

Predators induce egg retention in prey

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Abstract To prevent predation on their eggs, prey often avoid patches occupied by predators. As a result, they need to delay oviposition until they reach predator-free patches. Because many species allocate energy to egg production in a continuous fashion, it is not clear what kind of mechanism prey use to delay oviposition. We used females of the phytoseiid mite *Neoseiulus cucumeris* to study these mechanisms. Females were placed in patches with pollen, a food source they use for egg production, and they were exposed to another phytoseiid mite, *Iphiseius degenerans*, which is an intra-guild predator of *N. cucumeris* juveniles. We found

that the oviposition of *N. cucumeris* females on patches with the predator was lower than on patches without the predator. Cues left by the intraguild predator were not sufficient to elicit such behaviour. Females of *N. cucumeris* reduced oviposition when exposed to the predator by retaining the egg inside their body, resulting in a lower developmental rate once these eggs were laid. Hence, females are capable of retaining eggs, but the development of these eggs continues inside the mother's body. In this way, females gain some time to search for less risky oviposition sites.

Keywords Predator–prey interactions · Antipredator behaviour · Intraguild predation · Predatory mites · Parental care

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Introduction

The extent to which offspring survive predation is an important determinant of parental fitness. Vulnerability to predation is usually high in young developmental stages and decreases with age and size due to higher mobility and increased ability to defend (Aljetlawi et al. 2004; Chase 1999). Hence, we expect selection on parental behaviour to reduce the exposure of their young to predation risks. This prediction holds even if this behaviour entails a risk to the parents themselves, provided that it increases their overall reproductive success (Williams 1966; Trivers 1974; Bell 1980). Parents can protect their offspring by directly defending their nesting or oviposition sites from the attack of predators (Montgomerie and Weatherhead 1988; Koskela et al. 2000; Magalhaes et al. 2005a), and/or by actively searching for predator-free patches for nesting and egg

laying (Murphy 2003a; 2003b; Binckley and Resetarits 2002, 2003; Eitam and Blaustein 2004; Mokany and Shine 2003; Nomikou et al. 2003; Faraji et al. 2002; Kessler and Baldwin 2002; Angelon and Petranka 2002; Reguera and Gomendio 2002; Resetarits 2001; Stav et al. 1999; Mappes and Kaitala 1995).

Selection of alternative sites for nesting or oviposition is time-consuming, and females may have to decide whether to resorb the egg material for later use or to retain the eggs inside their body during the time spent searching for new sites. The distinction between these two tactics is not straightforward. In this article, we investigate whether predators can induce egg retention in prey. We chose a system composed of two species of phytoseiid mites: the prey *Neoseiulus cucumeris* (Oudemans) and the predator *Iphiseius degenerans* (Berl.). Phytoseiid mites are synovigenous organisms (i.e. they continue to allocate energy into oocytes during the adult stage). They can carry only one mature egg at a time, which represents more than 20% of the female body weight (Sabelis 1981). When under stress, the female prey could decide to reallocate her resources to somatic maintenance instead of reproduction, or she could retain the egg inside her body. Both strategies would result in an immediate decrease in the rate of oviposition. Moreover, a reduction in feeding rate due to antipredator behaviour of the prey (e.g. by escaping or reducing conspicuousness to predators by feeding less—Magalhães et al. 2005b) could also result in a decrease in oviposition rate. Therefore, a critical test is needed to discriminate egg retention from other possible mechanisms underlying a reduction in oviposition.

The two species studied here have overlapping distributions in the Mediterranean area (DeMoraes et al. 2004). *I. degenerans* poses a high mortality risk on all mobile juvenile stages of *N. cucumeris*, whereas eggs and adults of *N. cucumeris* are invulnerable. Populations of both species are capable of growing when feeding on pollen. Hence the interaction between them is characterized by resource competition and predation, i.e. intraguild predation (Polis and Holt 1992). Here, we first quantified mortality of juvenile *N. cucumeris* in the presence or absence of adult *I. degenerans* and in the presence or absence of the shared resource (pollen). Subsequently, we investigated whether the presence of a predator affected the oviposition rate of the prey, and whether the prey is able to tune the oviposition rate to changes in the predation risk. Next, we tested whether cues left by the predator in the patch (eggs, faeces, etc.) are sufficient to elicit the same response in the prey. Finally, we investigated whether the changes in the oviposition rates are caused by egg retention, egg resorption, or limited feeding.

