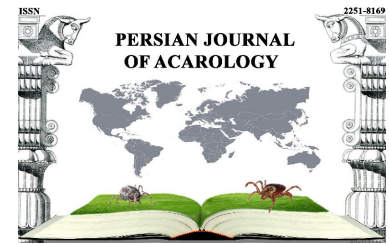




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Article

Reciprocal intraguild predation between *Neoseiulus barkeri* and *Amblyseius swirskii* (Mesostigmata: Phytoseiidae): Does experience affect anti-intraguild predation behaviors?

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ABSTRACT

In order to increase their inclusive fitness, animals predominantly probe their changing environment for predation cues to adopt appropriate antipredator strategies and decrease the costs of defensive behavior. Intraguild predation (IGP) occurs when a predator kills and consumes individuals of another predator which is its competitor for a shared prey. IGP is prevalent among predatory mites of the family Phytoseiidae which are used as biological control agents of agricultural pests worldwide. Phytoseiid mite mothers usually display antipredator behaviors to avoid or reduce IGP risk of their juveniles. When facing a novel IGP risk, experience may enable the mothers to display more efficient antipredator responses. We studied the effect of experience on reciprocal antipredator behaviors of an indigenous predatory phytoseiid mite, i.e., *Neoseiulus barkeri* Hughes, and an exotic one, i.e., *Amblyseius swirskii* Athias-Henriot, as biological control candidates for integrated pest management strategies in Iran. First, we determined the occurrence of IGP and mutual risk of the predators within the guild; IGP occurred reciprocally and *A. swirskii* was the stronger IG predator. Second, in choice situations between a patch with only shared prey and a patch with shared prey plus IGP risk cues, we scrutinized patch choice, oviposition site selection and ability to counterattack by females of each species that had either experienced the IGP risk or not. The experience did not affect patch choice and oviposition behaviors of the species whereas it elicited an increase in their predation on IG predator juveniles. We suggest that the presence of IG predator juveniles and cues may not significantly modify the distribution of the IG prey species. The reinforced counterattack behavior in experienced females showed that both species were able to tune their antipredator behavior after exposure to IG predators. Consequences of the antipredator behaviors in experienced IG prey females on distribution and possibilities of the coexistence of the study species are discussed.

KEY WORDS: Antipredator behavior; predation risk; predatory mites; role reversals; biological control.

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INTRODUCTION

Accurate enemy detection and appropriate and timely behavioral response are advantageous to increase the inclusive fitness of animals since any defensive response is costly (Chase 1999; Dicke and Grostal 2001). Trade-offs between food intake and predation avoidance play a crucial role in animal's survival (Kats and Dill 1998). In a changing environment with temporal variation in resources and threats, animals predominantly probe their habitat by their sensory structures to exploit the cues related to predators because predation has immediate consequences on survival (Lima and Dill 1990). Prey animal can avoid predators by choosing predator-free habitats for feeding and

reproduction (e.g. Walzer *et al.* 2006; Walzer and Schausberger 2011; Almeida and Janssen 2013), and in the times that they cannot avoid them, e.g. because they consume shared resources, they may reduce or delay reproduction (Montserrat *et al.* 2007; Abad-Moyano *et al.* 2010a) and/or counterattack the predators (e.g. Schausberger and Croft 2000; Janssen *et al.* 2002) to reduce the predation risk on their offspring.

Arthropods comprise the largest group of animals that provide essential services to agroecosystems. Mites of the family Phytoseiidae (Parasitiformes: Mesostigmata) are well-known examples of blind predators that exploit direct and indirect chemical cues to find prey and/or avoid predators. Currently, several species of phytoseiid mites are commercially available to control spider mites, thrips, and whiteflies on different vegetable crops in biological pest management programs in greenhouses worldwide. Because greenhouse crops are usually infested with more than one pest species, therefore, frequently multiple biological agents are released to manage pest populations which is the case with predatory phytoseiid mites. Intraguild predation (IGP, hereafter), i.e. competition for a shared prey plus predation on competitors, is a prevalent phenomenon when releasing multiple phytoseiid predators for pest control (e.g. Schausberger and Croft 2000; Çakmak *et al.* 2006; Abad-Moyano *et al.* 2010a, b).

Antipredator behavior to avoid or reduce IGP risk may vary geographically because behavioral responses to environmental information usually depend on the previous experience of the cue. Sympatric predators and prey with long-term co-evolutionary history are often more responsive than allopatric predators and prey (Kats and Dill 1998). Agricultural systems are not natural systems and releasing exotic natural enemies to control native or exotic pest results in the creation of synthetic guilds including predator species with little or no co-evolutionary history with the presumably short-lived association (Gerson *et al.* 2008). When confronting a new competitor for resources and also a threat for offspring, learning or behavioral shifts mediated by experience may enable the predator to reduce IGP risk by making faster foraging decisions (Papaj and Vet 1990; Bernays and Funk 1999). In this way, previous experience of the IG predators may result in more efficient antipredator responses in IG prey. Thus, learning to avoid certain patches to reduce IGP risk and assume safer patches for the acquisition of resources and/or oviposition when confronting a novel threat that did not exist before may result in modifications in predator distribution patterns and subsequently affect the interspecific interactions in food webs. A precondition for effective and successful application of biological control agents, when multiple species are released, is understanding the interactions between different natural enemies.

