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Integration of multiple cues allows threat-sensitive anti-intraguild predator responses in predatory mites

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Abstract

Intraguild (IG) prey is commonly confronted with multiple IG predator species. However, the IG predation (IGP) risk for prey is not only dependent on the predator species, but also on inherent (intraspecific) characteristics of a given IG predator such as its life-stage, sex or gravidity and the associated prey needs. Thus, IG prey should have evolved the ability to integrate multiple IG predator cues, which should allow both inter- and intraspecific threat-sensitive anti-predator responses. Using a guild of plant-inhabiting predatory mites sharing spider mites as prey, we evaluated the effects of single and combined cues (eggs and/or chemical traces left by a predator female on the substrate) of the low risk IG predator *Neoseiulus californicus* and the high risk IG predator *Amblyseius andersoni* on time, distance and path shape parameters of the larval IG prey *Phytoseiulus persimilis*. IG prey discriminated between traces of the low and high risk IG predator, with and without additional presence of their eggs, indicating interspecific threat-sensitivity. The behavioural changes were manifest in distance moved, activity and path shape of IG prey. The cue combination of traces and eggs of the IG predators conveyed other information than each cue alone, allowing intraspecific threat-sensitive responses by IG prey apparent in changed velocities and distances moved. We argue that graded responses to single and combined IG predator cues are adaptive due to minimization of acceptance errors in IG prey decision making.

Keywords

direct predator cues; intraguild predation; phytoseiid mites; risk-sensitive behaviour

1. Introduction

Intraguild predation (IGP), i.e., being killed and eaten by heterospecific food competitors, is a major source of predator mortality (Polis et al., 1989). Predator guilds are often composed of multiple predator species differing in the predation risk posed to each other in both terrestrial (Rosenheim et al., 1993; Glen et al., 2011; Lourenco et al., 2011; Walzer & Schausberger, 2011a) and aquatic ecosystems (Gustafson, 1993; Wissinger & McGrady, 1993; Hawley, 2009). Accordingly, the risk of intraguild (IG) prey to be killed and eaten may range from negligible to high. To avoid the costs accruing from over- or underestimation of IGP risk, IG prey should evolve in-traspecific threat-sensitivity, allowing to adjust their anti-predator behaviours to the level of IGP risk posed by a given species (Walzer & Schausberger, 2011a, 2013). Interspecific threat-sensitivity in mutual IGP has

recently been observed in plant-inhabiting predatory mites such as *Phytoseiulus persimilis* (Walzer & Schausberger, 2011a, 2013). However, regarding the threat posed by a given predator individual, species identity is only the first level in an interrelated set of hierarchically organized indicators of IGP risk. Analogous to classical predation, the risk posed by an individual of a given IG predator species may change with sex, life-stage, size, or motivational state, i.e., intraspecific characteristics (e.g., Persons & Rypstra, 2001; Lehmann et al., 2004; Walzer et al., 2004; Bell et al., 2006). For example, a developmentally advanced large juvenile individual or a hungry individual or a gravid female of a low risk predator species may be more dangerous for IG prey than a developmentally early small juvenile individual or a satiated individual or an unmated female of a high risk predator species. Thus, threat-sensitive prey including IG prey should not only be able to discriminate between different predator species but should also be able to grade the risk within species in dependence of the available predator-associated cues.

In any recognition system, a central challenge for the receiver is finding the optimal balance between acceptance errors (for IGP: mistaking a low risk IG predator for a high risk IG predator and vice versa) and rejection errors (for IGP: no response to an IG predator) (Reeve, 1989; Sherman et al., 1997; Liebert & Starks, 2004). In IGP, the risk of a predator may be indicated by various direct and indirect predator related cues. Indirect cues include alarm pheromones emitted by injured or killed conspecifics or extraguild prey. Direct cues may include physical encounters, specific behaviours, body odours, metabolic waste products, chemical footprints or eggs left by the predators (Chivers & Smith, 1998; Kats & Dill, 1998; Dicke & Grostal, 2001). Several signalling theories, albeit originally developed for other ecological contexts such as mate choice, may be conceptually applied to signalling in IGP contexts. All these theories predict that natural selection should favour IG prey individuals that integrate multiple cues for IG predator recognition. (1) The backup signal hypothesis suggests that perception of a second predator cue with the same information as the first predator cue may serve as a backup when background noise handicaps perception of the first cue (Johnstone, 1996; Hebets & Papaj, 2005). (2) The multiple message hypothesis predicts that multiple cues provide more detailed information about the predator (species, sex, developmental stage) than single cues (Johnstone, 1996). (3) The inter-signal interaction hypothesis applies to situations where only interactions of multiple cues but not single cues induce a prey response (Hebets & Papaj, 2005). Consequently, the ability to integrate multiple IG predator cues should reduce both acceptance errors (multiple message hypothesis) and rejection errors (backup signal hypothesis, inter-signal interaction hypothesis) by IG prey.

