as pollen, nectar, and thrips larvae. What is surprising is the observation that *I. degenerans* deposits most of its eggs on leaves and not in flowers (F. Faraji, pers. obs.). Moreover, the eggs are not deposited singly but in clusters containing up to hundreds of eggs. Because predatory mites deposit only one egg at a time, and need to feed between oviposition events, they need to search on leaves until they find a cluster of eggs. This makes this predator unique in comparison with many other arthropod predators that lay eggs close to where they feed. Because *I. degenerans* has to find a specific site for every oviposition and prefers to oviposit in clusters, it seems important that the mite recognises relatedness of the clusters to which it adds eggs. While forthcoming publications will deal with evolutionary reasons for discrimination and oviposition in clusters (i.e. resource exploitation strategies, avoidance of cannibalism, or production of female-biased sex ratios), here the ability to discriminate between kin and non-kin is reported. The experiment was started, however, by testing the ability to discriminate between conspecific and heterospecific eggs, because this is as important for oviposition decisions as being able to recognise kin. For example, to produce an optimal sex

ratio, it is as important to distinguish conspecific from heterospecific offspring as to discriminate among conspecific offspring with varying degrees of relatedness. Moreover, recognition of heterospecific eggs may lead to avoidance of intraguild predation.

Materials and methods

Rearing

A population of *I. degenerans* originating from Rabat, Morocco (van Houten *et al.*, 1995), referred to here as the M-strain, was reared on a diet of birch pollen *Betula pubescens* Ehrh. on plastic arenas (P. C. J. van Rijn and L. K. Tanigoshi, pers. comm.). Arenas consisted of a grey plastic sheet (30 × 21 cm) on a wet sponge. Paper tissues were wrapped over the edges of the arena, serving as a water source as well as a barrier. Each arena surface was divided into four using three narrow filter paper strips (1 × 30 cm). Prior to the experiments, the laboratory population had been cultured for 5 years and this may have led to a high degree of intra-strain relatedness. A second strain was obtained by releasing ≈ 35 adult females from the M-strain on to five flowering castor bean plants *Ricinus communis* L. in a greenhouse, where the mites were reared in isolation for about 18 months; this is referred to here as the G-strain. Females of this strain were transferred to the laboratory and reared on birch pollen, using the method described above. A third field population (I-strain) was obtained from *R. communis* in Givat Shmuel, Israel, and was also cultured on birch pollen in the laboratory for a few generations, following the same method. It was expected that this strain would harbour the largest genetic variation.

Heterospecific predators were represented by three species of predatory mites that were available in the laboratory. *Neoseiulus cucumeris* (Oudemans) and *Typhlodromus pyri* Scheuten were reared on small plastic arenas and fed with broad bean pollen *Vicia faba* L., as described by Overmeer *et al.* (1982). *Phytoseiulus persimilis* was reared on detached common bean *Phaseolus vulgaris* L. cv. Arena or cucumber leaves *Cucumis sativa* L. cv. Ventura infested with two-spotted spider mites *Tetranychus urticae* Koch. Of the three heterospecific predators, only the last occurs sympatric with *I. degenerans* in the Mediterranean, where they are reported on the same host plants, such as *Ricinus communis* (De Moraes *et al.*, 1986).

Experimental arenas

Experiments were performed on oval-shaped green plastic arenas (26 × 52 mm). Using a sharp pencil, two circles (5 mm diameter) were drawn on the arena, their centres 26 mm apart. Food consisting of birch pollen (similar to that used for rearing) was supplied at the centre of the arenas. Sets of five arenas were placed on water-saturated cotton wool. To compensate for any directionality in mite behaviour, arenas

were positioned randomly with respect to direction and the experimental arenas were shielded from direct light from above by a cheesecloth screen.

Experimental procedure

In no-choice experiments, two fresh eggs of either conspecifics or heterospecifics were placed in the centre of one of the circles; in choice experiments, the other circle was also occupied by two fresh eggs. Conspecific eggs were either from the experimental female itself (referred to as own eggs) or from one of the three strains of *I. degenerans*. Experiments started with the placement of a mated female predator from the M-strain or I-strain (10–14 days old) in a random location on the experimental arena. The mobility of these predators is so high that they can move easily from one end of an arena to the other within a minute.