If egg resorption or reduced feeding were to occur, the developmental rates of eggs produced in the presence or the absence of predators would not differ. Eggs that are retained, however, continue to develop, resulting in a shortened developmental period after oviposition. Hence, we expected no differences in the developmental rates of eggs in the presence or the absence of predators when eggs were resorbed or when the prey reduced its feeding activities, whereas egg retention would show differences in the developmental rates of eggs oviposited in the presence or in the absence of predators.

Materials and methods

Cultures and experimental conditions

The origin and culture methodology for *I. degenerans* and *N. cucumeris* is described in van Rijn and Tanigoshi (1999). In short, both species were reared on plastic arenas placed on top of sponges in water-containing trays. The edges of the arenas were covered with tissue paper that was in contact with the water, thus serving both as barrier and water source. *I. degenerans* cultures were fed twice per week with birch pollen (*Betula pubescens* Ehrh.), and *N. cucumeris* with *Typha* sp. pollen, supplied twice per week.

All females used in the experiments were 10–14 days old (from egg deposition). Experiments were carried out in a climate room at 25 ± 1 °C, 16:08 hours L/D, and 60 ± 5 RH.

Predation risk of prey offspring

The predation risk experienced by juvenile prey that emerged from eggs in presence of the predator was measured on plastic arenas similar to those used in the cultures (14.5×7.5 cm). Each arena was divided into eight cells (ca. 2×2 cm) with thin strips of filter paper that remained humid through contact with the paper covering the margins. Cells were isolated by a line of Tanglefoot applied on the filter paper. Each cell received five eggs of *N. cucumeris* (ca. 24 h old) and either one female of *I. degenerans* or no predator. Furthermore, cells were either supplied with *Typha* sp. pollen or without pollen to check whether the presence of food for both prey and predators affected predation rates. *Typha* pollen was used because it is a good food source for both predator species (van Rijn and Tanigoshi 1999). The number of replicates per treatment varied between 9 and 13. We counted the number of larvae alive or dead every day for a period of

three days. Differences in the number of dead larvae were analysed with a two-way repeated-measures ANOVA, with presence or absence of the predator and pollen as independent variables, and the number of dead larvae [transformed to $\log(x+1)$ to minimize heteroscedasticity among groups] as the dependent variable.

Oviposition in the presence of the predator

The experimental set-up consisted of oval plastic arenas (5.5×2.5 cm) with abundant *Typha* sp. pollen. The arenas were floating in petri dishes filled with water to prevent the mites from leaving the arena. A piece of cotton wool was deposited in the water film underneath each arena to prevent them from floating to the side of the petri dish. For two consecutive days, we measured the ovipositional rates of *N. cucumeris* that were either in the presence of a predator during the two days (+ +), with a predator during the first day, and alone the second day (+ –), alone during the first day and together with the predator during the second day (– +), alone during the two days (– –), or together with another female of *N. cucumeris* during the two days (two conspecifics), to account for density effects. The number of replicates varied between 16 and 23. To examine the effect of the presence of the predator on the oviposition rate of the prey, the number of eggs in the treatments was analysed with repeated measures ANOVA. Given that our expectations have a priori directionality, i.e. we expected oviposition to decrease in the presence of predators, we performed one-tailed paired *t*-tests for each treatment to assess differences between days, and ANOVAs for each of the two days followed by Fisher's LSD tests to assess differences among groups. This test was chosen because it does not require an equal number of replicates for groups, and it does not require large differences between means for significance. In our case, differences between treatments rely on small differences between means, due to the fact that females lay only 2–3 eggs per day.