We examined inter- and intraspecific threat-sensitivity in anti-predator behaviour in a subset of a plant-inhabiting predatory mite guild with mutual IGP, consisting of the IG prey larvae of *Phytoseiulus persimilis*, low risk IG predator females of *Neoseiulus californicus* and high risk IG predator females of *Amblyseius andersoni* (Walzer & Schausberger, 2011a, 2013). This guild occurs naturally in Sicily and elsewhere in the Mediterranean basin (De Moraes et al., 2004; authors personal observation) sharing host plants and spider mites as prey. *P. persimilis* is highly specialized to prey on spider mites producing dense webs, *N. californicus* is a diet generalist with a preference for spider mites and *A. andersoni* is a diet-generalist poorly adapted to exploit spider mites producing dense webs (McMurtry & Croft, 1997; Walzer & Schausberger, 2011b). IGP in phytoseiid guilds is commonly mutual but life-stage- and -phase-specific (Schausberger & Croft, 1999, 2000a; Walzer & Schausberger, 1999) with the small, little mobile larvae being the most endangered to fall victim to larger, more mature life stages, particularly the gravid IG predator females. We recently observed interspecific threat-sensitivity in IG prey larvae of *P. persimilis* physically confronted with low or high risk IG predators (Walzer & Schausberger, 2013). Direct predator encounter is the most reliable signal for IG predator recognition by prey but response only after

encounter is most risky because every direct encounter is possibly lethal for prey. Thus, a highly vulnerable and threat-sensitive IG prey should be able to recognize IG predator related cues before or without encountering the predators themselves and integrate multiple predator cues to precisely judge the associated risk.

Cues indicating IGP risk may be emitted directly from the predators or indirectly from injured or killed extraguild or conspecific prey. IG predator recognition based solely on indirect cues is prone to acceptance errors because the production of such cues can be induced by any predator including conspecifics. Direct IG predator cues such as chemical traces left by the predator females on the substrate (metabolic waste products or chemical footprints) or IG predator eggs are more reliable and likely IG predator species specific (Walzer & Schausberger, 2012). Moreover, integration of both IG predator cues should allow accurate risk assessment within IG predator species. Traces left by the females without eggs may be indicative of the presence of a non-ovipositing, perhaps unmated female posing a comparably low risk. Similarly, eggs without traces left by the females may indicate past presence of a gravid female, assuming that the traces left by the female vanish over time and, thus, a comparably low immediate risk. Only presence of eggs and traces left by the female indicate an immediate high risk.

To test for threat-sensitivity and cue integration ability, we videotaped the behaviour of single larval IG prey of *P. persimilis* held on bean leaf discs in the presence of eggs, chemical traces left by gravid predator females on the leaf surface, or eggs and chemical traces combined of the high or low risk IG predator, or IG predator cue absence and subsequently analyzed their behaviours using EthoVision Pro®. We asked (1) whether the IG prey larvae are able to discriminate between cues of the low and high risk IG predator, (2) if so, which cues mediate interspecific threat-sensitivity, (3) whether single separate cues convey the same (backup signal hypothesis) or different information (multiple message hypothesis) for IG prey and (4) whether cue combinations (inter-signal interaction hypothesis) provide different information than single cues?

2. Materials and methods

2.1. Species origin and rearing

Specimens of *P. persimilis*, *N. californicus* and *A. andersoni* used to found laboratory-reared populations were collected in the Trapani region, Sicily, in 2007. Since then, in the laboratory, the species were separately reared on arenas consisting of plastic tiles resting on water-saturated foam cubes in plastic boxes half-filled with water (for details, see Walzer & Schausberger, 2011a). To obtain similarly aged IG prey larvae or IG predator eggs, gravid *A. andersoni*, *N. californicus* or *P. persimilis* females were randomly withdrawn from the rearing units and placed on detached bean leaves infested with spider mites. The predator females were allowed to feed on the spider mites and lay eggs for 2 h. Then they were removed and the eggs laid by *A. andersoni* and *N. californicus* were used in the experiments as IG predator eggs from the high and low risk IG predators, respectively. For *P. persimilis*, the eggs were left on the arena until the larvae hatched. The newly hatched larvae were used as IG prey in the experiments.