In experiments on interspecific discrimination, conspecific eggs were taken from one of the cultures of the M-strain (but never from that of the female under test), and the females were transferred directly from the culture to the experimental arena. To obtain own eggs, females were isolated individually on an arena, where they oviposited for 2 days. Two freshly laid eggs were transferred to a new arena that was used for experiments the next morning (thus ≈ 18 h later). When females were subjected to tests involving eggs that were not their own, they were still treated in exactly the same way: they were isolated individually on experimental arenas for 2 days, but the eggs they produced were discarded.

One day after introducing the female to the experimental arena, the number of newly laid eggs was recorded. These were distinguished from the eggs that had been added by their lighter colour and greater stickiness. The distance of these eggs from the resident eggs (inside or outside the circle) was scored. Based on these data, the females were categorised into six groups: 1 and 2 – females only laid eggs inside either of the circles (complete preference); 3 and 4 – females laid at least one egg in either of the circles and the rest outside the circles (partial preference); 5 – females laid eggs in both circles and none outside (no preference); 6 – females only laid eggs outside the circles (no preference).

It was observed that females often displaced eggs that were placed on the arena by the experimenter; they were often turned around with the mouthparts. The function of this behaviour is unknown; it may represent unsuccessful attempts to feed on the eggs, females trying to hide their own eggs inside clusters of other eggs, or females assessing the identity of eggs in this way. Nevertheless it was recorded by noting the position of the oval-shaped eggs before and after exposure to ovipositing females. Displacement was recorded and eggs were considered to be displaced when either one or two of the eggs were rotated, placed at another position within the circle, or moved out of the circle. Hence, data on displacement were categorised on a per-female basis. In very few cases, females did not oviposit during the experiment, and data on displacement for these females were discarded. The experiments were conducted in a climate room at 25 °C, 60 ± 5% RH, and LD 24:0 h.

Statistical analysis

Under the null hypothesis of no discrimination, females are expected to distribute their eggs randomly over the arena, resulting in equal probabilities of ovipositing in either of the two circles. Each female that laid eggs in only one of the circles was considered as a separate trial for a binomial test of this null hypothesis, hence the numbers of females that oviposited exclusively in either of the two circles were compared. The same test was used to compare the total number of all females showing a preference (partial plus complete). For statistical analysis of displacement in the choice experiments, the data were also analysed on a per-female basis, as follows from the criteria used for recording displacement. These data were grouped in 2×2 contingency tables and comparisons were made using a chi-square test.

Results

Discrimination between conspecific and heterospecific eggs

When two conspecific and two heterospecific eggs (*N. cucumeris*, *T. pyri*, or *P. persimilis*) were offered, females of *I. degenerans* showed a significant preference for ovipositing close to the cluster of conspecific eggs (Fig. 1). Eggs were deposited much more often within the circle with conspecific

eggs than expected from the ratio of areas of the circle and the arena: 55–80% of the eggs were deposited inside the circle, the area of which was 1.6% of the total arena. On the arena half with heterospecific eggs, 5–10% of the eggs were oviposited inside the circle, suggesting that females preferred to oviposit close to heterospecific eggs rather than randomly on the arena. Displacement of heterospecific eggs occurred significantly more frequently than displacement of conspecific eggs. Ninety-eight, 74, and 84% of the eggs of *P. persimilis*, *T. pyri*, and *N. cucumeris* were displaced compared with only 6–22.5% of conspecific eggs (chi-square test, $P < 0.001$ for all three comparisons).

To investigate further whether females prefer to oviposit near heterospecific eggs rather than anywhere else on the arena, no-choice experiments were carried out where eggs of only one species (conspecific or heterospecific) were offered in one of the circles. Although the number of *I. degenerans* females that oviposited in the circle with eggs of *N. cucumeris* or *T. pyri* was higher than those ovipositing in the other circle without eggs, this preference was not significantly different from a 0.5:0.5 ratio (Fig. 2). There was however a significant preference to oviposit near eggs of *P. persimilis* and even more so near conspecific eggs of the same strain. Displacement of heterospecific eggs again occurred significantly more frequently than displacement of conspecific eggs (*I. degenerans*: 8%, *P. persimilis*: 86.5%, *T. pyri*: 92%, *N. cucumeris*: 88.57%).