We studied the effect of experience on reciprocal antipredator behaviors of an indigenous predatory phytoseiid mite, i.e., *Neoseiulus barkeri* Hughes, (Faraji *et al.* 2007; Rahmani *et al.* 2010; Mahjoori *et al.* 2015) and an exotic one, i.e., *Amblyseius swirskii* Athias-Henriot, as biological control candidates for integrated pest management (IPM) strategies in Iran. Although lethal effects such as prey stage preference and IGP rates by *A. swirskii* on the native species (and vice versa) are documented (Maleknia *et al.* 2016), knowledge about non-lethal effects of the two predatory mite species on each other is lacking. We scrutinized habitat selection, oviposition site selection and counterattack behaviors as three possible antipredator strategies in females of each of the two predator species and in the presence of direct and indirect cues of the other species. In order to elucidate the effect of experience on these behaviors, we compared the antipredator behaviors in experienced and naïve females of each species. Experienced females had previously encountered the other species, i.e., the IG predator during their development from egg to adult and in the role of IG prey whereas naïve females had not previously encountered the IG predator. We compared antipredator behaviors of experienced and naïve females to see whether experienced females change their distribution and tune their antipredator behaviors in response to the presence of the IG predator cues and juveniles.

MATERIAL AND METHODS

Plants and mites

We grew common bean plants (*Phaseolus vulgaris* L. (Fabaceae) var. Red Alamoti) in plastic pots in the greenhouse (soil: perlite; 50:50%) under controlled conditions (25 ± 5 °C, 16L: 8D photoperiod, $65 \pm 5\%$ RH). Plants were watered daily with tap water and fertilizer solution of NPK (20: 20: 20). Spider mites, *Tetranychus urticae* Koch were reared as a food source for the predatory mites on bean plants. Fresh plants were added to the rearing system regularly.

We kept the predatory mites, *Neoseiulus barkeri* and *Amblyseius swirskii* on masses of detached bean leaves, infested with *T. urticae*. Leaves were placed upside down on a plastic sheet (19×14 cm) on a water saturated sponge (20×15 cm) inside a plastic tray (25×20 cm) half-filled with water. The plastic sheet was surrounded by napkin tapes which were put into the water from another side so that the predatory mites could drink water. Fresh *T. urticae* infested leaves were added to the rearing system and the old predator-free leaves removed regularly. The cultures were kept in separate growth chambers under controlled conditions (25 ± 2 °C, 16L: 8D photoperiod, $65 \pm 5\%$ RH) in Acarology Laboratory at Jalal Afshar Zoological Museum, Department of Plant Protection, Faculty of Agriculture, University of Tehran, Karaj, Iran.

Reciprocal intraguild predation risk

To determine the occurrence of reciprocal IGP between *N. barkeri* and *A. swirskii* and their comparative predation risk on each other juveniles, predation of a group of 5 same-aged female IG predators of either *A. swirskii* or *N. barkeri* on a group of 20 intraguild prey immature stages of either *N. barkeri* or *A. swirskii* and in the presence of the extraguild prey *T. urticae* was monitored and survival of juveniles was assessed after their exposure to female IG predators (Choh *et al.* 2012). Experimental units consisted of a detached bean leaflet (6 cm^2 , approx.) put upside-down on water-saturated cotton and surrounded with strips of tissue paper in contact with water and placed inside Petri dishes (6 cm diameter). Twenty IG prey eggs of either *A. swirskii* or *N. barkeri* were placed on each experimental unit with 5 female IG predators (two weeks old) of either *N. barkeri* or *A. swirskii*, respectively and ad libitum spider mites (mixed stages) as shared prey (IG prey eggs + IG predators + spider mites). Treatment arenas with female IG predators were considered as risky arenas. All experimental arenas were kept in a climate room (25 ± 1 °C, $65 \pm 5\%$ RH and 16L: 8D). Ten days later, the number of surviving IG prey adults in each arena was recorded. In similar experimental units but without predators (IG prey eggs + spider mites), the numbers of surviving adults were recorded after ten days as controls for each treatment. Control arenas without female IG predators were considered as safe arenas. Each treatment and control was replicated 25 times.

Anti-intraguild predator behavior on behalf of experienced/naïve IG prey

The anti-intraguild predator behaviors in *N. barkeri* and *A. swirskii* were investigated with the juvenile IG prey that developed to females (in the previous experiment) either on arenas with IG predators (experienced females) or on the ones without IG predators (naïve females). Either one experienced/naïve gravid female from each risky/safe experimental unit was chosen randomly for behavioral studies within two choice tests (Walzer and Schausberger 2011). The experimental patches were prepared by putting two detached bean leaflets of similar size (6 cm^2 , approx.) upside-down and next to each other on water-saturated sponges inside a plastic box (15×20 cm) half-filled with water. Ten *T. urticae* females plus 30 active juveniles were added to each leaflet as extraguild prey. Twenty-four hours later, five IG predator females of either *N. barkeri* or *A. swirskii* were introduced to one of the leaflets which was considered as a risky patch. No predators were added to the neighboring leaflet and it was considered as a safe patch. Twenty-four hours later from introducing the predators, *T. urticae* adults on risky and safe patches and the predator females and probable deposited eggs on

risky patches were removed so that the risky patches were occupied by the female predator and *T. urticae* cues, survived nymphs and exuviae of the killed spider mites. The safe patches were occupied by only *T. urticae* cues and juveniles. The number of *T. urticae* eggs and nymphs were increased to 40 on each of the risky/safe patches in order to uniform the density of extraguild prey on both patches (Blackwood *et al.* 2001; Walzer and Schausberger 2011). Afterwards, 10 same-aged (2 hours old) IG predator larvae (the same species with the removed ones) were added to the risky patches as direct cues of IG predators. For safe patches, 10 larvae of *T. urticae* were used. After 15 minutes, the apical margins of the two leaflets were connected to each other using a wax bridge (2×5 mm) and the experiment was started by introducing a 24 hour starved gravid IG prey female of either *A. swirskii* or *N. barkeri* in the middle of the bridge. Monitorings were made at the first minute of release and 1, 2, 3, 4, 5, 6 and 12 hours after release. We recorded the location of the IG prey female and its predation rate on IG predator larvae in each monitoring. We also recorded the number of eggs deposited by IG prey female and the patch in which the eggs were deposited after 24 hours. Twenty five replicates were considered.

