SHORT COMMUNICATION

Predator cues have contrasting effects on lifespan of *Pardosa milvina* (Araneae: Lycosidae)

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Abstract.   Predators can affect prey indirectly by eliciting changes in behavior, morphology, and life history. These nonconsumptive effects are often mediated by predator cues used by prey to avoid capture. However, predator cues can cause stress responses in prey that negatively impact survival and reproduction. We explored responses of the wolf spider *Pardosa milvina* (Hentz 1844) to cues from the larger wolf spider *Tigrosa helluo* (Walckenaer 1837) and the ground beetle *Scarites quadriceps* Chaudoir 1843. We exposed *Pardosa* to cues from both predators and measured changes in body size, weight, consumption, and lifespan. We found significant effects of predator cues only on female longevity: females exposed to *Tigrosa* cues had shorter lifespans than those exposed to cues from *Scarites*. The lack of treatment effects on energy intake suggests that predator cues act through physiological pathways. Future experiments may uncover opposing hormonal mechanisms underlying the observed differences in lifespan.

Keywords: Nonconsumptive effects, foraging, predation, *Tigrosa helluo*, *Scarites quadriceps*

Predation is a ubiquitous ecological interaction that shapes the behavior, morphology, physiology, and life history of both predators and prey. Although traditionally focused on the consumption of prey by predators (i.e., consumptive effects), researchers have gained an appreciation for the impacts predators can have on prey without consuming them (i.e., nonconsumptive effects; Werner & Peacor 2003; Preisser et al. 2005). These nonconsumptive effects are frequently mediated by cues deposited by predators, often created as a by-product of interactions with prey (e.g., kairomones; Dicke & Grostal 2001). Prey have evolved the ability to respond to predator cues by altering their behavior and morphological traits (Benard 2004), but these modifications come with associated costs. Reduced foraging is a common trade-off made by prey responding to the risk of predation, and often translates into reduced growth, development, and survival (Lima 1998; Relyea 2007; Hawlena & Schmitz 2010a), though compensatory feeding is possible (Thaler et al. 2012; Hawlena & Schmitz 2010b).

Interestingly, stress induced by predator cues can decrease prey development and growth and increase prey mortality independent of changes in foraging (Stoks 2001; McCauley et al. 2011; Siepielski et al. 2014). If predator presence leads to a decrease in prey population sizes without directly consuming or changing the foraging success of their prey, then our conceptual models of predator-prey dynamics may be incomplete due to incorrectly attributing prey mortality to consumptive effects (Peckarsky et al. 2008; McCauley et al. 2011). Understanding the nonconsumptive effects predators have on their prey is an important goal in ecology, as prey responses to the risk of predation can affect processes at scales exceeding prey physiology and behavior by altering food web structure and ecosystem function (Hawlena & Schmitz 2010a). To further research on nonconsumptive predator effects, we explored the impacts of cues from two predators on the foraging, development, and survival of their shared prey using a well-studied system.

The wolf spider (Araneae: Lycosidae) *Pardosa milvina* (Hentz 1844) co-occurs with two larger predators: the wolf spider *Tigrosa helluo* (Walckenaer 1837), formerly *Hogna helluo* (Walckenaer 1837) (see Brady 2012), and the ground beetle (Coleoptera: Carabidae) *Scarites quadriceps* Chaudoir 1843 (study species hereafter referred to by genus). *Pardosa* has evolved a sophisticated sensory system able to detect nuanced information in cues deposited by *Tigrosa* indicating predator size (Persons & Rypstra 2001), sex (Lehmann et al. 2004), hunger level (Bell et al. 2006), diet (Persons et al. 2001), and residency

status (Barnes et al. 2002). Although not as well-characterized, *Pardosa* does respond to cues from *Scarites* with decreased patch residence time (Wrinn et al. 2012) and moderate increases in activity (Sitvarin, unpublished data). In contrast, *Pardosa* respond to *Tigrosa* cues with increased patch residence time (Wrinn et al. 2012) and decreases in activity (Persons et al. 2002; Sitvarin, unpublished data). Therefore, evidence suggests these predators are functionally inverse (i.e., cause opposing responses in prey, Herzog & Laforsch 2013), and thus are likely to cause conflicting responses in *Pardosa* foraging, development, and survival.

