

The Effect of Predator Hunger on Chemically Mediated Antipredator Responses and Survival in the Wolf Spider *Pardosa milvina* (Araneae: Lycosidae)

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Abstract

The wolf spider *Pardosa milvina* exhibits effective antipredator behavior (reduced movement) in the presence of silk and excreta from a larger co-occurring predatory wolf spider *Hogna helluo*. As the quantity and quality of the silk and excreta may vary with the hunger state of the predator, we tested if chemical cues from a hungry vs. satiated *H. helluo* affected the activity level and survival of *P. milvina*. *Pardosa milvina* response was measured on substrates containing chemical cues from (1) a satiated *H. helluo*, (2) a *H. helluo* that had been withheld food for 2 wk, (3) cues from adult domestic crickets (*Acheta domesticus*), or (4) a blank test substrate (20 replicates/treatment). *Pardosa milvina* activity level was recorded on each substrate over a 30-min period using video-tracking equipment (Videomex-I[®]; Columbus Instruments, Columbus, OH, USA). We then measured *P. milvina* survival in the presence of hungry or satiated *H. helluo* on cues from a hungry *H. helluo*, satiated *H. helluo*, or a blank control (2 × 3 design). *Pardosa milvina* significantly reduced activity in the presence of *H. helluo* cues and showed significantly less activity in the presence of cues from a hungry *H. helluo* compared with a satiated one. Cue type and predator hunger state significantly affected *P. milvina* survival in the presence of live predators. However, cues from hungry vs. satiated *H. helluo* resulted in no difference in *P. milvina* survival. *Pardosa milvina* can discriminate between hungry vs. satiated predators based on silk and excreta cues alone, but differences in behavior as a result of this discrimination did not translate into increased survival in the presence of a live predator.

Introduction

Many animals show defensive behavior in the presence of chemical cues produced by predators. These cues may take many forms including excreta, marking pheromones, or other metabolic by-products (Dicke & Grostal 2001). Antipredator responses, although of obvious survival benefit, are generally costly because they interfere with both foraging and reproduction (Hedrick & Dill 1993; Kats & Dill 1998;

Dicke & Grostal 2001). Chemically mediated defensive behavior may be particularly costly because prey may respond in the absence of an actual predator and therefore tend to overestimate risk (Kats & Dill 1998). Prey may mitigate these costs by showing graded levels of defensive behavior proportional to the perceived risk (Lima 1998; Lima & Bednekoff 1999). However, such fine-tuned responses are dependent upon the ability of prey to acquire accurate information about the motivational state of the

predator (Lima & Dill 1990). Chemical cues associated with predators may provide substantial information about the level of risk beyond simply the presence or absence of a predator. For example, information about the diet of the predator can be obtained from chemical cues alone (Chivers et al. 1996; Laurila et al. 1997; Chivers & Smith 1998; Madison et al. 1999; Murray & Jenkins 1999; Venzon et al. 2000; Mirza & Chivers 2001; Brown & Dreier 2002). Predator hunger state has been found to have an effect on antipredator response, with cues from food-withheld predatory fish causing antipredator behavior in smaller prey fish (Brown et al. 2001; Smith & Belk 2001).

The wolf spider, *Pardosa milvina*, detects silk and excreta associated with a larger co-occurring predatory wolf spider, *Hogna helluo*. *Pardosa milvina* shows increased vertical movement, immobility, and avoidance behaviors in the presence of these cues (Persons et al. 2001, 2002). These behaviors are likely to be adaptive as they increase *P. milvina* survival when in the presence of a live *H. helluo* (Persons et al. 2001, 2002; Barnes et al. 2002; Lehmann et al. 2004). Reduced activity by *P. milvina* is also costly because it interferes with mate searching, copulation, foraging efficiency, and egg production (Persons et al. 2002; Taylor et al. 2005). *Pardosa milvina* is particularly adept at extracting information about predation risk from *H. helluo* silk and excreta and adjusting its activity level accordingly, presumably to mitigate these costs. Adult female *P. milvina* grades their antipredator responses to *H. helluo* cues based on the size of the spider producing the cues (Persons & Rypstra 2001), the diet of the predator (Persons et al. 2001), and how recently the predator deposited the cues (Barnes et al. 2002). Thus, *P. milvina* may use qualitative and quantitative differences in silk and excreta to assess relative predation risk. However, it remains unclear if hungry predators produce smaller quantities of silk and excreta, and therefore compromise the early warning system of *P. milvina*, or, conversely if *P. milvina* can detect qualitative changes in the silk and excreta of a hungry *H. helluo* and respond in an adaptive way.

