Threat-sensitive anti-intraguild predation behaviour: maternal strategies to reduce offspring predation risk in mites

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Predation risk is a major selective force for the evolution of behavioural characteristics of prey. Predation among consumers competing for food is termed intraguild predation (IGP). From the perspective of individual prey, IGP differs from classical predation in the likelihood of occurrence because IG prey is usually more rarely encountered and less profitable because it is more difficult to handle than classical prey. It is not known whether IGP is a sufficiently strong force to evolve interspecific threat sensitivity in antipredation behaviours, as is known from classical predation, and if so whether such behaviours are innate or learned. We examined interspecific threat sensitivity in antipredation in a guild of predatory mite species differing in adaptation to the shared spider mite prey (i.e. *Phytoseiulus persimilis*, *Neoseiulus californicus* and *Amblyseius andersoni*). We first ranked the players in this guild according to the IGP risk posed to each other: *A. andersoni* was the strongest IG predator; *P. persimilis* was the weakest. Then, we assessed the influence of relative IGP risk and experience on maternal strategies to reduce offspring IGP risk: *A. andersoni* was insensitive to IGP risk. Threat sensitivity in oviposition site selection was induced by experience in *P. persimilis* but occurred independently of experience in *N. californicus*. Irrespective of experience, *P. persimilis* laid fewer eggs in choice situations with the high- rather than low-risk IG predator. Our study suggests that, similar to classical predation, IGP may select for sophisticated innate and learned interspecific threat-sensitive antipredation responses. We argue that such responses may promote the coexistence of IG predators and prey.

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spiders: Matsumura et al. 2004). Although the nutrient composition of IG prey per se seems favourable for IG predators (Denno & Fagan 2003; Matsumura et al. 2004), subduing, capturing and killing IG prey is energetically costly because IG prey are predators themselves and in mutual IGP may counterattack their predators. In extreme cases, the energetic costs of IGP may even exceed the benefits obtained (predatory mites: Lawson-Balagbo et al. 2008). In addition, true predators (carnivores and omnivores), and consequently potential IG prey, are usually less abundant than classical prey such as herbivores (Begon et al. 1996), reducing the predator—prey encounter frequency and making predator adaptations that help exploit IG prey more efficiently less likely than adaptations that improve exploitation of classical prey. Hence, although omnipresent in natural and artificial food webs (Pollis et al. 1989; Arim & Marquet 2004) IGP events should be rarer than classical predation events. It is not known whether IGP is enough of a selective force to evolve interspecific threat-sensitive anti-predation behaviours in IG prey, as is common in classical predation.

A precondition for displaying effective threat-sensitive anti-predation responses is the ability to recognize a given predator species by direct and/or indirect cues. In general, recognition of predator species can be innate or learned, or a combination of both, ranging from strictly innate recognition unaffected by experience (e.g. tadpoles: Gallie et al. 2001) to innate recognition modifiable by experience (e.g. fish: Hawkins et al. 2008) to recognition only after experience (e.g. rodents: Kindermann et al. 2009). However, most studies on interspecific threat-sensitive anti-predation behaviour do not allow discrimination between innate and learned predator recognition because of studying wild animals in the field (e.g. Edelaar & Wright 2006; Blumstein et al. 2008) or using either wild-caught or experienced experimental animals (Kiesecker et al. 1996; Stapley 2003; Botham et al. 2008; Monclús et al. 2009). Unambiguous evidence for learned threat sensitivity is rare and mostly relates to intraspecific threat sensitivity in aquatic or semiaquatic animals such as larval mosquitoes, tadpoles, fishes and water striders in classical predator—prey interactions (Ferrari et al. 2005, 2008; Ferrari & Chivers 2009; Hirayama & Kasuya 2009). Evidence for learned interspecific threat sensitivity in IGP and terrestrial animals is lacking.