2.2. Experimental units

Detached bean leaf discs (diameter 14 mm), punched out from the centre of detached trifoliate bean leaves including the mid vein, and were used as experimental units. Each leaf disc was placed on the surface of a water column in an acrylic glass cylinder (height 20 mm, inner diameter 16 mm) leaving a ~1 mm wide water film barrier between the leaf edge and the inner margin of the acrylic glass cylinder, preventing the mites from escaping. Before

the experiment, leaf discs were prepared according to one of seven treatments: (1) without IG predator cues (control, $N = 14$); (2) with traces of the low risk IG predator female ($N = 18$); (3) with traces of the high eggs of the low risk IG predator risk IG predator female ($N = 17$); (4) with ($N = 16$); (5) with eggs of the high risk IG predator ($N = 19$); (6) with both eggs and traces of the low risk IG predator ($N = 18$); (7) with both eggs and traces of the high risk IG predator ($N = 16$). To generate chemical traces of the IG predator females (treatments 2, 3, 6 and 7) a single IG predator female was placed on each leaf disc and removed again after 60 min. For treatments with IG predator eggs (4–7), three eggs were placed in a semi-circle on each leaf disc. After preparation of leaf discs, IG prey larvae were singly placed on the discs and allowed to acclimatize for approximately 10 min. Afterwards, IG prey behaviour was videotaped for 60 min.

2.3. Video-taping and -tracking

The behaviour of the mites was videotaped using an analogue colour camera (Leica ICA) integrated in a Leica M5 stereo-microscope. The video signal was fed into a computerized video tracking system consisting of a personal computer equipped with a frame grabber (HaSoTec, FG-33-II) and the Etho-Vision Pro®, version 3.1 software (Noldus et al., 2001). To increase the contrast between the mites and the leaf surface (the background in the video), fluorescent, magenta-coloured powder (Kurt Wolf & Co., Vienna, Austria) was dusted on the dorsum of the mites and the videos were shot under UV lighting using a red photographic filter. The powder did not affect the behaviour of the mites (personal observations). In the videos the mites appeared as light red dots moving on a dark grey background. Grey scaling was used as detection method. The sampling rate was 3.5 samples per second, which was a compromise of the requirements of the highest possible sample rate, the processor speed and the storage capacity of the computer (Bell, 1991). For analyses, each leaf disc arena was in-video subdivided into a leaf margin zone (a 1 mm wide ring along the edge of the leaf disc) and a refuge zone (including the mid vein and an approximately 0.5 mm strip on the left and right hand side from its longitudinal axis). The leaf margin is a zone of high predator activity because of the edge-oriented searching behaviour of many plant-inhabiting phytoseiid predators (e.g., Sabelis & Dicke, 1985), including *N. californicus* and *A. andersoni* (Walzer & Schausberger, 2013). The angle between the leaf veins and blade is used by many phytoseiid larvae as a refuge from biotic and abiotic hazards (e.g., Norton et al., 2001).

2.4. Time, distance and path shape parameters

Four time and distance parameters (time spent in each zone, total distance moved, mean velocity and activity) and three path shape parameters (absolute turning angle, absolute angular velocity and absolute meander) were computed from track data using EthoVision Pro® (for detailed algorithms of parameter calculation, see Noldus Information Technology, 2005). Time spent in zones is the time spent by the mites in the margin and refuge zones in seconds (s). Total distance moved is the total length of the path moved by the mites (mm). Mean velocity is the average speed at which the mites moved (mm/s). Activity is the time (s) spent moving. Absolute turning angle (°) is the absolute change in direction of a moving mite and corresponds to the difference in direction of an individual's movement between two consecutive samples. Absolute angular velocity (°/s) is calculated by dividing the turning angle by the sample interval and is an indicator how fast an object is changing its direction. Absolute meander (°/mm) is the turning angle divided by the distance moved, which gives an estimation of the level of path tortuosity (Bell, 1991). All three path shape parameters range from 0 to 180°. To prevent small movements caused by noise of the system or pivoting on the spot to be scored as genuine movement by the mites, a minimum distance filter of 0.5 mm, which corresponds to 1.5 times body length plus first pair of legs, was used in the analyses of all time and distance parameters except for time spent in zones.