Oviposition in the presence of predator cues

To test whether cues produced by the intraguild predator were sufficient to elicit a decrease in the oviposition rate of prey, we used the same type of arenas as in the previous experiments. A female of *I. degenerans* was added to half of the arenas for 24 h. Subsequently, the female was removed, but cues (eggs, faeces, etc.) associated with the presence of the predator were left on the arena. One female of *N. cucumeris* was added to

each of the arenas (hence, with or without predator cues). Oviposition was measured after 24 h, and the females were subsequently transferred to another arena; those that had been exposed to cues of the predator were placed on clean arenas (treatment c+ c–), and females that had been on a clean arena were transferred to an arena with predator cues (c– c+). The number of eggs produced by each prey was counted again 24 h later. Differences in the number of eggs were analysed using the same procedure as described above, including the data of females that were without predators for two days from the previous experiment (– –, see above), as control.

Egg retention as a response to the presence of the predator

Based on data from the literature (De Courcy Williams et al. 2004; Zhang et al. 2000), we estimated the developmental time of eggs of *N. cucumeris* at 25 °C to be in the range of 58–72 h. When eggs are retained, they are older at oviposition, and if embryonic development proceeds in the retained eggs, they are expected to hatch earlier than eggs that followed a normal development. Because females lay only 2–3 eggs per day, detection of egg retention using individual females is potentially hampered by low statistical power. We therefore used groups of five females to test for egg retention. Five females of *N. cucumeris* and two females of *I. degenerans* ($N=18$), or five females of *N. cucumeris* only ($N=17$) were put on a plastic arena with abundant *Typha* sp. pollen. The arenas were similar to but larger than those used in the two previous experiments (5×5 cm), because of the higher number of individuals present per arena. After 24 h, we removed the predators and the eggs of both species. Subsequently, females of both treatments were allowed to oviposit for another 24 h, at which point they were removed. The eggs were further incubated, and the fraction of eggs that hatched was assessed after another 28 and 44 h (therefore the oldest eggs were 52 and 68 h old, respectively). At the first observation, no eggs were expected to have hatched, unless egg retention and development of the retained eggs had occurred, whereas some eggs were expected to have hatched 44 h after the females were removed. The fractions of eggs that hatched 44 h after the removal of the females were compared between treatments using a one-tailed *t*-test, because our hypothesis was that eggs would hatch earlier when prey females were exposed to predators. No analysis was done with the fraction of eggs hatched after 28 h, because no eggs had hatched by this time in the treatment with females that had not been previously exposed to predators.

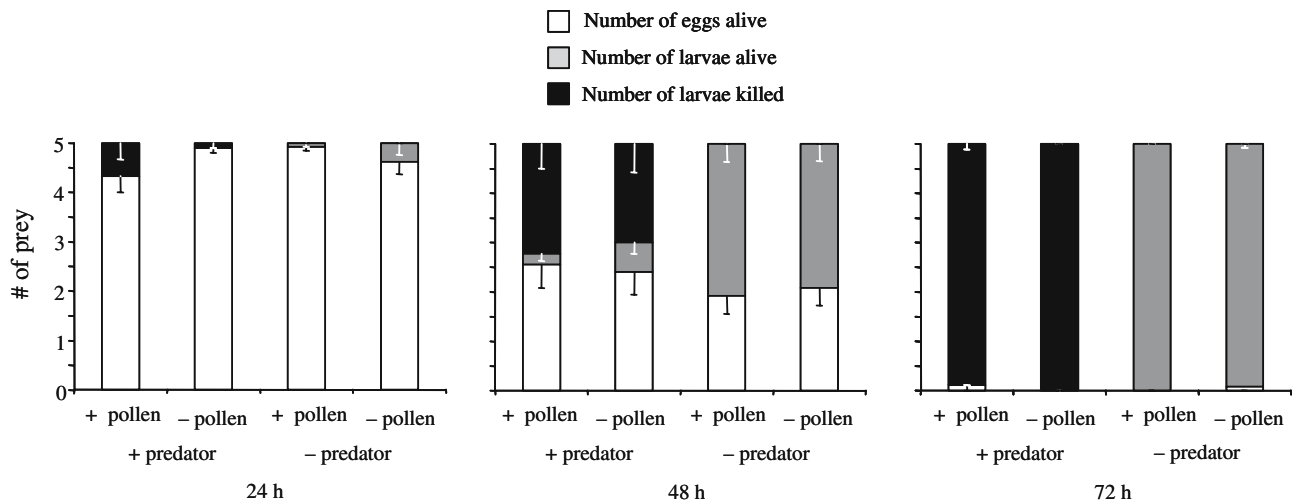


Fig. 1 Rates of predation (larvae/day) of juvenile *N. cucumeris* by adult female *I. degenerans* (\pm SE). Five eggs of the prey were incubated on arenas with or without a predator, and with-

out food (pollen). The fate of the larvae of *N. cucumeris* emerging from the eggs was recorded over a period of three days