Differences in *H. helluo* maturity, and thus size would be expected to result in varying amounts of chemical cues produced. *P. milvina* have shown a graded response between juvenile and adult *H. helluo* cues, but not between the cues of multiple juveniles and cues from an adult (Persons & Rypstra 2001). Presumably, the quantity of excreta is likely to decrease with the increasing hunger state of *H. helluo*. Additionally, it is known that the chemical com-

position of silk changes as a function of diet among web-building spiders (Craig et al. 2000) and thus both qualitative and quantitative changes are possible with silk cues as well as excreta as a result of recent feeding patterns. This, in turn, may affect the information available to *P. milvina* about the presence of a predator and subsequently impact both its behavior and survival in the presence of a live *H. helluo*.

We addressed two questions: (1) can *P. milvina* discriminate between a hungry and satiated *H. helluo* based on silk and excreta cues alone?; and (2) how does hunger state of the predator and direct chemical cues interact to influence *P. milvina* behavior and survival in the presence of live predators? We hypothesized that the satiated *H. helluo* would produce more silk and excreta and that variation in cue quantity would be detectable by *P. milvina*. If *P. milvina* relies primarily on cue quantity, this would result in a more intense antipredator response among satiated predators. If they are instead able to detect motivational state of the predator through the cues, and hungry predators are indeed more dangerous, they may show an elevated antipredator response in the presence of hungry predators. Response to quantity alone may ultimately compromise the effectiveness and adaptive value of using silk and excreta as an early warning system as hungry predators are presumably more dangerous than satiated ones. Although it seems obvious that a hungry predator would be more dangerous than a satiated one, this may not be the case as spiders frequently engage in superfluous killing by continuing predation even while fully satiated (Sunderland & Greenstone 1999; Persons 1999; Maupin & Riechert 2001).

General Methods

Collection and Maintenance

Adult and subadult female *P. milvina* and *H. helluo* were collected from the field during the summer and fall of 2001 and 2002 and raised to maturity in the laboratory. The spiders were collected near the hedgerows in hayfields, corn, and soybean fields in Snyder County, Selinsgrove, Pennsylvania. Spiders were kept in individual containers on a moist peat moss substrate of 4–5 cm for *H. helluo*, and 2–3 cm for *P. milvina*. The peat moss was used to provide a source of water and humidity to prevent desiccation. *Hogna helluo* were housed in round white plastic containers (8-cm high × 11 cm in diameter) and

P. milvina were maintained in round translucent plastic containers (5-cm high \times 8 cm in diameter). *Hogna helluo* were maintained in the lab on a weekly diet of 2–4 subadult domestic house crickets (*Acheta domesticus*) while *P. milvina* were maintained on a weekly mixed diet of 4–5 *Drosophila melanogaster* and 2–4 two-week-old domestic house crickets. Both species were kept on a 13 h:11 h light:dark cycle at room temperature (23–25°C).

Hogna helluo of two different hunger states was prepared prior to being used to deposit silk and excreta cues. The first treatment group of spiders was fully satiated 24-h prior to the experiment. The second treatment group was fully satiated for 24-h after which any live prey were removed and the spiders were withheld food for 14 d prior to silk and excreta deposition. Spiders were considered satiated if they had live prey available 24 h after feeding. All of the *P. milvina* were fed *D. melanogaster* to satiation 24-h prior to the experiment.