By that way, a parameter per sample was only scored when the object had moved 0.5 mm away from the point at which the parameter had been scored the previous time.

2.5. Statistical analyses

SPSS 15.0.1 (SPSS, 2006) was used for all statistical analyses. Separate generalised estimating equations (GEE, normal distribution with identity link function, exchangeable correlation structure between leaf zones) were used to compare the influence of IG predator species (no, low, or high risk for IG prey) and cue type (without cues, IG predator eggs, IG predator traces, eggs and traces of the IG predators) on time, distance and path shape parameters of IG prey in two leaf zones (margin and refuge, used as correlated within subject variable). The proportional parameters residence time and activity were arcsin square root transformed before analyses. To detail differences between leaf zones among IG predator species and cue types within IG predator species, the estimated marginal means were compared pairwise by LSD tests if needed.

3. Results

3.1. Time and distance parameters

Residence time of IG prey was neither affected by IG predator species, cue type, and leaf zone, nor by their interactions (Table 1, Figure 1).

Velocity of IG prey was influenced by zone but not cue type and IG predator species. None of the two-way interactions was significant, but the three-way interaction was (Table 1). IG prey moved more slowly in the leaf margin than in the refuge. However, this behavioural shift of IG prey depended on cue type and IG predator species. Presence of both eggs and traces of the low risk IG predator female reduced velocity of IG prey in the leaf margin (pairwise LSD tests: no cues vs. eggs + traces: $p = 0.033$; eggs vs. eggs + traces: $p = 0.644$; traces vs. eggs + traces: $p = 0.145$; no cues vs. eggs: $p = 0.152$; no cues vs. traces: $p = 0.778$; eggs vs. traces: $p = 0.397$). Conversely, IG prey velocity in the leaf margin was higher in the presence of the cue combination of the high risk IG predator than that of the low risk IG predator (low vs. high risk: $p < 0.001$; no vs. high risk: $p = 0.361$) (Figure 1).

Distance moved by IG prey was affected by IG predator species, cue type, and leaf zone. None of the interaction terms was significant (Table 1). IG prey covered a longer distance in presence of high risk IG predator cues (pairwise LSD tests: no vs. low risk: $p = 0.302$; no vs. high risk: $p = 0.009$; low vs. high risk: $p = 0.047$). Distance moved by IG prey increased only when both eggs and traces of the IG predator females were present (eggs + traces vs. no cues: $p = 0.001$; eggs + traces vs eggs: $p = 0.001$; eggs + traces vs. traces: $p = 0.010$; no cues vs. eggs: $p = 0.714$; no cues vs. traces: $p = 0.284$; eggs vs. traces: $p = 0.392$). IG prey covered longer distances in the refuge than in the leaf margin (Figure 1).

Activity of IG prey was only influenced by IG predator species (Table 1). Cues of the high risk IG predator induced higher activity in IG prey than cues of the low risk IG predator (pairwise LSD tests: no vs. low risk: $p = 0.466$; no vs. high risk: $p = 0.520$; low vs. high risk: $p = 0.010$) (Figure 1).

3.2. Path shape parameters

The absolute turning angles of IG prey were influenced by zone but not by IG predator species and cue type. The interaction terms were not significant except the interaction between IG predator species and cue type (Table 2). The turning angles of IG prey were higher in the leaf margin than in the refuge. Traces of high risk IG predator females reduced the turning angles of IG prey compared to the other cue types of the high risk IG predator

(pairwise LSD tests: traces vs. eggs: $p = 0.038$; traces vs. eggs + traces: $p = 0.002$; eggs vs. eggs + traces: $p = 0.577$) and compared to the control treatment and corresponding data of low risk IG predator cues (no vs. high risk: $p = 0.017$; no vs. low risk: $p = 0.147$; low vs. high risk: $p = 0.004$; Figure 2).