We expected exposure to predator cues to alter prey consumption, development, and survival of *Pardosa*. Specifically, we predicted that cues from *Tigrosa* would elicit responses opposite those seen in spiders exposed to *Scarites* cues, with *Tigrosa* cues resulting in increased prey consumption due to lower body condition (Lima & Bednekoff 1999; Persons et al. 2002), slower development, and decreased lifespan due to documented negative effects of *Tigrosa* cues on *Pardosa* (Persons et al. 2002; Taylor et al. 2005; Folz et al. 2006; Rypstra et al. 2007). Furthermore, we expected that longer exposure to predator cues would strengthen responses as chronic predator stress has larger effects than acute exposure (Lima 1998; Hawlena & Schmitz 2010a). Finally, we predicted males to be more strongly affected by the treatments due to previously documented differences between sexes in responses to experience with predator cues (Sitvarin & Rypstra 2012).

We collected all study organisms from Miami University's Ecology Research Center (39° 31′ 33″ N, 84° 43′ 20″ W). Female *Pardosa* carrying eggsacs were maintained individually in translucent containers (5.5 cm high × 5.5 cm diameter) with a 2 cm deep layer of moistened soil/peat moss mixture. Adult female *Tigrosa* and adult *Scarites* were maintained individually in larger containers (8 cm high × 12 cm diameter) with the same substrate type. Water was available *ad libitum*, and two crickets (*Acheta domesticus* Linnaeus, 1758), approximately half the size of the predator, were provided weekly. All containers were maintained in an environmental chamber on a 13L:11D light cycle at 25°C.

When *Pardosa* spiderlings dispersed (approximately two weeks after eggsacs hatched), we took no more than 12 spiderlings from each clutch (n = 21 clutches) and placed them individually into separate cultures containing collembolans (*Sinella curviseta*) as prey. After three molts, we transferred spiderlings to new containers and fed them two appropriately-sized crickets weekly. *Pardosa* reached the penul-

Table 1.—The effects of cue source (none, *Tigrosa helluo*, or *Scarites quadriceps*), exposure duration (1 or 3 days), and their interaction on female and male *Pardosa milvina* lifespan.

	Females			Males		
	df	F	P	df	F	P
Cue source	2	4.02	0.030	2	1.60	0.224
Duration	1	0.17	0.683	1	0.33	0.574
Cue source*Duration	2	3.13	0.060	2	1.42	0.264

timate stage after 70.8 ± 2.9 days (mean $\pm$ SE) and were randomly assigned to one of six treatments in a factorial design: one of three predator cue exposures (none, *Tigrosa* cues, or *Scarites* cues) and one of two exposure durations (1 or 3 days). We used penultimate spiders because the transition to adulthood may represent an especially sensitive period in life history (McCauley et al. 2011).

Three weeks prior to experimentation, we provided each *Tigrosa* and *Scarites* three crickets and then deprived them of food until trials were completed. We exposed *Pardosa* to predator cues by removing *Tigrosa* and *Scarites* from their containers and placing a single *Pardosa* into each container, thus preventing predation while allowing *Pardosa* to sense predator cues (i.e., silk, feces, and other excreta). To evaluate potential stress effects on body condition, we measured the abdomen width and weight of each *Pardosa* before and immediately after the exposure period 1 d or 3 d. Additionally, we provided each spider with two crickets after exposure and recorded change in abdomen width and weight after two days. We returned *Pardosa* to their original containers after the exposure period, recorded the number of days required to reach the final molt to adulthood, and monitored survival three times weekly until death.