Experiment 1: Behavioral Responses of *P. milvina* to Silk and Excreta From Hungry vs. Satiated *H. helluo*

Stimulus Preparation

To test the effect of predator hunger state on the antipredator response of *P. milvina*, we established four different chemical cue treatments. Cue treatments consisted of silk and excreta deposited by: (1) a single hungry adult female *H. helluo*, (2) a single satiated adult female *H. helluo*, (3) excreta and other metabolic waste produced by a single adult house cricket (*A. domesticus*) and (4) nothing. The cues were deposited by a single adult cricket or adult female *H. helluo* in white plastic deli dishes (8-cm high \times 11 cm in diameter), which were previously rinsed with 95% ethanol. Prior to placing stimulus animals in each dish, the ethanol was allowed to fully evaporate. To establish chemical cues, a food-deprived *H. helluo*, a satiated *H. helluo*, or a cricket was placed in the container for 12 h, during which time it was allowed to deposit silk and excreta undisturbed. At the end of the 12-h session, the individuals were removed and placed back in their original containers. Only a single individual was used to lay down cues in each container and no *H. helluo* or cricket was used more than once as a stimulus. Immediately upon removal of *H. helluo* or crickets, we tested *P. milvina* activity level. A stratified randomization procedure was used during testing. We tested spiders across all

four treatments daily and randomized the order in which we ran each treatment each day to control for time of day, sequence, or other possible confounding effects.

Experimental Protocol

A single adult female *P. milvina* was introduced into the center of each substrate-treated container. Each of the following behaviors was recorded during a 30-min trial ($n = 20$ /treatment): (1) total time spent walking during the trial period (s), (2) distance traveled (cm), (3) total time spent immobile (s), (4) total time spent stationary while participating in non-forward motion (leg waving, grooming, pivoting, or other motion that did not involve forward motion), and speed, which was derived by dividing distance traveled by the time spent walking (cm/s). Time spent immobile is equivalent to time spent freezing and constitutes an important antipredator response (Persons et al. 2001). *Pardosa milvina* behavior was tracked using an automated video tracking system (Videomex-I[®]) and a black and white video camera (see Persons et al. 2001 for a complete description of the video tracking system).

Four of five categories of behavior (time spent walking, non-forward motion, time spent immobile, and speed) were found to approximate a normal distribution and were not transformed. Distance traveled was natural log-transformed to conform to assumptions of normality. Results were then statistically analyzed with a one-way ANOVA for each of the five behaviors measured. Behaviors that were statistically significant across treatments were further analyzed using a Tukey post hoc comparison of means test. We then used a sequential bonferroni adjustment to the alpha level to correct for the number of ANOVA tests performed.

Experiment 2: Survival of *P. milvina* in Containers With Hungry or Satiated *H. helluo* and Associated Chemical Cues

Stimulus Preparation

We sought to determine if hungry *H. helluo* and satiated *H. helluo* present different levels of risk to *P. milvina* and to measure if predator silk and excreta mitigates any possible difference in risk. The procedures used to establish the feeding treatments for both *H. helluo* and *P. milvina* in the first experiment were repeated here. As in expt 1, we allowed a single adult female *H. helluo* to deposit silk and excreta;

however, we used moistened peat moss as a substrate and larger containers than those used in expt 1. This allowed a more natural approximation of a predator-prey encounter as these spiders were collected on the ground in habitat with exposed soil. These round containers were nearly twice the diameter (20 cm) of those used in expt 1, and made of a translucent plastic. The substrate consisted of a thin layer (1–2 cm) of moist compressed peat moss, sufficient to cover the bottom, but not enough for effective burrowing into the substrate by the spider. Because the container was larger, the cues were allowed to be laid down by the *H. helluo* for 24 h to ensure adequate coverage at a density comparable with that of expt 1.

We used a 2 × 3 design with six treatments (20 replicates/treatment): (1) blank substrate with a single satiated adult female *H. helluo*, (2) blank substrate with single hungry adult female *H. helluo*, (3) hungry cue substrate with satiated predator, (4) hungry cue substrate with hungry *H. helluo*, (5) satiated cue substrate with satiated predator, and (6) satiated cue substrate with hungry predator. For each trial (except in the blank control treatment), two different *H. helluo* were used, one to generate the cues, and the other as the predator in that container.

Live *H. helluo* and *P. milvina* were placed under inverted clear plastic vials at opposite sides of the container and allowed 1 min to acclimate to the container. The vials were removed simultaneously and each pair of spiders was allowed to run freely for 3 h or until the *P. milvina* was preyed upon by the *H. helluo*. The number surviving and predation latency for each *P. milvina* were recorded.