Statistical analysis

All statistical analyses were carried out using SPSS 22. To determine the predation risk of a group of 5 IG predator females on a group of 20 IG prey immature stages, generalized linear models (GLM; Poisson distribution) was used to compare the numbers of surviving juvenile IG prey that reached adulthood in risky or control arenas.

The effect of experience on IG prey patch choice and proportion of eggs deposited on risky patches were analyzed through generalized linear models (GLM; counts of events; binomial distribution with logit link function).

Differences in the numbers of deposited eggs by IG prey females in risky or safe patches were analyzed by Wilcoxon signed-ranks test due to non-normality of data. Effect of experience on total oviposition (log-transformed to improve normality) was analyzed by one-way ANOVA.

Differences in predation of IG prey females (experienced or control) on larvae of the IG predators were analyzed separately for each species with one-way repeated measurements (RM) ANOVAs, correcting for violation of sphericity in data when needed, with "Treatment" as explanatory variable and data of the six one-hour intervals as the repeated measurements. Data used for the analyses were the cumulative number of larvae killed through time. We performed RM ANOVAS including data of all the treatments and used the between-subjects post-hoc HSD Tukey tests to evaluate differences among treatments.

RESULTS

Reciprocal intraguild predation risk

For both species as IG prey, the numbers of surviving juveniles that reached to adulthood were significantly different on risky and safe arenas. The number of *N. barkeri* Juveniles that developed to adults after confronting *A. swirskii* females was estimated 7.52 ± 0.40 individuals (mean number of adults \pm SE), 42.80% less than the same juveniles on the safe arenas which was 16.08 ± 0.25 ($P < 0.0001$, $n = 25$ per treatment and control; Fig. 1a).

The number of *A. swirskii* juveniles that reached to adulthood on risky arenas with *N. barkeri* females as IG predator was estimated as 11.44 ± 0.37 individuals (mean number of adults \pm SE), 29.60% less than the juveniles on safe arenas which was 17.36 ± 0.23 ($P < 0.0001$, $n = 25$ per treatment and control; Fig. 1b).

The survivorships of IG prey were not significantly different between control arenas of *N. barkeri* and *A. swirskii* juveniles ($X^2 = 1.225$, $df = 1$, $P = 0.268$). Thus we compared the numbers of surviving adults on risky arenas for both IG prey species to determine the reciprocal risk of IG predators. The

mean survivorship of *N. barkeri* juveniles in risky arenas with *A. swirskii* females was significantly less than the survivorship of *A. swirskii* juveniles in risky arenas with *N. barkeri* females (GLM with Poisson errors; mean number of surviving adults \pm SE: 7.52 ± 0.40 and 11.44 ± 0.37 respectively, $P \ll 0.0001$; Fig. 2).

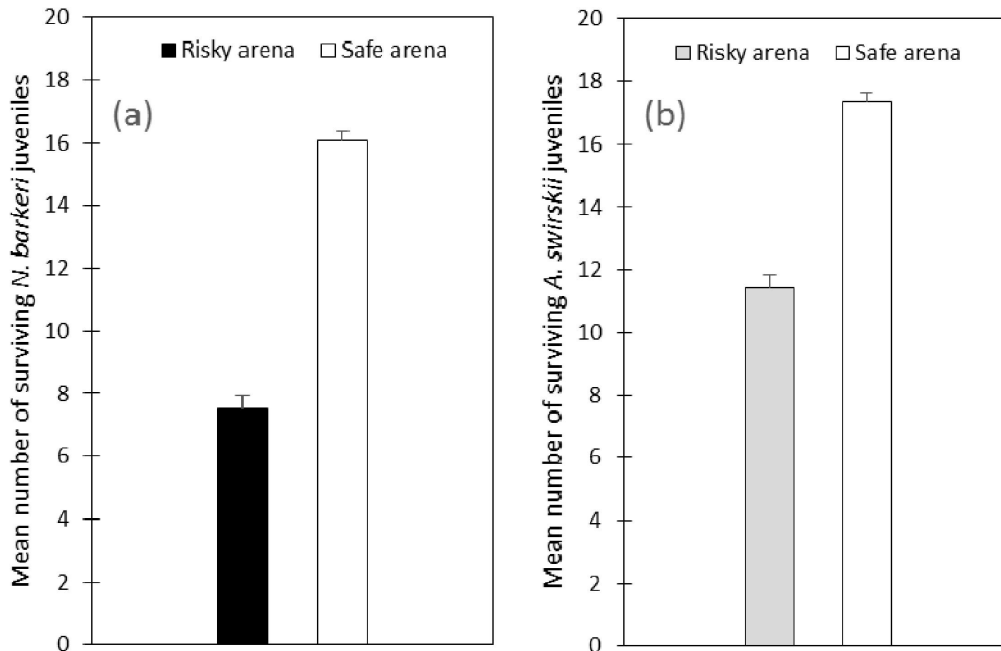


Figure 1. Survival to adulthood (mean number \pm SE) of 20 IG prey eggs of either *N. barkeri* (a) or *A. swirskii* (b) on arenas with only spider mites (control arenas, white bars) or with spider mites and 5 IG predator females (risky arenas, black and grey bars).