Results

Predation risk of prey offspring

The number of prey larvae killed by the predator increased with time (Fig. 1), and the predation rate was not affected by the presence of pollen (see interaction terms in Table 1). All larvae survived in the treatment without predator (Fig. 1).

Oviposition in the presence of a predator

The prey oviposition rate was different depending on the treatment and on the day (Table 2). The univariate analysis revealed that the prey laid fewer eggs in presence of the predator than in its absence (Fig. 2).

Table 1 Two-way repeated measures ANOVA of the $[\log(x+1)]$ number of dead larvae of *N. cucumeris*, depending on the presence of the predator *I. degenerans* and the presence of other food (pollen)

Source	$df_{(source, error)}$	F	P
Between-subjects			
Predator	1, 41	411.20	<0.001
Pollen	1, 41	0.75	0.391
Predator \times pollen	1, 41	0.75	0.391
Within-subjects			
Day	2, 82	118.50	<0.001
Day \times predator	2, 82	118.50	<0.001
Day \times pollen	2, 82	0.39	0.679
Day \times predator \times pollen	2, 82	0.39	0.679

The mortality of the larvae was assessed during three consecutive days

Females exposed to the predator on the first day but not the second had a lower oviposition rate during the first day (Fig. 2, second group of bars; $t_{17}=-2.637$, $P=0.017$), whereas the opposite was found for those females that were without the predator the first day and with the predator the second day (Fig. 2, third group of bars; $t_{15}=3.560$, $P=0.003$). Oviposition rates did not vary between days in the treatments where females were exposed to the same regime during the two days (Fig. 2, first and fourth group of bars; P values >0.3). Thus, prey tuned their oviposition rate to the risk posed by the presence of the predator, and the oviposition rate was recovered within one day of the removal of the predator. If females had fed less during exposure to a predator, we would have expected the oviposition rate on the next day to be lower than that for unexposed females, because the conversion of food into eggs takes time. Hence, the prey probably foraged normally in the presence of the predator. This was expected, because adult prey females are not vulnerable to predation by *I. degenerans*.

The analysis of the effect of density on the oviposition rate of the prey showed differences among the treatments but not within days (Table 3). Fisher LSD tests revealed that the oviposition rates of female prey that were together with a conspecific or alone during the two consecutive days (treatments: two conspecifics and --, respectively) were not significantly different. However, their oviposition rates were significantly different from those of the females that were together with the predator (Fig. 2, compare first, fourth and fifth pair of bars). Additionally, we performed a power test for each of the two days, calculating the root mean

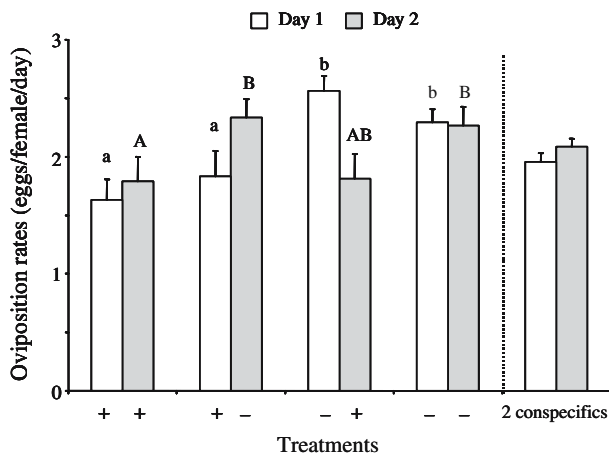


Fig. 2 Average number (\pm SE) of *N. cucumeris* eggs laid during two consecutive days, in presence (+) or absence (–) of the intraguild predator *I. degenerans*. Female *N. cucumeris* were either in the presence of *I. degenerans* for two days (first pair of bars), only during the first day (second pair of bars), only during the second day (third pair of bars), or were without *I. degenerans* for both days (fourth pair of bars). Different small and capital letters above the bars account for statistical differences among treatments for each of the two days. The last pair of bars of the figure shows the number (average \pm SE) of eggs laid per female for two females of *N. cucumeris* that were together during the two days