We studied the influence of predation risk and experience on anti-predation strategies within a guild of three predatory mite species: Phytoseiulus persimilis, Neoseiulus californicus and Amblyseius andersoni (Acari: Phytoseiidae). All three species are plant-inhabiting predators of phytophagous mites (e.g. McMurtry & Croft 1997; De Moraes et al. 2004). They naturally co-occur in the Mediterranean basin (De Moraes et al. 2004; A. Walzer, personal observation), presumably share a long coevolutionary history and interact with each other via competition for shared prey, such as the two-spotted spider mite, Tetranychus urticae (Acari: Tetranychidae), and mutual IGP. They differ in diet breadth and adaptation to, and strength in competition for, spider mites. Phytoseiulus persimilis is a highly specialized predator of spider mites and the strongest competitor; N. californicus is a generalist predator with a ranked preference for spider mites and an intermediate competitor while A. andersoni is a generalist predator poorly adapted to utilize spider mites as prey and therefore the weakest competitor for spider mites (McMurtry & Croft 1997). Regarding the propensity to engage in IGP, the ranking is reversed, with A. andersoni being a highly aggressive IG predator, followed by the intermediate N. californicus. Phytoseiulus persimilis is a comparably weak IG predator, only occasionally preying on other predatory mites (Walzer & Schausberger 1999; Schausberger & Croft 2000b). Thus, owing to a joint natural history and presumable differences in the IGP risk posed to each other, the three predatory mites are perfectly suitable animals to test for threat-sensitive anti-IGP behaviours.

As with many other animals (Polis et al. 1989), IGP among phytoseiid mites is mutual but asymmetric with respect to size. Small/younger juveniles are usually preyed upon by larger/older juveniles and/or adult females, whereas adult females and eggs are relatively invulnerable to IGP (Croft et al. 1996; Schausberger 1997; Walzer & Schausberger 1999; Schausberger & Croft 2000b). The larva is the smallest and least mobile juvenile stage and most in danger of falling victim to larger IG predators (Walzer & Schausberger 1999; Schausberger & Croft 2000b). The IGP risk for larvae may be reduced by antipredation behaviours of the larvae themselves (e.g. Schausberger 2003) or by maternal investment in reducing larval predation risk (Faraji et al. 2001; Walzer et al. 2006). Here, we focused on the latter. Foraging gravid phytoseiid females facing IG predators have several possibilities for decreasing the predation risk of their offspring. They may avoid prey patches with IG predators and choose predator-free patches for oviposition (e.g. Walzer et al. 2006); they may kill potential IG predators of their offspring (e.g. Schausberger & Croft 2000b); or they may reduce/postpone oviposition in the presence of IG predators (e.g. Montserrat et al. 2007; Abad-Moyano et al. 2010a) and resume oviposition when conditions improve.

We investigated the influence of IGP risk and IG predator experience of IG prey on the above-mentioned three maternal strategies to reduce offspring IGP risk. In the first experiment, we assessed the relative risk that Phytoseiulus persimilis, N. californicus and A. andersoni posed to each other in IGP, allowing categorization of each species as a low- or high-risk IG predator of another species. In the second experiment, we scrutinized prey patch choice and oviposition behaviour of IG predator-naïve and predator-experienced females of P. persimilis, N. californicus and A. andersoni when confronted with low- and high-risk IG predators.

METHODS

Species Origin and Rearing

Phytoseiulus persimilis, N. californicus and A. andersoni are indigenous, co-occurring species in Sicily (De Moraes et al. 2004). All three species were sampled from herbs and trees in the state of Trapani in 2007. About 20—30 specimens of each species were used to initiate populations reared in the laboratory. Rearing arenas consisted of plastic tiles resting on water-saturated foam cubes in plastic boxes half-filled with water. The edges of the tiles were covered with moist tissue paper to confine the predators to the rearing arenas. Cotton wool fibres under coverslips served as shelter and oviposition sites for A. andersoni. To prevent contamination of the predator populations, an adhesive (Raupenleim, Avenarius Agro, Wels, Austria) was applied to the rim of the plastic boxes and the boxes were placed in a tray containing water with dishwashing detergent. The predators were fed in 2—3-day intervals with T. urticae, reared on whole bean plants (Phaseolus vulgaris), by adding bean leaves infested with spider mites (for P. persimilis, N. californicus) or by brushing spider mites from infested leaves (for A. andersoni) onto arenas.