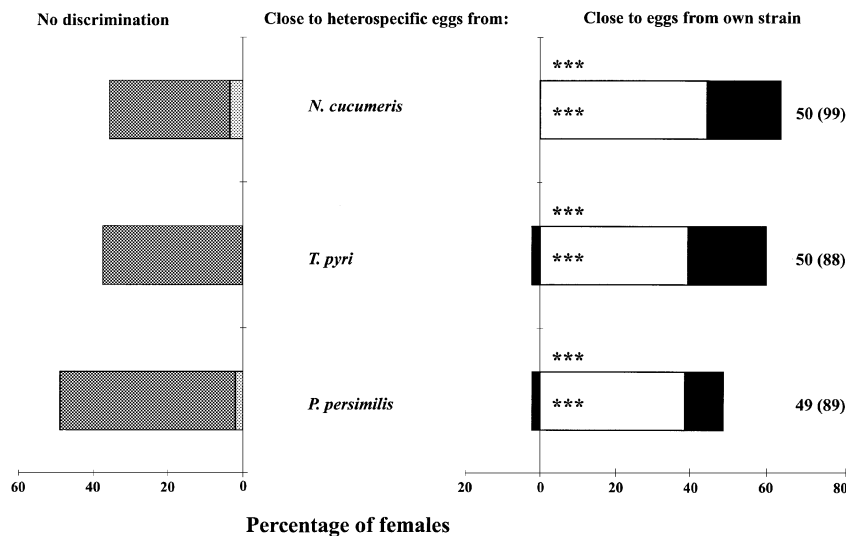


Fig. 1. Oviposition behaviour of *Iphiseius degenerans* females on experimental arenas with a cluster of two conspecific eggs and another cluster of two heterospecific eggs (i.e. *Neoseiulus cucumeris*, *Typhlodromus pyri*, and *Phytoseiulus persimilis*). The right-hand bar graph shows results of females that had complete preference, i.e. females that only oviposited close to one of the two clusters (open bars), and females that had partial preference, i.e. at least one egg was oviposited close to one of the clusters and the rest elsewhere (black bars). Bars extending to the left show percentages with preference for clusters of heterospecific eggs, those extending to the right show percentages of females with preference for clusters of eggs from their own strain. Asterisks inside the bars indicate significance levels of the binomial test against expected proportion of females of 0.5 for either of two clusters. Asterisks above bars indicate significance levels of the binomial test for the proportion of females with complete and partial preference: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, two-sided binomial test. The numbers outside and inside the parentheses refer to the number of females tested and the number of eggs that they produced, respectively. The left-hand graph shows percentages of females without preference, i.e. females that either oviposited close to both clusters (light grey bars) or females that did not oviposit close to any of the two clusters (dark grey bars).

Discrimination between related and unrelated conspecific eggs

When eggs of the I-strain were offered as an alternative, females of the M-strain showed a significant preference for ovipositing in the circle with eggs from other females of their own strain (Fig. 3). Eggs were deposited much more often within the circle with eggs from the own strain than expected from the ratio of areas of the circle and the arena (50.4% of all eggs were in this circle). The circle with eggs from the other

strain received 5.1% of all eggs. In contrast to the experiments with heterospecific eggs, displacement of eggs of both strains was observed only occasionally.

In an additional set of experiments, the females were offered a choice between own eggs and those of conspecifics of the same and other strains. If either the females with complete preference or females with complete and partial preference are considered, there is a significant preference for laying eggs close to own eggs, rather than close to I-strain eggs (Fig. 4). If the alternative eggs were of the same (M) strain, the preference

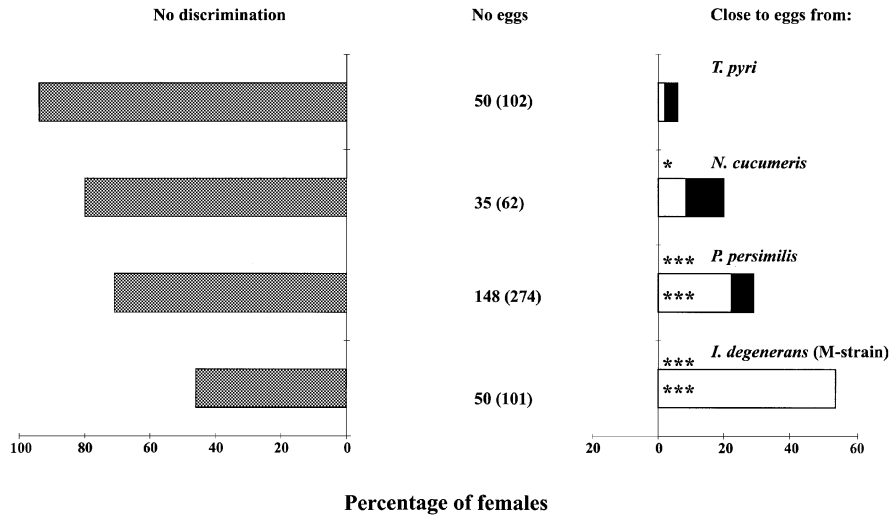


Fig. 2. Oviposition behaviour of *Iphiseius degenerans* females on experimental arenas with a cluster of two conspecific or heterospecific eggs only. See Fig. 1 for further explanation.