Zone but not IG predator species and cue type influenced the absolute angular velocity of IG prey, which was higher in the leaf margin than in the refuge. However, the effect of zones on angular velocity of IG prey depended on IG predator species and cue type (Table 2). Only traces of low but not high risk IG predator females induced faster turning by IG prey in the leaf margin (pairwise LSD tests: no vs. high risk: $p = 0.087$; low vs. high risk: $p = 0.002$; traces vs. eggs: $p = 0.003$; traces vs. eggs + traces: $p = 0.003$; eggs vs. eggs + traces: $p = 0.999$), which was also marginally faster than in the control (no vs. low risk: $p = 0.076$). Conversely, angular velocity of IG prey in the leaf margin was marginally significantly reduced by traces of the high risk IG predator female compared to the control (no vs. high risk: $p = 0.087$) (Figure 2).

The absolute meander of IG prey was influenced by zone but not by IG predator species and cue type. The interaction terms were not significant, except the interaction between IG predator species and cue type (Table 2). IG prey meandered more in the leaf margin than in the refuge. Only traces of high risk IG predator females reduced meandering of IG prey (pairwise LSD tests: no vs. high risk: $p = 0.051$; no vs. low risk: $p = 0.156$; low vs. high risk: $p = 0.007$; traces vs. eggs: $p = 0.023$; traces vs. eggs + traces: $p = 0.004$; eggs vs. eggs + traces: $p = 0.899$) (Figure 2).

4. Discussion

Our study indicates that the IG prey larvae of *P. persimilis* are able to discriminate between traces left by IG predator females on the substrate, with and without additional presence of their eggs, of the low risk IG predator *N. californicus* and the high risk IG predator *A. andersoni*, indicating interspecific threat-sensitivity. The behavioural changes were manifested in distance moved, activity time, turning angle, angular velocity and meander of IG prey. IG predator eggs alone did not allow IG predator recognition by the IG prey larvae. Thus, different direct IG predator cues presented alone conveyed different information for IG prey, which is in accordance with the multiple message hypothesis (Johnstone, 1996). The cue combination of traces and eggs of the IG predator females conveyed yet another information than each cue alone, which is in accordance with the inter-signal interaction hypothesis (Hebets & Papaj, 2005), allowing intraspecific threat-sensitive responses by IG prey manifested in changes in velocity (both low and high IGP risk) and distance moved (only high IGP risk). The majority of behavioural shifts of IG prey such as velocity, distance moved, turning angles, angular velocity, and meander occurred in the leaf margin but not in the refuge zone. A likely cause was the spatiotemporal distribution of the IG predators, which spend more time in the leaf margin than in the refuge zone (Walzer & Schausberger, 2013). As a consequence, the amount and/or concentration of chemical traces left by the IG predators were/was higher in the leaf margin than in the refuge zone.

Presence of IG predator eggs alone without chemical traces left by the IG predator female on the substrate may indicate that the IG predator female left the site some time ago. Chemical traces left by the IG predator females on the substrate are partly volatile (e.g., Janssen et al., 1997 for *P. persimilis*) and presumably diminish over time. Thus, IG predator eggs alone do not indicate an immediate risk for IG prey. Lack of response by IG prey larvae to IG predator eggs may either indicate that IG prey larvae were unable to recognize the eggs of heterospecific phytoseiid mites, or, more likely, that they perceived them as prospective prey (Walzer & Schausberger, 1999). In the situations tested, the larvae of *P. persimilis* would

have a temporally limited advantage in IG interactions with the juveniles emerging from the eggs of their predators *N. californicus* and *A. andersoni*, because they are developmentally more advanced and develop more quickly (Walzer & Schausberger, 2011b). Thus, for a limited time period, the roles of IG prey and predators would be shifted with *P. persimilis* nymphs being the IG predators and the hatching larvae of *A. andersoni* and *N. californicus* being the IG prey.

Presence of IG predator female traces alone without IG predator eggs may indicate the presence of a non-ovipositing, possibly unmated, female with lower prey needs than an ovipositing female. Under such conditions, an elaborate anti-IGP response does not pay for the IG prey larvae. Indeed, traces left by the IG predator female alone induced only a change in the path shape parameters of IG prey with increased angular velocity in presence of low risk IG predator traces and reduced angular velocity, turning angles and meander in presence of high risk IG predator traces. These predator-specific IG prey responses could be due to predator-specific movement patterns resulting in a differing distribution of the chemical traces released by the females on the substrate. Both IG predator species spend similar time moving, but the high risk IG predator runs faster and, thus, covers longer distances in the same time period than the low risk IG predator (Walzer & Schausberger, 2013). Therefore, the traces left by the high risk IG predator were probably more homogeneously distributed on the leaf surface than those of the low risk IG predator.