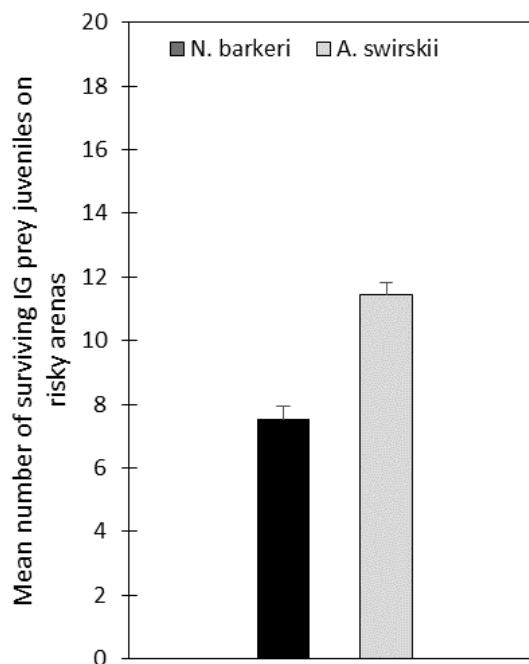


Figure 2. Comparative survival to adulthood of 20 IG prey eggs of either *N. barkeri* (black bar, $n = 25$) or *A. swirskii* (grey bar, $n = 25$) on arenas with 5 IG predator females of *A. swirskii* or *N. barkeri*, respectively.

Anti-intraguild predator behavior on behalf of experienced/naïve IG prey

IG prey patch choice

The number of times that naïve *N. barkeri* females were found on risky patches was significantly more than those on safe patches (Wald $\chi^2 = 13.20$, $df = 1$, $P \ll 0.001$). The number of times that experienced *N. barkeri* females were found on risky patches showed no difference with those on safe ones (Wald $\chi^2 = 1.61$, $df = 1$, $P = 0.20$). Experience marginally affected the residence frequency of adult IG prey in patches with IG predator cues and juveniles. Experienced females were found on risky patches less often than naïve females (GLM: Wald $\chi^2 = 2.97$, $df = 1$, $P = 0.085$; Fig. 3).

Naïve *A. swirskii* IG prey females resided more on risky patches (Wald $\chi^2 = 3.89$, $df = 1$, $P = 0.048$) whereas the experienced females were similarly distributed between risky and safe patches (Wald $\chi^2 = 0.08$, $df = 1$, $P = 0.77$). Although experienced females were found on risky patches less often than naïve ones, experience showed no significant effect on patch choice behavior of *A. swirskii* IG prey females (GLM: Wald $\chi^2 = 1.44$, $df = 1$, $P = 0.22$; Fig. 3).

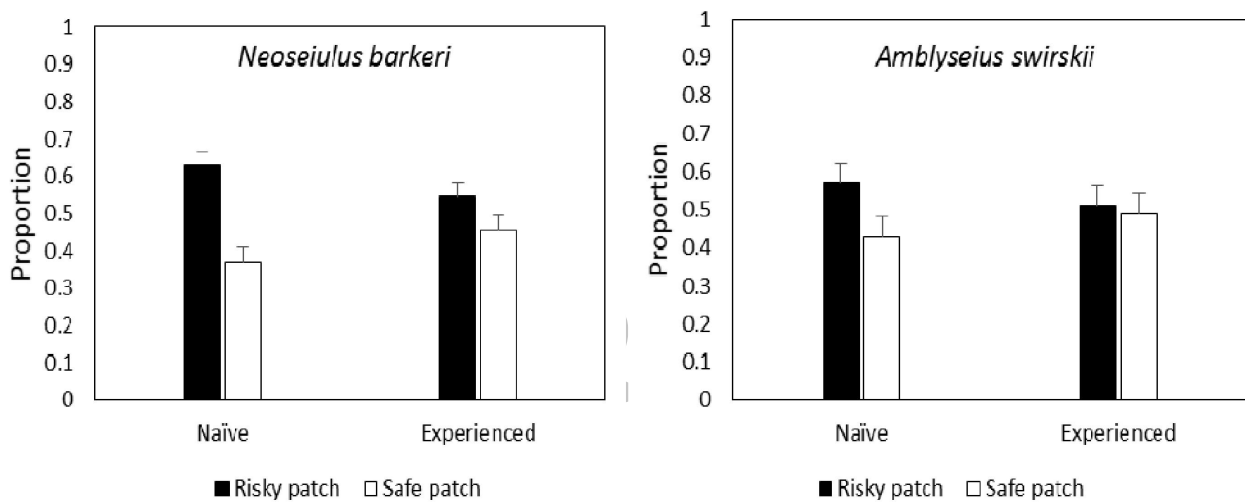


Figure 3. Effect of experience on patch choice behavior of *N. barkeri* and *A. swirskii* IG prey females within choice experiments. Shown are mean fractions (\pm SE) for residence frequency of either experienced or naïve females in risky patches with IG predator cues and juveniles (black bars) or in safe patches with only spider mites (white bars).

IG prey oviposition patch

The numbers of eggs laid by experienced or naïve IG prey females of *N. barkeri* showed no significant difference between risky and safe patches (Wilcoxon signed-ranks test; naïve female: $Z = -0.20$, $N = 25$, $P = 0.83$, experienced female: $Z = -0.74$, $N = 25$, $P = 0.45$) and experience did not influence the proportion of eggs deposited on risky patches (GLM; Wald $\chi^2 = 0.01$, $df = 1$, $P = 0.91$; Fig. 4).

The numbers of eggs deposited by experienced or naïve IG prey females of *A. swirskii* was not significantly different between risky and safe patches (Wilcoxon signed-ranks test; naïve female: $Z = -0.16$, $N = 25$, $P = 0.86$, experienced female: $Z = -0.39$, $N = 25$, $P = 0.69$). The proportion of eggs deposited on risky patches was not affected by experience (GLM; Wald $\chi^2 = 0.13$, $df = 1$, $P = 0.71$; Fig. 4).

IG prey oviposition rate

The mean number of eggs (\pm SE) produced per experienced or naïve *N. barkeri* females was estimated 1.12 ± 0.06 and 1.08 ± 0.05 , respectively. The numbers of eggs produced per *N. barkeri*

females was not significantly different between experienced and naïve IG prey (ANOVA; $F_{1,49} = 0.21$, $P = 0.64$; Fig. 4).