Due to differences in longevity (Foelix 1996) and previously documented behavioral and developmental differences between males and females (Sitvarin & Rypstra 2012), we analyzed each sex separately. We evaluated the effects of predator cue source, exposure duration, and their interaction on *Pardosa* lifespan using linear mixed-effects models. We used cue source and exposure duration as fixed effects and clutch as a random effect to predict post-exposure lifespan, where a significant interaction between cue source and exposure duration indicates that the effect of predator cues depends on how long *Pardosa* is exposed. Differences in longevity between treatments were tested using one-way ANOVA followed by pairwise Tukey HSD comparisons. Changes in abdomen width and weight due to cue exposure and post-exposure feeding were tested separately with two-way ANOVA, using predator cue source and exposure duration as factors. The number of days required until the final molt to adulthood was similarly analyzed with two-way ANOVA. All analyses were conducted using R (R Core Team 2013).

Female *Pardosa* post-exposure longevity (144.9 ± 8.8 days) was significantly affected by predator cue source and marginally impacted by the interactive effects of predator cue source and exposure duration (Table 1). Specifically, females had shorter lives after encountering *Tigrosa* cues for three days compared to those exposed to *Scarites* cues for three days, though neither treatment was significantly different from the blank treatments (Fig. 1a). Exposure to cues from these predators for one day had no effect on female longevity, and spiders from those treatments had comparable lifespans to those in the blank treatments. In contrast to the effects on female spiders, male post-exposure lifespan (87.3 ± 4.7 days) was unaffected by any experimental treatment (Table 1, Fig. 1b).

There was no effect of predator cue source or exposure duration on changes in abdomen width or weight after exposure or after feeding on crickets (females: all $P > 0.4$, males: all $P > 0.2$) or the number of days required for spiders to reach adulthood (females: $P > 0.5$, males: $P > 0.7$) (Table 2).
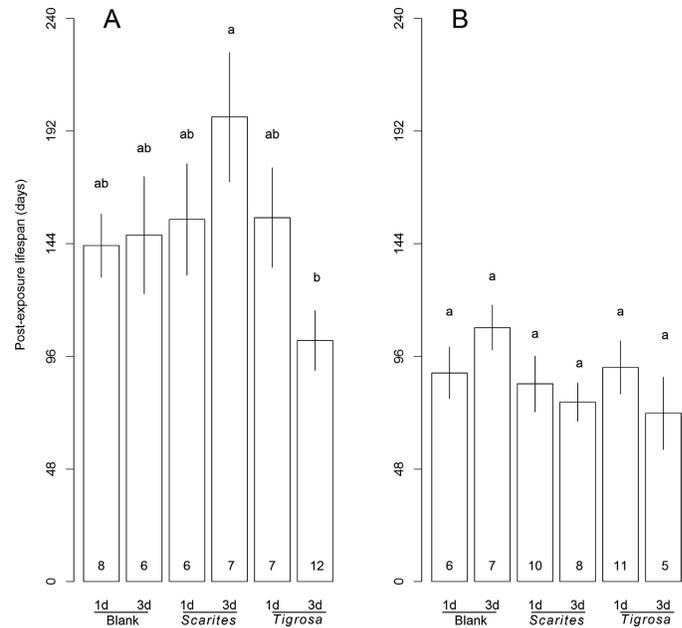

Figure 1.—The effects of exposure to cues from *Tigrosa helluo*, *Scarites quadriceps*, or no cues for one or three days on the mean ($\pm$SE) post-exposure lifespan of *Pardosa milvina* females (A) and males (B). Treatments sharing the same letter do not differ significantly. Sample sizes appear in bars.

We have demonstrated that exposure to cues from predators can have lifespan-altering effects on prey. Interestingly, the two predators used induced opposite responses that were sex-specific. Female *Pardosa* exposed to *Tigrosa* cues had significantly shorter lifespans than those exposed to cues from *Scarites*, though male spiders were unaffected by predator cues. To our knowledge, a predator cue-based increase in longevity has never been demonstrated before, though reduced lifespans after exposure to predator cues are known (e.g., McCauley et al. 2011).