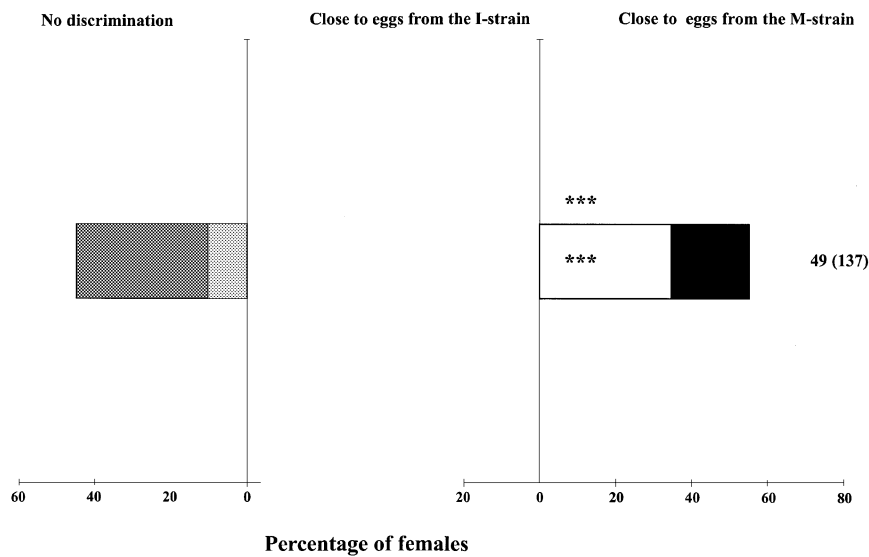


Fig. 3. Oviposition behaviour of *Iphiseius degenerans* females on experimental arenas with a cluster of two eggs from the own (M) strain and a cluster of two eggs from the I-strain. See Fig. 1 for further explanation.

of females was less clear. Of all females with complete preference (eggs in only one of the two circles), 61.5% oviposited near their own eggs. For females with a partial preference, this percentage was 63.6. For the G-strain, which was derived from the M-strain, the preference to oviposit close to own eggs was significant (Fig. 4). Because the I-strain was obtained from the field recently, it was expected to have the highest genetic variation. This strain showed significant discrimination between own and conspecific eggs (Fig. 5).

Discussion

The results show clearly that females of *I. degenerans* can discriminate between conspecific and heterospecific eggs. Females oviposited significantly more frequently near conspecific than near heterospecific egg clusters when these were offered simultaneously. Moreover, females displaced heterospecific eggs much more often than conspecific eggs. Displacement of eggs may result from attempts by the females

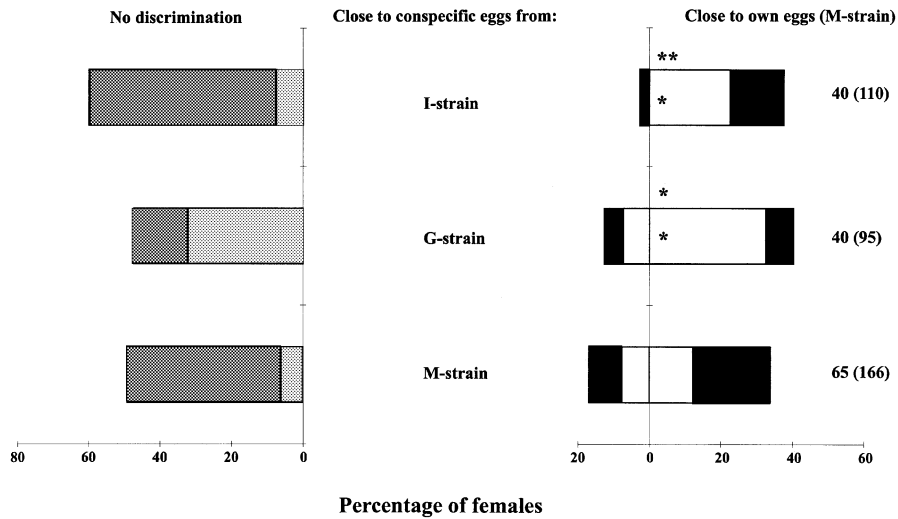


Fig. 4. Oviposition behaviour of *Iphiseius degenerans* females on experimental arenas with a cluster of two own eggs and two eggs from conspecifics (i.e. I-strain, G-strain, or M-strain). See Fig. 1 for further explanation.