The mean number of eggs (\pm SE) produced per experienced or naïve *A. swirskii* females was estimated 1.20 ± 0.08 and 1.16 ± 0.07 , respectively. The oviposition rates of *A. swirskii* females was not significantly different between experienced and naïve IG prey (ANOVA; $F_{1,49} = 0.13$, $P = 0.72$).

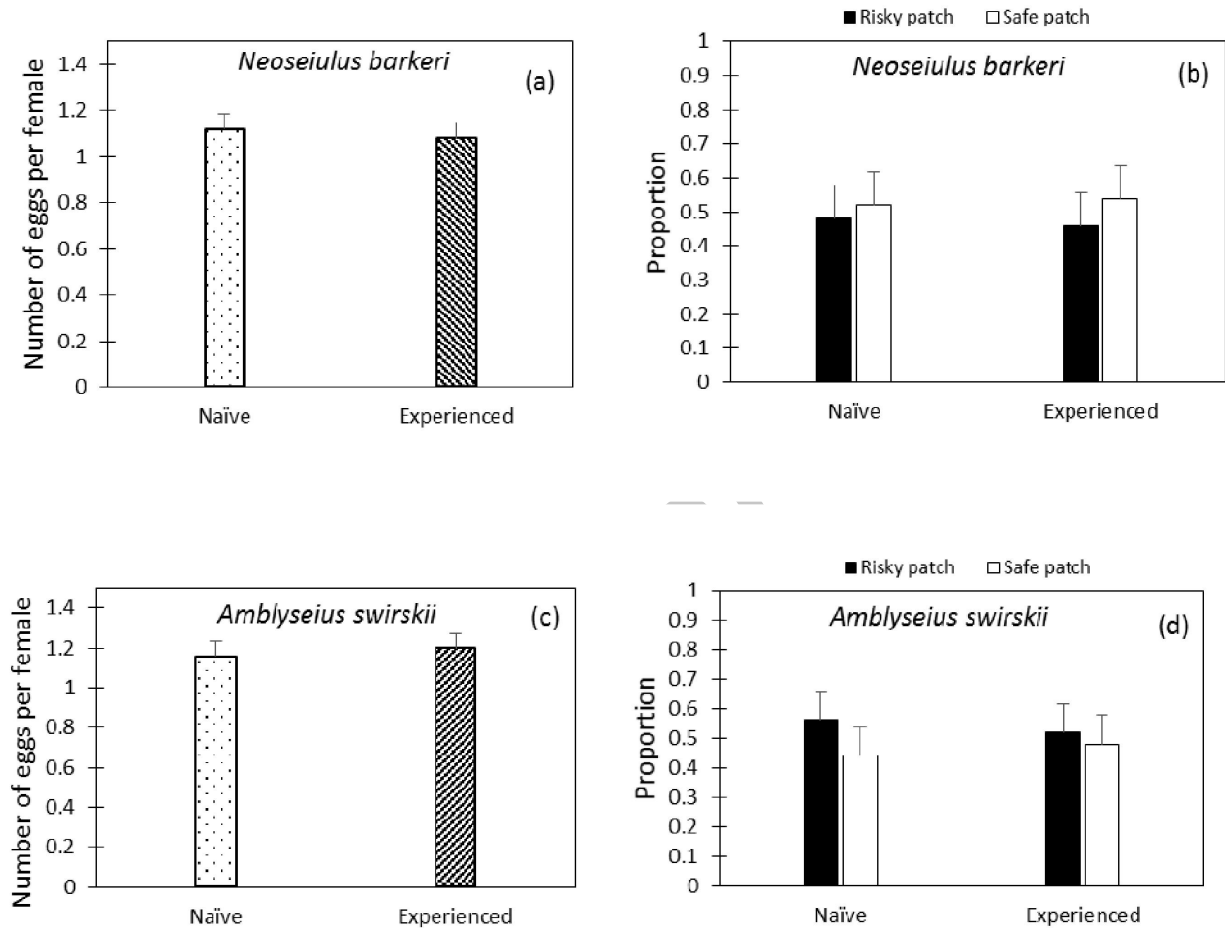


Figure 4. Total oviposition and proportion of eggs laid by experienced or naïve IG prey females *N. barkeri* (a, b) and *A. swirskii* (c, d) in risky (black bars) and safe (white bars) patches.

Predation on juvenile IG predators

Experienced *N. barkeri* females killed more larvae of the IG predator *A. swirskii* than naïve ones (Table 1, Fig. 5).

The same pattern was observed in *A. swirskii* females. Experienced females killed more larvae of the IG predator *N. barkeri* than naïve ones (Table 1, Fig. 5).

The overall analysis with all four treatments and subsequent post-hoc tests showed that predation rates were significantly different between two treatments (experienced *N. barkeri* vs. experienced *A. swirskii*: $P = 0.040$, experienced *A. swirskii* vs. naïve *N. barkeri*: $P < 0.0001$; Fig. 6). Differences in predation rates between the two other treatments were not significant (naïve *N. barkeri* vs. naïve *A. swirskii*: $P = 0.30$, experienced *N. barkeri* versus naïve *A. swirskii*: $P = 0.79$; Fig. 6).

Table 1. Predation by experienced or naïve IG prey females of either *N. barkeri* or *A. swirskii* on ten IG predator larvae in choice experiments. Shown are the results of the Repeated Measurements ANOVA applied to a cumulative number of IG predator larvae killed at six one-hour intervals (repeated measures) with treatment (experienced or naïve IG prey females) as an explanatory variable.