Table 2 One-way repeated measures ANOVA of the number of eggs laid by females of *N. cucumeris* during two consecutive days, in the presence of the intraguild predator *I. degenerans* for zero, one or two days. Univariate analyses for each of the two days are also shown

Source	<i>df</i> (source, error)	<i>F</i>	<i>P</i>
Between-subjects			
Treatment	3, 66	4.21	0.009
Within-subjects			
Day	1, 66	0.04	0.835
Treatment \times day	3, 66	5.49	0.002
Univariate day 1			
Treatment	3, 66	6.65	<0.001
Univariate day 2			
Treatment	3, 66	3.03	0.035

square standardized effect (RMSSE) averaging the standard deviation of the three groups, to ensure that there was enough power to detect departures from the null hypothesis. This resulted in a power of $P=0.834$ for the first day, and a power of $P=0.921$ for the second day. Therefore, we concluded that our test had sufficient power, thus that density had no effect on the oviposition rate of prey.

Oviposition in the presence of predator cues

The ovipositions of females exposed to cues left by the predator (eggs, faeces) on either the first or the second

Table 3 One-way repeated measures ANOVA to assess the effect of density on the number of eggs laid by the prey *N. cucumeris* during two consecutive days

Source	<i>df</i> (source, error)	<i>F</i>	<i>P</i>
Between-subjects			
Treatment	2, 56	9.04	<0.001
Within-subjects			
Day	1, 56	0.79	0.378
Treatment \times day	2, 56	0.20	0.819

day of the experiment [treatments: (c+ c–) and (c– c+), respectively] did not differ significantly from the control without predator cues (treatment – –, Table 4). Additional power tests for each of the two days, that used the average of the standard deviations of the three groups to calculate the RMSSE, resulted in powers of $P=0.829$ and $P=0.875$ for the first and second days, respectively. Hence, we concluded that predator cues did not affect the oviposition behaviour of the prey (Fig. 3).

Egg retention as a response to the presence of the predator

Eggs that were laid by *N. cucumeris* females in the presence of the predator hatched earlier than those laid by females in its absence. After 28 h, an average

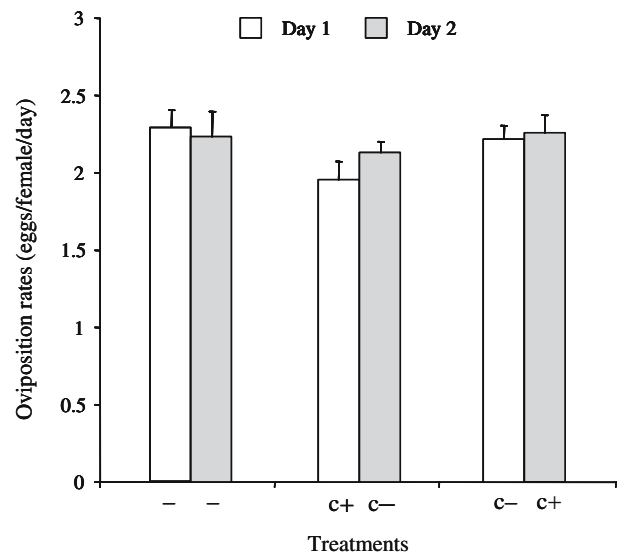


Fig. 3 Average number (\pm SE) of *N. cucumeris* eggs laid during two consecutive days, in relation to the presence (+) or absence (–) of cues (eggs, faeces, etc.) of the predator *I. degenerans*. Females of *N. cucumeris* were in arenas with cues of *I. degenerans* only during the first day (first pair of bars), or only during the second day (second pair of bars). The treatment from the previous experiment, where females were alone for two consecutive days, was taken as the control (third pair of bars)