Categorization of IG Predators

In the first experiment, we assessed the IGP risk posed by adult females to larvae to categorize each species as a low- or high-risk predator of another species (Schausberger & Croft 2000b). We measured the attack probability and attack latency of IG predator females on IG prey larvae confined in closed acrylic cages. Each cage consisted of a cylindrical cell (15 mm in diameter and 3 mm in
ments were all possible combinations of *P. persimilis*, *A. andersoni* and *N. californicus* as IG predators and prey. Gravid females randomly taken from the rearing units were singly placed into closed cages and starved for 12 h. Subsequently, a single hetero-specific larva was added to each cage. Each female and each larva was used only once. Each cage was checked for the first successful attack of the predator female on larval prey (killed and sucked out) every 10–15 min for 6 h at the longest. Each treatment (predator–prey combination) was replicated 19–20 times.

**Prey Patch Choice and Oviposition Behaviour**

In the second experiment, we assessed prey patch choice and oviposition behaviour of IG predator-naïve and predator-experienced females of *P. persimilis*, *N. californicus* and *A. andersoni* given a choice between a spider mite patch with and without cues (traces of foraging females and their eggs) from a low- or high-risk IG predator. We used a full 3 (IG prey female species) × 2 (naïve and experienced) × 2 (cues of high- and low-risk IG predator) factorial design. Each choice situation was replicated 20–31 times.

**Generating Naïve and Experienced Prey Females**

To obtain naïve and experienced prey females for experiments, three groups of 13–15 eggs each of *A. andersoni*, *N. californicus* and *P. persimilis* were randomly taken from the rearing units and placed on separate leaf arenas for development. Each leaf arena consisted of a detached bean leaf (5 × 5 cm) placed upside down on a water-saturated foam cube in a plastic box half-filled with water. Water-saturated cellulose strips (1 cm height) at the edge of the leaf confined the arena and prevented the mites from escaping. For each species, one group of eggs was placed on a leaf with only spider mites (to be used as naïve IG prey females in experiments), and the second and third groups of eggs were placed on separate leaves with spider mites and either five low- or high-risk IG predator females, respectively (to be used as experienced IG prey females in experiments). The developmental progress of IG prey was observed above the above-mentioned pre-experimental procedure, the presence of an IG predator in a given spider mite patch was indicated by traces left by the foraging and ovipositing IG predator (e.g. metabolic waste products and/or chemical footprints), eggs laid and killed spider mites (Grostal & Dicke 1999).

Before we ran the choice experiments, each experimental IG prey female was singly placed into a closed acrylic cage (described above) and starved for 12 h. Only females producing at least one egg during the starvation period were used for experiments. Subsequently, each female was singly released in the middle of the wax bridge and given a choice between a prey patch with only spider mites and a prey patch with spider mites and cues of either a low-risk or a high-risk IG predator (determined for each species in experiment 1). Each choice unit and each IG prey female was used only once. The position of the IG prey female was checked eight times during the experiment (immediately after release (first choice), and then after 1, 2, 3, 4, 5, 6 and 24 h). After 24 h we recorded eggs deposited in each prey patch and predation by the IG prey female on IG predator eggs.

**Statistical Analyses**

Statistical analyses were carried out for each species separately using SPSS 15.0.1 (SPSS, Chicago, IL, U.S.A.). In experiment 1, larval survival functions (combination of cumulative survival and survival time), used as indicators of the relative IG risk posed by the other two species, were analysed by the Kaplan–Meier procedure and pairwise Breslow tests (Bühl 2008). In experiment 2, the influence of experience (naïve versus experienced) and predation risk (low versus high risk) on the residence frequency of IG prey females in prey patches with IG predator cues during the experiment (presence in the prey patch with IG predator cues out of eight observation points) was analysed using generalized linear models (GLM; counts of events; binomial distribution with logit link function; Bühl 2008). Within each choice situation, the numbers of eggs laid in the prey patch with and without predator cues were compared by Wilcoxon signed-ranks tests owing to non-normality of data. The influence of experience and predation risk on total egg production (eggs laid in both prey patches combined; log-transformed) and the number of IG eggs preyed upon by the IG prey...
females were analysed using two-factorial (experience and predation risk) ANOVAs. The proportion of eggs laid by the IG prey females in prey patches with IG predator cues (eggs in patch with IG predator cues out of total egg production; females producing no eggs were removed from the analysis) were compared among treatments using GLMs (counts of events; binomial distribution with logit link function; Bühl 2008).