Species		Source of variation	Df	F (*)	P
<i>Neoseiulus barkeri</i>	Between subjects	Intersection	1	79.82	< 0.0001
		Treatment	1	5.52	0.023
		Error	48		
	Within subjects	Time	2.96	56.76	< 0.0001
		Time × treatment	2.96	1.43	0.23
		Error	142.09		
<i>Amblyseius swirskii</i>	Between subjects	Intersection	1	115.79	< 0.0001
		Treatment	1	6.68	0.013
		Error	48		
	Within subjects	Time	3.40	77.73	< 0.0001
		Time × treatment	3.40	1.72	0.15
		Error	163.57		

(*) When sphericity was not met, degrees of freedom were corrected according to the Huynh-Feldt test

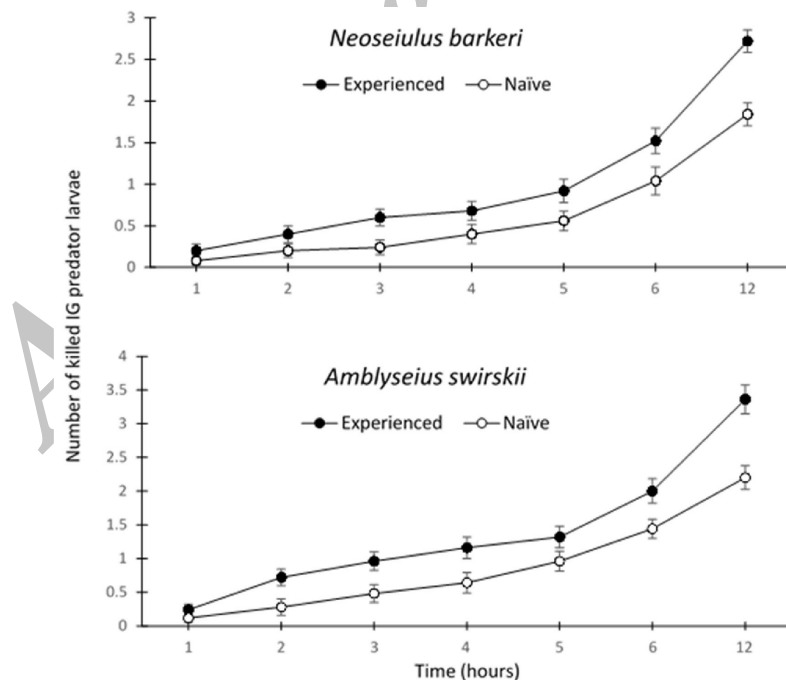


Figure 5. Survival of ten IG predator larvae of either *A. swirskii* (above) or *N. barkeri* (below) in choice experiments with naïve or experienced IG prey females of *N. barkeri* and *A. swirskii*, respectively.

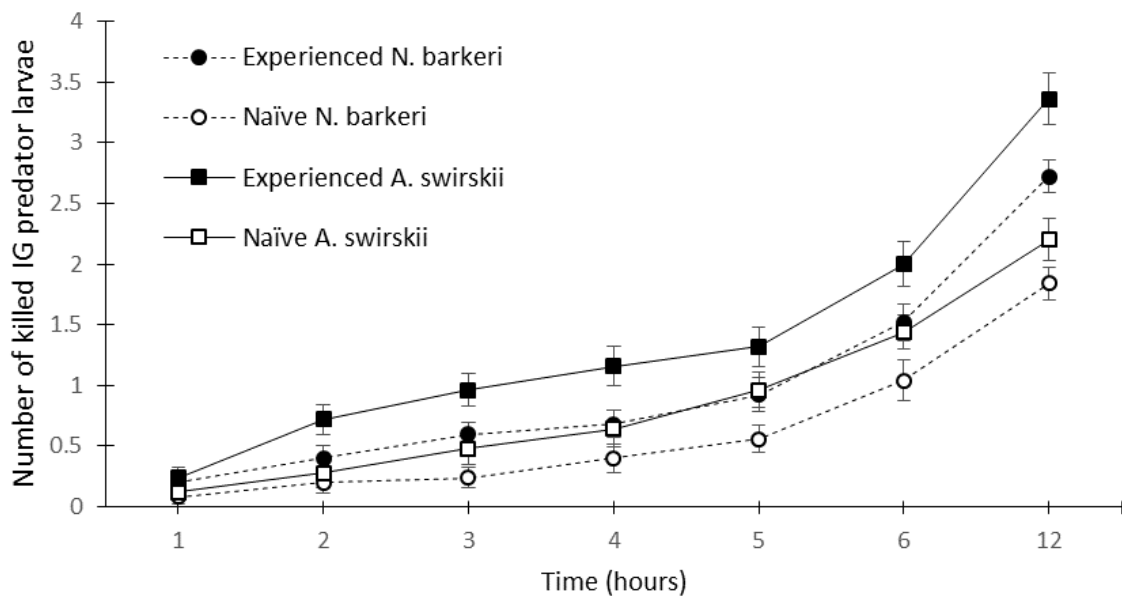


Figure 6. Comparative survivorship of ten IG predator larvae of either *A. swirskii* or *N. barkeri* in choice experiments with experienced or naïve IG prey females of *N. barkeri* or *A. swirskii*, respectively.

DISCUSSION

When females of *Neoseiulus barkeri* and *Amblyseius swirskii* were offered sufficient extraguild prey together with juveniles of the other species on risky arenas, both predatory mite species preyed upon juveniles of the heterospecific predator resulting in a substantial difference between the numbers of juveniles that developed to adult mites on risky arenas with that on safe ones. This shows that the two generalist predatory mites (type III life styles) are potentially engaged in reciprocal intraguild predation. IGP is a prevalent phenomenon among predatory phytoseiid mites especially those belonging to life style types III and IV (Schausberger 1997; Schausberger and Croft 2000; Hatherly *et al.* 2005; Montserrat *et al.* 2007; Seelmann *et al.* 2007).