Table 4 One-way repeated measures ANOVA of the $[\log(x+1)]$ number of eggs laid by the prey *N. cucumeris* during two consecutive days, in the presence or absence of cues (eggs, faeces, etc.) of the intraguild predator *I. degenerans*

Source	$df_{(source, error)}$	F	P
Between-subjects			
Treatment	2, 60	2.72	0.074
Within-subjects			
Day	1, 60	0.31	0.579
Treatment \times day	2, 60	0.49	0.614

(\pm SE) fraction of 0.05 ± 0.02 eggs of the females previously exposed to predators had hatched, whereas no larvae were found in the treatment without predator exposure. After 48 h, the average fraction of larvae emerging from eggs of prey females exposed to predators was higher than that of females that were not (0.48 ± 0.05 vs 0.32 ± 0.04 , respectively. One-tailed t -test: $t_{33} = 2.85$, $P = 0.007$). This indicates that females retained the eggs as a response to the presence of predators, and that embryonic development proceeded in the retained egg.

Discussion

The predator *I. degenerans* posed a high risk of predation to juveniles of *N. cucumeris*, even when a shared food resource (pollen) was available. In the presence of this predator, females of *N. cucumeris* were found to be reluctant to lay eggs. Because eggs laid by females previously exposed to predators had a significantly shorter developmental time than eggs laid by unexposed females, it can be concluded that the presence of a predator elicited egg retention in prey females. Egg retention was elicited only when the predator was present; predator cues (faeces, pheromones, etc.) were not sufficient to elicit such a behaviour.

The ability of females to find patches where their offspring will run a low risk of being killed may be a crucial determinant of their fitness. Retaining eggs is one possible mechanism by which prey females can protect their offspring from predators. This behaviour could therefore be considered to be a rudimentary form of parental care (Trivers 1972).

There are many methods by which prey can take care of their offspring. Apart from avoiding patches occupied by predators and delaying oviposition, prey females could also actively defend their offspring, chase away predators, or even kill the predator's offspring. These strategies are not mutually exclusive, and prey females could adopt any of them, depending

on the context. For instance, *I. degenerans*, one of the species studied here, oviposits nearby food patches when a predator of its eggs, the thrips *Frankliniella occidentalis* Pergande, is absent. In the presence of the thrips, however, they oviposit away from the food source (Faraji et al. 2001; Janssen et al. 2002). When predators have already laid eggs, the presence of counterattacking prey does not elicit avoidance of the patch; on the contrary, females stay closer to their eggs and protect them by killing thrips larvae in the vicinity of their offspring (Magalhães et al. 2005a). In addition to these two strategies, it has been recently observed that these predators are probably also able to retain their eggs (T. van der Hammen, personal communication). In variable environments, this flexibility in strategies adopted by species is probably a crucial determinant of their reproductive success. However, such flexibility also requires the utilisation of specific cues. Our results suggest that the presence of the predator is necessary to trigger egg retention, which is not the case in the strategies defined above. This suggests that either the species use different cues, or that different strategies require different cues. Intuitively, the more costly the behaviour, the more it should be displayed only when cues are sufficiently reliable. Egg retention is probably very costly, since delaying oviposition impedes the formation of a new egg. Therefore, it should be displayed only in the presence of very reliable cues, such as encounters with predators. In contrast, killing counterattacking prey is probably less costly, because predators are acquiring nutrients while defending their offspring. In agreement with our reasoning, they also display this defensive behaviour only in the presence of predator cues (Magalhães et al. 2005a).

Egg retention should be distinguished from phenotypic variation in oviposition rate and in egg maturation rate. A population may consist of individuals that each have different fixed rates of egg maturation (Boutreau-Merle and Fouillet 2002), but this does not imply that individuals can retain eggs. Egg retention, in contrast, is characterised by individual flexibility in oviposition rate and the residual rate of egg maturation after egg deposition. To our knowledge, this is the first paper demonstrating that the developmental state at which eggs are deposited can vary within one individual, and that this can be controlled by external cues such as the presence of predators. It is rather spectacular that such a basal characteristic of species (oviparity) is not as fixed as previously thought.

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