Differences in survival distribution were analyzed statistically using failure-time analysis (survival regression). We used the non-parametric Kaplan–Meier product limit estimator to test for a significant treatment effect of the median survival time for each

treatment. We then made pair-wise comparisons of the survival distributions using the log-rank (Mantel–Cox) test. Alpha levels for statistical significance were adjusted using a sequential bonferroni to control for the number of pair-wise comparisons performed between treatments.

Results

Results: Experiment 1

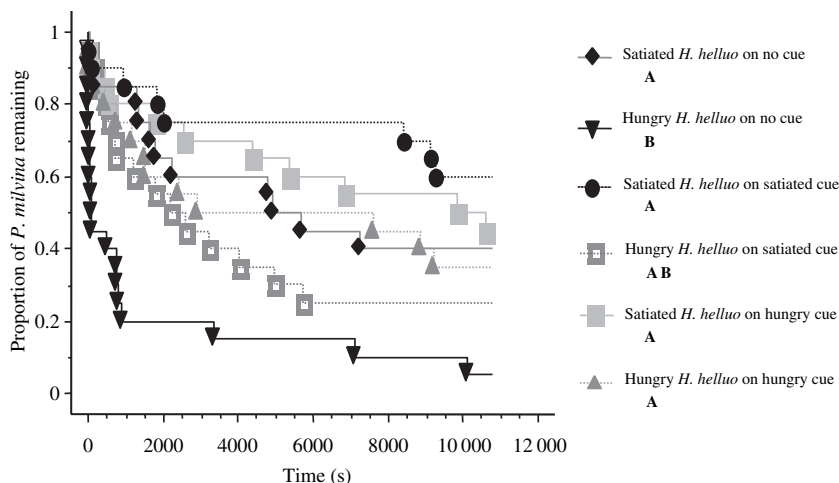
Pardosa milvina showed a significant reduction in activity in the presence of predator cues, and showed a significantly greater reduction of activity in the presence of hungry predator cues. Spiders spent the greatest amount of time moving and traveled the greatest distance on substrate treatments in which predator cues were not present. *Pardosa milvina* moved a significantly shorter distance on substrates treated with predator cues compared with a blank substrate as well as on hungry *H. helluo* cues compared with satiated *H. helluo* cues (Table 1). The time spent walking was found to be significantly different between the blank substrate and those containing predator cues, and also between the hungry and satiated *H. helluo* treatments (Table 1). Test spider speed was also significantly different between cues from hungry vs. satiated predators, with *P. milvina* moving slowest on silk and excreta from hungry *H. helluo*. A Tukey post hoc comparison of means test revealed that *P. milvina* spent significantly more time immobile on substrates with either hungry or full *H. helluo* compared with the blank control or cricket treatment. However, we did not find a significant difference in time spent immobile between the hungry and satiated predator treatments or a significant difference in time spent moving in non-forward motion among treatments (Table 1). Although an initial significant difference in speed was found across treatments ($p = 0.03$, Table 1), this difference

Table 1: Movement behaviors ($\bar{x} \pm SE$) measured for an adult female *Pardosa milvina* in the presence of silk and excreta chemical cues from a single adult female *Hogna helluo* that varied in hunger level (satiated or 14 d without food) compared with cues from a domestic house cricket (*Acheta domesticus*) or blank control substrate

Behavior	Blank control	Cricket cues	Satiated <i>Hogna</i> cues	Hungry <i>Hogna</i> cues	$F_{3,71}$	p
Distance traveled (cm)	588.1 ± 72.7 ^a	479.8 ± 88.9 ^{a,b}	345.5 ± 82.9 ^b	87.1 ± 21.2 ^c	8.15	0.0001*
Time spent walking(s)	391.4 ± 34.5 ^a	369.6 ± 48.4 ^a	215.3 ± 40.3 ^b	97.7 ± 20.3 ^c	12.62	0.0001*
Non-forward motion(s)	595.8 ± 34.6	664.8 ± 45.3	570.6 ± 48.9	602.2 ± 85.3	0.55	0.6507
Time spent immobile(s)	812.8 ± 52 ^a	769.8 ± 46.5 ^a	1010.4 ± 66.1 ^b	1100.2 ± 87.3 ^b	5.97	0.0011*
Speed (cm/s)	1.43 ± 0.13 ^a	1.21 ± 0.12 ^a	1.25 ± 0.25 ^a	0.71 ± 0.11 ^b	3.14	0.0306

F-values based on one-way ANOVAS for each behavior. Different letters indicate significant differences between treatments based on a Tukey post hoc comparison of means test. * = significant difference based on a sequential bonferroni correction of the α level for multiple tests.