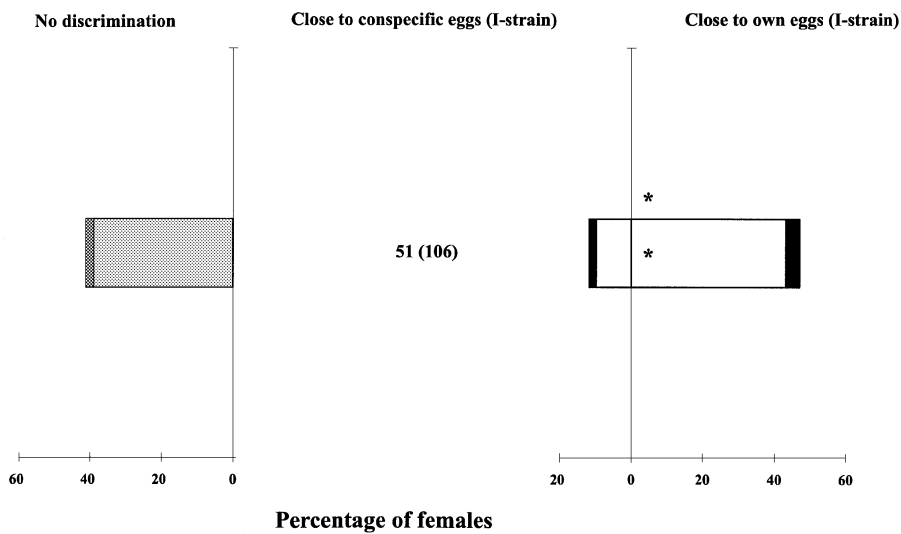


Fig. 5. Oviposition behaviour of *Iphiseius degenerans* females from the I-strain on experimental arenas with a cluster of two own eggs and a cluster of two eggs from conspecifics (I-strain). See Fig. 1 for further explanation.

to feed on them (Yao & Chant, 1989) but, except for very few cases, females were not observed piercing or feeding on eggs (whether conspecific or heterospecific). Females have, however, been observed feeding on larvae (F. Faraji, pers. obs.).

Preference was also strong when unrelated conspecific eggs (from the I-strain) and closely related eggs (M-strain) were offered simultaneously. When own eggs were compared with eggs that were more distantly related (e.g. the G- and I-strain), it was found that preference to oviposit near own eggs increased with decreasing relatedness to the alternative egg cluster. This suggests that females are able to discriminate between conspecific eggs that differ in relatedness. The experiments with own eggs and conspecific eggs from the same strain showed the same trend, but the results were not significant. This may be due partly to a reduced genetic variation within this strain. The preference of females to oviposit close to eggs of their own rather than those of the G-strain, however, suggests that, at the time of creating the G-strain from the M-strain, there was still genetic variation in the M-strain. Females of the I-strain, which was assumed to harbour the greatest genetic variation, showed a significant preference to oviposit near their own eggs over eggs of conspecific females of the same strain.

There seems to be a general tendency for the predatory mites to oviposit preferentially near egg clusters when the alternative is no egg cluster at all: there was a slight but significant preference to oviposit close to clusters of *P. persimilis* eggs, but less so when eggs were of the other two heterospecifics. This may be because egg size of *P. persimilis* and *I. degenerans* is similar whereas the eggs of the other two species are smaller. Hence, one of the characteristics that *I. degenerans* may use to discriminate between conspecific and heterospecifics is egg size.

Apart from egg size, however, there may well be other factors involved in discrimination. It was observed frequently that females contact their own eggs with mouthparts and palps just after oviposition. Much the same behaviour was observed when encountering and displacing other eggs. In this way, females can learn to recognise the physical and chemical properties of their own and other eggs, which may help in discriminating between closely related and distantly related eggs. Choice experiments with washed and unwashed eggs showed that water-soluble cues covering the eggs are used for discrimination (F. Faraji, pers. obs.). Freshly laid eggs are covered with a sticky material, which is removed by washing and may serve as or contain a cue for discrimination.