Only the presence of eggs and traces of the IG predator female unambiguously indicate spatial and temporal proximity of a gravid IG predator female. Under such circumstances, IG prey faces a high risk of being attacked because the IG predator female profits twofold from IGP. First, she eliminates a future food competitor and predator of her offspring (Walzer et al., 2006). Second, IG prey provide valuable nutrients for survival, development and reproduction of generalist predators such as *A. andersoni* and *N. californicus* (Walzer & Schausberger, 1999; Schausberger & Croft, 2000b). Accordingly, the IG prey larvae responded in a threat-sensitive manner to the presence of the cue combination by increased velocity and distance moved at high IGP risk and reduced velocity at low IGP risk. The response under high IGP risk but without immediate physical presence of the IG predator can be interpreted as an attempt to leave a risky area homogeneously contaminated with predator cues as quickly as possible. Reduced velocity under low IGP risk may again be a consequence of trying to avoid entering places with predator cues, assuming that these are more heterogeneously distributed on the surface than those of *A. andersoni*.

Perception of multiple IG predator cues with different information content enabled IG prey to respond in both an interspecific and an intraspecific threat-sensitive manner to IGP risk. Differential response to single and combined cues from the same species suggests that different cues did not act as backup signals. In backup signalling different cues provide similar information, to reduce the likelihood of rejection errors by the receiver (i.e., non-response to an IG predator). Using different cues as back-up signals might be selected for in IG prey that is usually threatened by only a single IG predator species. However, *P. persimilis* is specialized to exploit the patchily distributed spider mite *T. urticae*. This spider mite is exploited by various predators such as other predatory mites, spiders and insects (e.g., Chazeau, 1985; Gerson, 1985), some of which are also IG predators of *P. persimilis*. Thus, similarly responding to each predator cue, no matter of the risk associated with the predator, would increase acceptance errors and entail disproportionally high fitness costs.

Comparison of this study and Walzer & Schausberger (2013) suggest that *P. persimilis* larvae also modulate their anti-predator response to immediate and latent IGP risk. Walzer & Schausberger (2013) measured the response of *P. persimilis* larvae to physically present IG predators, which represent an immediate life-threatening risk. Predator cues in physical

absence of the predator, as used in this study, indicate only the past presence of a predator, which may or may not appear again and, thus, indicate a latent risk. There are only few examples from classical prey-predator interactions comparing prey responses to immediate and latent predation risk. For example, stingless bees avoided more likely webs with spiders than webs without spiders (Rao et al., 2008). The perception of barn owl calls by its prey, spiny mice, increased the cortisol level of prey but did not change their behaviour (Eilam et al., 1999), while owl presence induced a complex defence response (Edut & Eilam, 2003). Along the same line, IG prey *P. persimilis* larvae responded quantitatively and qualitatively different to physical IG predator presence (Walzer & Schausberger, 2013) and IG predator cues in predator absence (this study). Physical presence of the low risk IG predator *N. californicus* triggered an escape response in IG prey, manifested in covering longer distances at higher velocity (Walzer & Schausberger, 2013), whereas predator cues perceived in predator absence reduced the velocity of IG prey (this study). Conversely, presence of the high risk IG predator *A. andersoni* resulted in lower IG prey activity (Walzer & Schausberger, 2013), whereas IG prey responded to high risk IG predator cues with an escape behaviour (this study). At low IGP risk, a costly anti-predator response such as escaping may only pay under immediate predation risk, i.e., presence of the IG predator. At high but latent IGP risk, detection of predator cues in predator absence allows IG prey to move away from dangerous zones. Such a response would be maladaptive in physical presence of the high risk IG predator *A. andersoni*, because it moves about three times faster than the IG prey *P. persimilis* larvae making a successful escaping unlikely. Reducing activity by being more or less immobile seems to be a more effective strategy for IG prey to avoid encounters with the high risk IG predator (Walzer & Schausberger, 2013). Thus, we argue that the IG prey *P. persimilis* larvae are able to differentiate between immediate and latent IGP risk and modulate their behavioural strategies accordingly.

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Figure 1.