We found reductions in female lifespan despite a lack of impact on body size, weight, or development. Similarly, larval odonates exposed to predator cues have been found to have increased mortality rates compared to unexposed individuals (Stoks 2001; McCauley et al. 2011; Siepielski et al. 2014). In one study, reduced damselfly lifespan was accompanied by slower growth and development rate, and smaller, more asymmetric wings after metamorphosis (Stoks 2001). However, these detrimental effects on prey beyond decreased longevity are not always present: prey exposed to predator cues had lower survival but did not differ from the control treatment in terms of body size as larvae or adults (McCauley et al. 2011; Siepielski et al. 2014). Interestingly, we did not find evidence for reduced foraging to explain how predator cues may reduce prey lifespan; odonates were also found to have unaltered energy intake in the presence of predator cues (Stoks 2001; McCauley et al. 2011; Siepielski et al. 2014). Prey typically must make trade-offs between anti-predator behavior and foraging, so most responses (e.g., reduced body size, slower development) are attributed to decreased energy intake (Lima 1998; Persons et al. 2002; Benard 2004; Relyea 2007; Hawlena & Schmitz 2010b; but see Davenport et al. 2014). However, in our study and the odonate studies described above, prey had *ad libitum* access to food (Stoks 2001; McCauley et al. 2011; Siepielski et al. 2014) or were provided a standardized amount of food without the presence of competitors, thus making reduced energy intake an unlikely explanation for decreased longevity. Although increased survival has been observed in response to predator cues, this effect is due to thinning (*sensu* Relyea 2007), a phenomenon unrelated to our results due to the lack of interactions among spiders.

Table 2.—Mean (±SE) change (post – pre) in abdomen width (abd., mm) and weight (wgt., μg) after exposure (exp.) to cues from *Tigrosa helluo*, *Scarites quadriceps*, or no cues for one or three days and after foraging (feed) and number of days to reach adulthood for female and male *Pardosa milvina*.

	Females					Males				
	Abd. exp.	Wgt. exp.	Abd. feed	Wgt. feed	Days	Abd. exp.	Wgt. exp.	Abd. feed	Wgt. feed	Days
Blank 1d	−0.07	−8.4	0.08	58.8	226.7	−0.16	−7.2	0.16	6.6	173.8
	(0.06)	(5.4)	(0.03)	(4.6)	(13.4)	(0.06)	(1.7)	(0.03)	(2.9)	(14.2)
Blank 3d	−0.14	−9.7	0.10	103.3	225.2	−0.02	−4.3	−0.23	−6.5	191.0
	(0.05)	(1.7)	(0.02)	(2.8)	(24.6)	(0.05)	(2.5)	(0.27)	(14.2)	(10.7)
Tigrosa 1d	−0.11	−15.4	0.09	85.7	241.1	−0.03	−4.6	0.09	4.6	174.6
	(0.06)	(4.1)	(0.04)	(2.3)	(21.4)	(0.07)	(5.3)	(0.04)	(2.7)	(12.3)
Tigrosa 3d	−0.08	−5.0	0.09	40.0	187.0	−0.08	−7.6	0.03	6.0	160.2
	(0.03)	(3.7)	(0.03)	(3.7)	(12.4)	(0.06)	(2.7)	(0.05)	(2.5)	(17.9)
Scarites 1d	−0.11	−2.0	0.13	122.5	236.5	−0.11	−1.9	0.12	6.1	169.5
	(0.14)	(2.8)	(0.07)	(4.2)	(24.5)	(0.09)	(2.1)	(0.03)	(2.1)	(10.4)
Scarites 3d	−0.18	−11.7	0.02	116.7	289.0	−0.12	−0.7	0.03	−2.0	153.8
	(0.09)	(6.3)	(0.09)	(3.2)	(28.0)	(0.05)	(11.2)	(0.07)	(11.3)	(9.5)