RESULTS

Categorization of IG Predators

For each species, the survival functions of larvae differed significantly between the two IG predator species (Fig. 1; Breslow tests within Kaplan–Meier analyses). Based on these differences we categorized the two IG predators of a given species as low- and high-risk predators: for Amblyseius andersoni, low-risk P. persimilis and high-risk N. californicus (chi-square test: $\chi^2 = 4.507$, $P = 0.034$); for Neoseiulus californicus, low-risk P. persimilis and high-risk A. andersoni ($\chi^2 = 9.743$, $P = 0.002$); for P. persimilis, low-risk N. californicus and high-risk A. andersoni ($\chi^2 = 13.875$, $P < 0.001$).

Prey Patch Choice and Oviposition Behaviour

Amblyseius andersoni

Prey patch choice by A. andersoni females was influenced by experience but not by predation risk (Table 1). Experienced females resided in prey patches with IG predator cues less often than naïve females (Fig. 2).

Within choice situations, experienced females confronted with cues of the high-risk predator deposited more eggs in the patch with predator cues (Wilcoxon signed-ranks exact test: $Z = -2.822$, $N = 28$, $P = 0.005$). In the other choice situations the numbers of deposited eggs did not differ between patches with and without predator cues ($P > 0.05$; Fig. 3). Total egg production was not affected by experience, predation risk or the interaction of the two sources of variation (ANOVA experience: $F_{1,96} = 0.159$, $P = 0.691$; predation risk: $F_{1,96} = 0.353$, $P = 0.554$; experience*predation risk: $F_{1,96} = 0.889$, $P = 0.348$). The proportion of eggs laid in the prey patch with IG predator cues was marginally influenced by experience (GLM: Wald $\chi^2 = 3.446$, $P = 0.063$) but not by predation risk (Wald $\chi^2 = 0.001$, $P = 0.995$) or the interaction between experience and predation risk (Wald $\chi^2 = 1.057$, $P = 0.304$). Experienced females laid a slightly higher proportion of eggs in prey patches with IG predator cues than naïve females (Fig. 3).

The IGP rates of A. andersoni were not influenced by experience (ANOVA: $F_{1,96} = 1.999$, $P = 0.161$) and predation risk ($F_{1,96} = 0.317$, $P = 0.575$) as main effects but were influenced by the interaction of

| Table 1 | Generalized linear model for the influence of predation risk (low versus high) and experience (naïve versus experienced) on prey patch choice (residence frequency in the prey patch with IG predator cues out of eight observation points) by IG prey females of A. andersoni, N. californicus and P. persimilis |
|---------|---------------------------------------------------------------|
| Species | Variables          | $df$ | Wald $\chi^2$ | $P$   |
| A. andersoni | Experience          | 1   | 14.083        | <0.001|
|           | Predation risk      | 1   | 0.413         | 0.091 |
|           | Experience*predation risk | 1 | 0.246       | 0.620 |
| N. californicus | Experience          | 1   | 4.080         | 0.043 |
|           | Predation risk      | 1   | 0.792         | 0.373 |
|           | Experience*predation risk | 1 | 5.043       | 0.015 |
| P. persimilis | Experience          | 1   | 2.415         | 0.120 |
|           | Predation risk      | 1   | 4.087         | 0.043 |
|           | Experience*predation risk | 1 | 8.025       | 0.005 |

Figure 1. Survival of singly caged IG prey larvae of (a) A. andersoni, (b) N. californicus and (c) P. persimilis when confronted with a high-risk (solid line) or low-risk (dotted line) IG predator female for 360 min.
and a prey patch with cues of a low-risk (white bars) or high-risk (black bars) IG predator. Each female was given a choice between a prey patch with only spider mites or without IG predator cues, except experienced females subjected to the choice with the high-risk IG predator A. andersoni, which were more often found in the prey patch with only spider mites (Table 1, Fig. 2).