The influence of cues (eggs, chemical traces left by a female on the substrate, traces and eggs) from the high risk IG predator *A. andersoni* (black bars), the low risk IG predator *N. californicus* (grey bars) and absence of IG predator cues (white bars) on time and distance parameters (mean + SE) of the IG prey larvae of *P. persimilis* in zones of leaf discs with high (leaf margin, A) and low (refuge, B) predator activity.

Figure 2.

The influence of cues (eggs, chemical traces left by a female on the substrate, traces and eggs) from the high risk IG predator *A. andersoni* (black bars), the low risk IG predator *N. californicus* (grey bars) and absence of IG predator cues (white bars) on path shape parameters (mean + SE) of the IG prey larvae of *P. persimilis* in zones of leaf discs with high (leaf margin, A) and low (refuge, B) predator activity.

Table 1

Generalized estimating equations (GEE, normal distribution with identity link function, exchangeable correlation structure between the leaf zones) for the influence of predator species (no, low or high risk for IG prey) and cue type (without cues, IG predator eggs, IG predator traces, eggs and traces of the IG predators) on time and distance parameters of IG prey in two leaf zones (margin and refuge).

Parameter	Source of variation	df	Wald χ^2	P
Residence time	IG predator species	1	0.803	0.370
	Cue type	2	2.028	0.363
	Zone	1	0.002	0.964
	Cue type $\times$ IG predator species	2	2.025	0.363
	Cue type $\times$ zone	2	1.200	0.549
	IG predator species $\times$ zone	1	0.858	0.354
	IG predator species $\times$ cue type $\times$ zone	2	3.609	0.165
Distance moved	IG predator species	1	3.937	0.047
	Cue type	2	11.859	0.003
	Zone	1	4.615	0.032
	Cue type $\times$ IG predator species	2	2.257	0.324
	Cue type $\times$ zone	2	1.539	0.463
	IG predator species $\times$ zone	1	0.001	0.990
	IG predator species $\times$ cue type $\times$ zone	2	1.263	0.532
Velocity	IG predator species	1	0.877	0.349
	Cue type	2	1.930	0.381
	Zone	1	13.245	<0.001
	Cue type $\times$ IG predator species	2	0.244	0.885
	Cue type $\times$ zone	2	2.484	0.289
	IG predator species $\times$ zone	1	0.045	0.832
	IG predator species $\times$ cue type $\times$ zone	2	6.826	0.033
Activity	IG predator species	1	6.585	0.010
	Cue type	2	2.554	0.279
	Zone	1	0.273	0.601
	Cue type $\times$ IG predator species	2	0.119	0.942
	Cue type $\times$ zone	2	3.696	0.158
	IG predator species $\times$ zone	1	1.517	0.218
	IG predator species $\times$ cue type $\times$ zone	2	0.356	0.837

Table 2

Generalized estimating equations (GEE, normal distribution with identity link function, exchangeable correlation structure between the leaf zones) for the influence of predator species (no, low or high risk for IG prey) and cue type (without cues, IG predator eggs, IG predator traces, eggs and traces of the IG predators) on path shape parameters of IG prey in two leaf zones (margin and refuge).

Parameter	Source of variation	df	Wald χ^2	P
Turning angle	IG predator species	1	1.716	0.190
	Cue type	2	0.067	0.967
	Zone	1	31.432	<0.001
	Cue type $\times$ IG predator species	2	7.829	0.020
	Cue type $\times$ zone	2	1.512	0.470
	IG predator species $\times$ zone	1	0.220	0.639
	IG predator species $\times$ cue type $\times$ zone	2	1.787	0.409
Angular velocity	IG predator species	1	0.013	0.909
	Cue type	2	2.137	0.344
	Zone	1	7.384	0.007
	Cue type $\times$ IG predator species	2	13.564	0.001
	Cue type $\times$ zone	2	5.682	0.058
	IG predator species $\times$ zone	1	1.061	0.303
	IG predator species $\times$ cue type $\times$ zone	2	9.154	0.010
Meander	IG predator species	1	1.773	0.183
	Cue type	2	0.239	0.887
	Zone	1	38.270	<0.001
	Cue type $\times$ IG predator species	2	6.300	0.043
	Cue type $\times$ zone	2	0.677	0.713
	IG predator species $\times$ zone	1	0.171	0.680
	IG predator species $\times$ cue type $\times$ zone	2	1.877	0.391