The number of *N. barkeri* juveniles that reached adulthood on risky arenas with the IG predator *A. swirskii* was significantly less than that of *A. swirskii* juveniles in risky arenas with the IG predator *N. barkeri*. This indicates that although IGP occurs reciprocally between the two species, the predation risk of females on juveniles of the other species is different. Based on these differences we showed that *A. swirskii* females pose a higher predation risk on juveniles of *N. barkeri* and are the stronger IG predator in our system. The latter finding is in consistent with previous studies that have shown that *A. swirskii* is a highly voracious predatory mite. Choh *et al.* (2012) exposed twenty eggs of *N. cucumeris* to five *A. swirskii* females in the presence of ample amounts of pollen as shared food and reported that *A. swirskii* was highly voracious and none of the juveniles could reach adulthood. Maleknia *et al.* (2016) reported that *A. swirskii* and *N. barkeri* are IG predators on each other and *A. swirskii* seems to be a stronger IG predator because it consumes more eggs, larvae, and nymphs of *N. barkeri*.

Juveniles that reached adulthood on risky arenas, were subjected to IGP risk cues (direct and indirect) whereas those that reached adulthood on safe arenas were not subjected to such cues. Thus, adult IG prey from the risky arenas was experienced whereas those from safe arenas were naïve. We used surviving IG prey females (experienced/naïve) to see whether IG prey change their antipredator behavior after experiencing the risk of IG predator. When these females were offered a choice between a safe patch with only the shared prey and a risky patch with shared prey plus larva of the IG predator and indirect cues of prior activity of the female IG predators, experienced females of both

N. barkeri and *A. swirskii* were found on risky patches less often than naïve ones. However, experience marginally affected the presence of *N. barkeri* on risky patches and presence of *A. swirskii* on risky patches was not affected by the experience. This is consistent with results of Walzer and Schausberger (2011) who showed that experienced *Amblyseius andersoni* females were found on patches with their IG predator cues less often than naïve females. They furthermore showed that the effect of experience on patch choice behavior of *Neoseiulus californicus* was dependent on predation risk. Experienced females avoided the patches with IGP risk when the predation risk of the IG predator was high but did not change their distribution when the predation risk was low. One explanation for the marginal effect of experience on patch choice behavior of *N. barkeri* females and its nonsignificant effect on patch choice behavior of *A. swirskii* females could be related to the differences in the degrees of predation risk experienced by IG prey females. Experienced *N. barkeri* females suffered a higher predation risk during their development than that endured by experienced females of *A. swirskii*. We suggest that the overall predation risk of *A. swirskii* females on *N. barkeri* juveniles was high enough to trigger an even weak avoidance behavior in *N. barkeri* females whereas the predation risk of *N. barkeri* females on *A. swirskii* juveniles was not too high to trigger such a response in females.

Oviposition patterns of IG prey in choice experiments between risky and safe patches was not affected by experience neither in *N. barkeri* nor in *A. swirskii*. We expected the IG prey to lay more eggs on safe patches after experiencing the IGP risk but experienced females showed no preference to lay their eggs on safe patches. We suggest that patch choice and oviposition behaviors of IG prey species could be explained by their feeding habits. Both species are type III phytoseiid mites that are well-adapted to utilize different types of food resources such as spider mites, small insects, their eggs and juveniles and pollen (McMurtry and Croft 1997). Juvenile IG predators are a threat to the offspring but at the same time, they are an alternative prey for generalist phytoseiid mites. Schausberger and Croft (2000) showed that phytoseiid mites are even a higher quality prey than spider mites for *A. andersoni*. Indeed, Walzer and Schausberger (2011) showed that experienced females of *A. andersoni* laid more eggs on patches with IG predator eggs and cues than on patches without IG predator eggs and cues and this occurred when females resided on risky patches less often than clean patches. It can be suggested that IG prey did not avoid to reside and lay their eggs on risky patches because it provided them with a food source which supplemented their diet and satisfied their feeding habits. Whether the larva of IG predators is a food with higher quality for *N. barkeri* and *A. swirskii* is unknown but because the oviposition rates of experienced IG prey that consumed more IG predator larva than naïve ones was not increased, it seems unlikely.

In contrast to patch choice and oviposition behaviors, predation of IG prey females on larvae of IG predators was significantly affected by experience both in *N. barkeri* and *A. swirskii*. Choh *et al.* (2012) showed that experienced IG prey females of *I. degenerans* killed the juveniles of the IG predator *N. cucumeris* at a significantly higher rate than naïve females. Consistently, experienced females of both species in our study showed higher predation rates on IG predator larvae than naïve ones. Although patch choice and oviposition behaviors in experienced IG prey females seems counter-adaptive the reinforced counterattack behavior in these females may explain these behaviors. IG prey may adopt appropriate antipredator strategy depending on the situation because there are costs associated with each strategy (Montserrat *et al.* 2007). Moreover, it is known that antipredator responses in phytoseiid mites depend on the ontogeny of IG prey; vulnerable developmental stages of IG prey are expected to escape when facing the IG predator cues whereas the invulnerable adults are expected to counterattack (Choh *et al.* 2012). In consistent with this prediction, experienced females in our study did not avoid to settle and lay their eggs on risky patches but they provided a safer environment for their offspring by killing more IG predator juveniles and reducing the future predation risk. Almeida and Janssen (2013) showed that when *A. swirskii* females laid their eggs near their counterattacking prey, *Frankliniella occidentalis*, they killed more larva of the prey than females that laid their eggs in the neighboring patch which was without counterattacking prey. The authors

suggested that because such higher predation on the larva of the prey did not result in higher oviposition in *A. swirskii*, thus females killed the larva to protect their offspring. Indeed, because the oviposition rates of experienced *N. barkeri* and *A. swirskii* that consumed more IG predator larvae was not increased, it can be suggested that they killed the larvae to protect their progeny.