Within choice situations, experienced females confronted with cues of the high-risk predator deposited more eggs in the prey patch with only spider mites (Wilcoxon signed-ranks exact test; \( Z = -2.658, N = 31, P = 0.008 \)). In the other choice situations, the numbers of deposited eggs did not differ between patches with and without predator cues (GLM: Wald \( \chi^2 = 3.382, P = 0.070 \); Fig. 3). Total egg production was unaffected by experience and predation risk (ANOVA: experience: \( F_{1,110} = 0.112, P > 0.05 \); predation risk: \( F_{1,109} = 0.354, P = 0.556 \); experience*predation risk: \( F_{1,110} = 0.253, P = 0.616 \); Fig. 3). Irrespective of experience, the proportion of eggs laid in prey patches with predator cues was higher in choice situations with the low-risk IG predator than in those with the high-risk IG predator (GLMs: experience: Wald \( \chi^2 = 0.121, P = 0.728 \); predation risk: Wald \( \chi^2 = 8.928, P = 0.003 \); experience*predation risk: Wald \( \chi^2 = 2.710, P = 0.100 \); Fig. 3).

The IGP rates of N. californicus were not influenced by experience (ANOVA: \( F_{1,111} = 0.002, P = 0.951 \)) and predation risk (\( F_{1,111} = 0.612, P = 0.330 \)) as main factors but were influenced by the interaction of these two sources of variation (\( F_{1,111} = 3.010, P = 0.032 \)). Irrespective of predation risk, experienced females killed similar numbers of eggs of the low- and high-risk IG predator (mean \( \pm SE = 0.6 \pm 0.2, N = 27 \) versus 0.5 \( \pm 0.1, N = 30 \)), whereas naïve females killed more eggs of the high-risk IG predator than of the low-risk IG predator (0.8 \( \pm 0.2, N = 27 \) versus 0.3 \( \pm 0.1, N = 31 \)).

Phytoseiulus persimilis

The influence of predation risk on prey patch choice by P. persimilis females was dependent on experience (Table 1, Fig. 2). Experienced females resided more often in the predator-free prey patch in choice situations with the high-risk IG predator compared with the other choice situations (Fig. 2).

Within each choice situation P. persimilis deposited more eggs in the prey patch without predator cues than in the prey patch with predator cues (Wilcoxon signed-ranks exact test: naïve female/harmless predator: \( Z = -3.106, N = 26, P = 0.002 \); naïve female/harmful predator: \( Z = -3.382, N = 22, P = 0.001 \); experienced female/harmless predator: \( Z = -2.519, N = 27, P = 0.012 \); experienced female/harmful predator: \( Z = -4.193, N = 23, P < 0.001 \); Fig. 3). Total egg production was affected by predation risk but not by experience (ANOVA: experience: \( F_{1,94} = 0.354, P = 0.533 \); predation risk: \( F_{1,94} = 7.533, P = 0.007 \); experience*predation risk: \( F_{1,94} = 0.045, P = 0.833 \)). Irrespective of experience, P. persimilis females produced fewer eggs in choice situations with the high-risk IG predator than in choice situations with the low-risk IG predator (GLM: Wald \( \chi^2 = 7.377, P = 0.007 \)) but not experience (GLM: Wald \( \chi^2 = 2.647, P = 0.104 \)).

Figure 2. The influence of experience and IGP risk on residence of (a) A. andersoni, (b) N. californicus and (c) P. persimilis females in the prey patches with spider mites and IG predator cues (eggs and traces such as metabolic waste products and/or chemical footprints of an IG predator female; mean proportion \( \pm SE \) calculated from eight observations during 24 h). Each female was given a choice between a prey patch with only spider mites and a prey patch with cues of a low-risk (white bars) or high-risk (black bars) IG predator.
the patch with predator cues in choice situations with the high-risk IG predator but not in choice situations with the low-risk IG predator (Fig. 3).