Because food supply (pollen and young thrips larvae) is much higher in flowers than on leaves, *I. degenerans* spends much time feeding in the flowers, however it was found that the predation risk of predatory mite eggs by thrips was much higher in sweet pepper flowers than on leaves (F. Faraji, pers. obs.). This would explain the occurrence of oviposition on leaves, away from the predator's food. Because females only oviposit one egg at a time and need to feed between ovipositions, the females commute between flowers and leaves. Hence, it is still not clear why the females oviposit eggs in clusters, a behaviour common in *I. degenerans*, because it would involve searching for a cluster each time the

female has to oviposit. The fact that females spend time and energy in locating egg clusters suggests that ovipositing in clusters should have a selective advantage. Females may prefer to add their eggs to clusters because these provide some protection against predation and abiotic factors. Alternatively, clustering may not be the aim of the females, but a by-product of the fact that suitable oviposition sites are scarce. On sweet pepper, for instance, egg clusters are found predominantly in the tufts of hair at the base of the leaf, where leaf veins bifurcate. In the experimental design, however, all places were equal in quality with respect to oviposition, but the predators preferred to oviposit near other eggs. It is believed by the present authors that *I. degenerans* prefer to oviposit near conspecific eggs because clusters provide some protection (see Stamp, 1980 for advantages of ovipositing in clusters).

This leaves unexplained why females discriminate between kin and non-kin and prefer to oviposit next to related eggs. As mentioned already, one explanation involves the production of female-biased sex ratios in the absence of unrelated females, as has been found in spider mites (Roeder *et al.*, 1996). Another explanation involves cannibalism among juveniles. Juveniles were observed to feed on younger stages. Because egg clusters are large and oviposition rates are low, clusters consist of eggs of various developmental stages, and juveniles are probably present in the vicinity. Because juveniles cannibalise each other, a female adding an egg to a cluster with her own eggs and offspring may gain from the fact that cannibalism on kin is avoided. This then requires the ability of juveniles to recognise kin, a topic that deserves further study. Alternatively, even when cannibalism among kin takes place as a consequence of ovipositing in clusters, it is always better to be fed upon by kin than by non-kin. Note, however, that under the last scenario there should be an additional advantage of ovipositing in clusters, such as reduction of predation risk, that should outweigh the disadvantage of cannibalism. The evolutionary reasons for ovipositing in clusters will be dealt with in subsequent papers. A third explanation for kin recognition involves the opportunity for producing female-biased sex ratios when ovipositing in clusters of own eggs. The ability of females to distinguish between kin and non-kin allows them to adjust the sex ratio of the eggs in an adaptive manner (Nagelkerke *et al.*, 1996). In conclusion, it is expected that oviposition in clusters increases survival of offspring, whereas ovipositing in clusters of conspecific or even own eggs has an added advantage, such as the possibility of avoiding cannibalism by non-kin and/or adjusting sex ratio.

The experiments with the predatory mite *I. degenerans* show clearly that females are not only capable of interspecific discrimination but also of discrimination between closely and distantly related conspecifics. Only a few other studies show that nonparasitoid arthropods are capable of recognising kin (Fellowes, 1998). It is expected that kin recognition plays an important role in the oviposition behaviour of other arthropods with relatively immobile offspring, especially because cannibalism on younger stages and oviposition in clusters occur frequently and because many arthropods are capable of regulating offspring sex ratio. Kin recognition in nonsocial arthropods therefore deserves more attention (Fellowes, 1998).

Acknowledgements

We thank Maria Nomikou, Angelo Pallini and Madelaine Venzon for fruitful discussions. We also thank Jan Bruin, Sam Elliot, Takatoshi Ueno and two anonymous referees for helpful comments and critical reviews of this manuscript. Theo Overzier, Ľuděk Tikovský and Jaap Fontijn arranged greenhouse space and took care of the castor bean plants. M.W.S. thanks A. Rubin for supplying *I. degenerans*. The Agricultural Ministry of Iran supported F.F. A.J. was supported by the Life Sciences Foundation (NWO/SLW). P.C.J.v.R. was supported by the Dutch Technology Foundation (NWO/STW).

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Accepted 12 July 1999