The precise proximate mechanism underlying changes in longevity after exposure to predator cues is unknown. Changes in foraging are unlikely (see above), and we saw no evidence of mortality attributable to pathogens (e.g., fungi or nematodes), both of which are mechanisms previously implicated as explanations for shortened lifespan after exposure to predator cues (McCauley et al. 2011). Stress hormones are likely involved, as the stress response diverts resources from other processes such as body maintenance, growth, and reproduction (Hawlena & Schmitz 2010a). We detected no effects on growth or development, so changes in behavior (e.g., Persons et al. 2002) or hormone-driven metabolic processes are likely mechanisms underlying the observed responses. Spiders exposed to predator cues may have altered assimilation efficiencies (Thaler et al. 2012), thus allowing differences in physiology that may translate into differential survival despite similar rates of growth and development.

Hormones coordinate large suites of behavioral processes and are known to regulate activity patterns in spiders. Specifically, the neurohormones serotonin and octopamine have contrasting effects on the huddle response of the orb-weaver *Larinioides cornutus* (Clerck 1757) (Araneae: Araneidae), lengthening and shortening the anti-predator behavior, respectively (Jones et al. 2011). Thus, there is a possibility that the contrasting effects of *Tigrosa* and *Scarites* cues on female longevity are driven by hormones acting in opposition. Discovering the hormonal underpinnings of this response could also provide insight on previously described opposing responses to cues from these predators in both emigration (Wrinn et al. 2012) and overall activity (Sitvarin, unpublished data). Increased longevity in response to predator cues has not previously been documented, but may be related to interactions between *Tigrosa* and *Scarites*. *Tigrosa* is the more dangerous predator for *Pardosa* (Sitvarin, unpublished data), though *Scarites* is capable of interfering with and consuming *Tigrosa* (Sitvarin & Rypstra 2014). Therefore, *Pardosa* may interpret *Scarites* cues as a forthcoming reduction in predation risk, leading to decreased levels of stress hormones or elevated levels of hormones that counter the effects of stress hormones.

We only found impacts of predator cues on lifespan for female spiders, a phenomenon likely tied to differences in life history between the sexes. Our sample sizes were modest, so the lack of effect on males may be a statistical artifact. However, males had significantly shorter lives than females, and so may also have less plasticity in lifespan. The sexes differ fundamentally in ecology (Foelix 1996) and in their growth and development trajectories (Sitvarin & Rypstra 2012). Furthermore, males have a higher metabolic rate than females (Walker & Irwin 2006), a fact that may put a limit on changes in longevity due to predator cues. Despite the lack of effect on males,

they do exhibit a greater behavioral response to predator cues (Schonewolf et al. 2006; Sitvarin & Rypstra 2012) than females.

Further work is necessary to fully elucidate the interactions among these species. It would be worthwhile to characterize the way *Pardosa* responds to the simultaneous presentation of cues from *Tigrosa* and *Scarites*, as both activity and anti-predator behavior can change when cues from both predators are present (Sitvarin, unpublished data). There may also be interesting interactions with other stressors, such as food stress or autotomy (Stoks 2001), that provide insight into how prey cope with multiple demands in nature. Cues from *Tigrosa* are known to reduce courtship (Taylor et al. 2005) and foraging (Rypstra et al. 2007) in *Pardosa*, but the impact of *Scarites* cues remain largely unexplored. Furthermore, cues from these predators may have opposing effects on reproductive success of *Pardosa*, with the potential for differential effects on males and females. We still have much to learn about predation risk-induced stress hormones in invertebrates (Preisser 2009), which is particularly profound considering the potential for nonconsumptive interactions to drive evolution (Siepielski et al. 2014).

ACKNOWLEDGMENTS

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