The IGP rates of *P. persimilis* (mean ± SE = 0.11 ± 0.06, N = 26 versus 0.12 ± 0.06, N = 29 and 0.04 ± 0.04, N = 22 versus 0.09 ± 0.06, N = 23 eggs of the high- and low-risk IG predator for naïve and experienced females, respectively) were unaffected by experience and predation risk (ANOVA: experience: $F_{1,94} = 0.599, P = 0.441$; predation risk: $F_{1,94} = 0.189, P = 0.665$; experience*predation risk: $F_{1,94} = 0.132, P = 0.718$).

**DISCUSSION**

Our study shows that IGP is a sufficiently strong force to select for interspecific threat sensitivity in antipredation behaviours. It documents innate and learned interspecific threat-sensitive anti-IGP responses and provides experimental evidence for learned threat-sensitive antipredation in a strictly terrestrial animal (e.g. Kats & Dill 1998). We observed three maternal strategies to reduce predation risk of offspring. These strategies are common in classical predator–prey interactions but are less well documented for IGP, that is, killing predators (for classical predation: Saito 1986; for IGP: Walzer & Schausberger 2009), decreasing and postponing oviposition (for classical predation: Skaloudova et al. 2007; for IGP: Montserrat et al. 2007) and oviposition site avoidance (for classical predation: Grostal & Dicke 1999; Murphy 2003; for IGP: Walzer et al. 2006). However, the strategies adopted, threat sensitivity and the influence of predator experience differed between species. First, IG prey females of all three species killed IG predator eggs. IG egg predation was most pronounced in *A. andersoni* and negligible...
in *P. persimilis*. Only naïve *N. californicus* females behaved in a threat-sensitive manner in IG egg predation. Second, both naïve and experienced *P. persimilis* females laid fewer eggs in the presence of the high-risk IG predator than in the presence of the low-risk IG predator, indicating innate threat sensitivity. Egg production by *A. andersoni* and *N. californicus* was unaffected by predation risk and experience. Third, both *N. californicus* and *P. persimilis* were threat sensitive in oviposition site selection. Both laid a lower proportion of eggs in prey patches with the high-risk predator than in those with the low-risk IG predator. However, threat sensitivity in oviposition site selection was induced by experience in *P. persimilis* but not in *N. californicus*.

Species-specific Threat Sensitivity

*Amblyseius andersoni* females were threat insensitive in prey patch selection and oviposition behaviour. A possible interpretation is that *A. andersoni* is not able to discriminate between low- and high-risk IG predators. More likely, the lack of threat sensitivity in *A. andersoni* was specific to the IGP risks posed by *P. persimilis* and *N. californicus*, respectively. The risks posed by *P. persimilis* and *N. californicus* to *A. andersoni* were lower and their difference smaller than those in the other IG predator–prey combinations. Therefore, it could be that the overall predation risk was too low and the difference between risks too small to trigger a threat-sensitive response in *A. andersoni*. Alternatively or additionally, experiment 1 indicates that larvae of *A. andersoni* are better able to escape from or defend themselves against IGP than are the larvae of *N. californicus* and *P. persimilis* (see also Zhang & Croft 1995). Experienced *A. andersoni* females preferred to deposit their eggs in prey patches with cues of the high-risk IG predator. At first glance such behaviour seems maladaptive. However, IG predator eggs are not only potential future predators and competitors of offspring but also an alternative prey for *A. andersoni*. Phytoseiid mites are a higher quality prey for *A. andersoni* than are *T. urticae*, allowing rapid juvenile development and sustained oviposition (Schausberger & Croft 2000a). Therefore, experience may have enhanced acceptance and utilization of IG predator eggs as food by *A. andersoni* females. Higher predation by experienced females on eggs of *P. persimilis* than *N. californicus* may be explained by differing nutritional quantity of single eggs. Eggs of *P. persimilis* are about one-third larger than those of *N. californicus* (Croft et al. 1999). Whether the eggs of *N. californicus* and *P. persimilis* also differ in nutritional quality is unknown.