Our findings suggest that of all strategies tested here (patch choice, oviposition site selection and counterattacking IG predator juveniles), IG prey females of both species adopted the counterattack strategy which probably incurs a lower fitness cost because by killing juvenile IG predators, apart from acquiring nutrients and eliminating their competitors for shared prey, they also protect their offspring (Montserrat *et al.* 2007). Although experience weakened the tendency of *N. barkeri* to settle on patches occupied by *A. swirskii* cues and juveniles we predict that the presence of IG predator cues and juveniles may not significantly affect the distribution of IG prey species because the effect of experience on patch choice and distribution of eggs by females was not significant. The increased predation rates by experienced females on IG predator larvae show that both species are able to avoid invasion of their occupied patches with IG predators. Although *A. swirskii* is a stronger IG predator *N. barkeri* seems to be able to avoid the invasion of its occupied patches by killing IG predator juveniles which indeed may reduce the strength of IGP. Taken together, such antipredator responses may have density-mediated effects on population dynamics of IG predators and preys which are often complex and difficult to predict and quantify (Abrams 2008).

In conclusion, the reinforced counterattack behavior in experienced IG prey females shows that both species tune their antipredator behavior after experiencing the IGP risk. The ability of IG prey to tune antipredator behaviors according to the risk of IG predators may enhance the coexistence of IG prey and predators and subsequently stabilize the persistence of food webs with IGP (Walzer and Schausberger 2011). Furthermore, it is known that killed juvenile predators deter the adult predators and such antipredator behaviors may further stabilize the persistence of systems with IGP by prompting the IG prey and predators to occupy patches of their shared prey (Choh *et al.* 2012). Although we did not explore the effect of such interspecific predation on avoidance of IG prey for patches that harbored their killed conspecifics by IG predator such behavioral responses may facilitate the spatial segregation of IG predator and prey and further contribute to the coexistence of IG predator and prey. However and in larger scales, the stage structure of the resident population and the orders of invasion determine the outcome of IG interactions (van der Hammen *et al.* 2010; Choh *et al.* 2012; Montserrat *et al.* 2012). We suggest that the deterrent effect of predation by IG prey females on adult IG predators and effect of invasion orders on IG interaction between *A. swirskii* and *N. barkeri* should be the subject for further investigations to draw more firm conclusions.


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شکارگری درون‌رسته‌ای متقابل بین *Amblyseius swirskii* و *Neoseiulus barkeri* (Acari: Phytoseiidae): آیا تجربه رفتارهای ضدشکارگری درون‌رسته‌ای را تحت تاثیر قرار می‌دهد؟

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چکیده

موجودات زنده در راستای افزایش شایستگی و کاهش هزینه‌های رفتار ضدشکارگری، پیوسته محیط متغیر پیرامون خود را برای آگاهی از نشانه‌های شکارگری و به‌کارگیری راهبردهای مناسب برای رویارویی با آن می‌پایند. شکارگری درون‌رسته‌ای پدیده‌ای است که در آن یک شکارگر افراد شکارگر دیگر را که رقیب آن برای یک شکار مشترک است مورد حمله و تغذیه قرار می‌دهد. شکارگری درون‌رسته‌ای پدیده‌ای فراگیر در بین کنه‌های خانواده *Phytoseiidae* است که به‌عنوان عوامل کنترل بیولوژیک آفات محصولات کشاورزی در سراسر جهان مورد استفاده قرار می‌گیرند. کنه‌های فیتوزئید ماده می‌توانند با رفتارهای ضدشکارگری خطر شکارگری درون‌رسته‌ای روی نتاج‌شان را کاهش دهند. هنگام برخورد با گونه جدیدی از شکارگرهای درون‌رسته‌ای، تجربه برخورد با شکارگر می‌تواند بروز رفتارهای کارآمدتری را در پی داشته باشد. در این پژوهش تاثیر تجربه بر رفتارهای ضدشکارگری شکارگر غیر وارداتی *Neoseiulus barkeri* Hughes و شکارگر وارداتی *Amblyseius swirskii* Athias-Henriot به‌عنوان گزینه‌های کنترل بیولوژیک در برنامه‌های مدیریت تلفیقی آفات در ایران، بررسی شد. ابتدا وقوع پدیده شکارگری درون‌رسته‌ای و خطر متقابل شکارگرها برای یکدیگر مورد ارزیابی قرار گرفت. شکارگری درون‌رسته‌ای به‌صورت متقابل اتفاق افتاد و *A. swirskii* شکارگر قوی‌تری بود. سپس در آزمایش‌های انتخابی بین پیچ‌کنه‌های تارتن با نشانه‌های شکارگر درون‌رسته‌ای و پیچ‌کنه‌های تارتن بدون نشانه‌های شکارگر درون‌رسته‌ای رفتارهای انتخاب پیچ، انتخاب محل تخم‌گذاری و حمله متقابل در ماده‌هایی که تجربه‌ی خطر شکارگری را داشتند با ماده‌هایی که فاقد این تجربه بودند مطالعه و مقایسه شد. تجربه تأثیری بر رفتارهای انتخاب پیچ و انتخاب محل تخم‌گذاری گونه‌های شکارگر نداشت اما موجب افزایش میزان شکارگری ماده‌ها با تغذیه از مراحل رشدی جوان شکارگر درون‌رسته‌ای در هر دو گونه شد. به نظر نمی‌رسد نشانه‌های شکارگر درون‌رسته‌ای تأثیر زیادی بر پراکندگی این گونه‌ها داشته باشد. تقویت رفتار حمله متقابل در گونه‌های شکارگر نشان از توانایی ماده‌ها در تنظیم رفتار ضدشکارگری دارد. به نظر می‌رسد این توانایی می‌تواند شرایط همزیستی این شکارگرها را در سامانه‌های کشاورزی بهبود بخشد.

واژگان کلیدی: رفتار ضدشکارگری؛ خطر شکارگری؛ کنه‌های شکارگر؛ تغییر جایگاه؛ مهار زیستی.

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