Both *N. californicus* and *P. persimilis* females responded in a threat-sensitive manner in prey patch selection and oviposition behaviour. However, the relative contribution of innate and learned components to threat sensitivity differed between the two species. Only *N. californicus* experienced with the high-risk IG predator avoided residence in the patch with IG predator cues. By contrast, both naïve and experienced *P. persimilis* females avoided patches with IG predator cues, but only experienced females were threat sensitive in patch selection. In *P. persimilis*, oviposition site selection matched prey patch selection. Irrespective of predation risk and experience, *P. persimilis* laid more eggs in predator-free patches, but experience induced threat sensitivity and fine-tuned oviposition site selection. To our knowledge, only one previous study dealt with threat-sensitive oviposition site selection influenced by experience in a classical predator–prey interaction. Water striders, *Aquarius paludum insularis* learned to adjust the oviposition depth to the risk of egg parasitism (Hirayama & Kasuya 2009b). The total number of eggs laid by *P. persimilis* was lower in choice situations with the high-risk IG predator than in those with the low-risk IG predator. Proximate explanations for decreased egg production in the presence of a high-risk IG predator include reduced feeding and/or egg retention (Montserrat et al. 2009; Abad-Moyano et al. 2010). In *N. californicus*, oviposition site selection and prey patch selection did not exactly match. Experience induced threat sensitivity in prey patch selection, whereas threat sensitivity in oviposition site selection was innate and unmodified by experience. A likely explanation is that offspring are much more vulnerable to IGP than are the adult females themselves (Croft et al. 1996), rendering oviposition site selection a much stronger selective force than prey patch selection.

Threat-sensitivity and Mutual IGP Risk

The species-specific strategies to reduce IGP on offspring and their complexities and magnitudes reflect the species ranking in mutual predation (experiment 1; Schausberger & Croft 2000b). They further indicate that IGP, which contains elements of both predation and competition, and not merely competition for spider mites, has been the selective force driving the evolution of these behaviours. If competition for spider mites was the driving force, the weakest competitor *A. andersoni* would have had the strongest response, and the strongest competitor *P. persimilis* the least, respectively, to the presence of the other species. However, the opposite was true. The lack of threat-sensitive behaviours in *A. andersoni* may indicate that their juveniles are the least endangered IG prey within the guild studied. Moreover, killing potential IG predator eggs by *A. andersoni* IG prey females both yields nutritional benefits and relaxes offspring predation and competition risks. Cues from killed conspecifics may prevent further IG predators from entering prey patches, as for example shown for the predatory mite *Iphiseius degenerans* (Faraji et al. 2001). *Neoseiulus californicus* females were threat sensitive in IGP and oviposition site selection. However, the latter was only evident in prey patches with the high-risk IG predator *A. andersoni*, indicating that *P. persimilis* represents a negligible risk for *N. californicus* offspring. *Phytoseiulus persimilis* is the most vulnerable to IGP within the guild studied. The females responded to both IG predators under all circumstances, indicating that both predators constitute a considerable risk for their offspring. Experience drastically increased threat sensitivity of *P. persimilis*, which was reflected in almost complete oviposition avoidance in prey patches with cues of the high-risk IG predator (only two of 51 eggs were placed in the patch with IG predator cues).

Implications for Population and Community Dynamics

Threat sensitivity in IGP may have important implications for population and community dynamics. For example, graded oviposition avoidance may result in graded direct trait-mediated IG interactions (Luttbeg & Kerby 2005; Preisser et al. 2005; Abad-Moyano et al. 2010b). Oviposition site selection affects spatial distribution of IG prey independent of the level of IGP risk, which in turn may trigger indirect trait-mediated effects on the shared prey (e.g. Werner & Peaco 2003; Walzer et al. 2009). The ability to perform threat-sensitive anti-IGP behaviours should have stabilizing effects on the coexistence of IG predators and prey. Currently, the general theoretical prediction deduced from IGP models is that coexistence of IG predators and prey within communities at ecological timescales is unlikely at high productivity levels (Janssen et al. 2006), but there is sparse empirical support for this assumption (e.g. Amarasekare 2008). Threat sensitivity in prey patch and oviposition site selection could be a mechanism promoting the coexistence of IG predators and prey (Heithaus 2001; Amarasekare 2008).
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