Fig. 1: *Pardosa milvina* survival curves in the presence of live *H. helluo*. Each point on the graph indicates a predation event and a subsequent decrease in the number of surviving members of that treatment. There was a significant difference in median survival time by treatment. Different letters next to each treatment group indicate significant differences between treatments after pair-wise comparisons (log rank tests) and a sequential bonferroni correction of the α level to control for the number of tests



did not persist after a sequential bonferroni adjustment of the alpha level.

Results: Experiment 2

We found a significant effect of substrate treatment on median *P. milvina* survival time (Mantel–Cox $\chi^2_5 = 34.31$; $p < 0.0001$). *Pardosa milvina* that were introduced onto a blank substrate with a live hungry *H. helluo* were quickly preyed upon, with a significant difference between this and all treatments except hungry *H. helluo* on satiated *H. helluo* cues (Fig. 1).

There were also considerable differences in the number that survived each treatment. Only one individual survived the duration of the experiment (3 h) in the treatment with hungry *H. helluo* and no predator cues available compared with eight that survived with the satiated *H. helluo* without cues present. In the presence of a live hungry *H. helluo*, *P. milvina* showed a sevenfold increase in mean survival time on hungry predator cues over no cues.

In a pair-wise comparison of the treatments, we found a significant difference in *P. milvina* median survival time in the hungry *H. helluo* on blank cues and satiated *H. helluo* on blank cues treatments (log rank test $\chi^2 = 13.150$; $p < 0.0003$). There was also a significant difference between *P. milvina* survival with hungry *H. helluo* on blank cues and satiated *H. helluo* on satiated *H. helluo* cues (log rank test $\chi^2 = 20.524$; $p < 0.0001$). Statistical differences in pair-wise comparison were also found between hungry *H. helluo* on blank cues vs. satiated *H. helluo* on hungry cues (log rank test $\chi^2 = 14.342$; $p < 0.0002$), and hungry *H. helluo* on blank cues vs. hungry *H. helluo* on hungry cues (log rank test $\chi^2 = 9.598$; $p < 0.0019$). The pair-wise comparisons remained

statistically significant after a table-wide sequential bonferroni adjustment of the alpha level was performed (Fig. 1).

Discussion

Our results demonstrate that *P. milvina* is able to discriminate between chemical cues from hungry and satiated *H. helluo* wolf spiders, showing significantly reduced activity when exposed to cues from hungry *H. helluo* compared to when exposed to satiated *H. helluo* cues. Our second experiment demonstrated that hungry *H. helluo* is indeed a significantly more dangerous predator than satiated individuals and that reduction in activity in the presence of *H. helluo* silk and excreta increases survival of *P. milvina*. This suggests that *P. milvina* may gain important information about the motivational state of *H. helluo* through chemical cues alone and respond appropriately according to the level of risk. Cues deposited by *H. helluo* elicited a stronger reduction in activity than did cues from domestic crickets or a blank container, consistent with previous studies of *P. milvina* response to *H. helluo* silk and excreta (Persons & Rypstra 2000; Persons et al. 2001; Barnes et al. 2002). *Pardosa milvina* activity levels in the presence of cricket cues were no different than the control container lacking cues. Although studies have found that wolf spiders show a preference for substrates previously occupied by crickets over clean sheets of paper (Persons & Uetz 1996; Persons & Rypstra 2001; Hoefler et al. 2002), our study used satiated *P. milvina*, so their motivation for seeking prey may have been exceptionally low.

We originally predicted that *P. milvina* antipredator behavior may be compromised because of a lack of

predator chemical cues among hungry predators. For example, hungry *H. helluo* are much less likely to establish silk laden burrows than are well-fed individuals (Walker et al. 1999a). However, our results demonstrate that *P. milvina* can distinguish and reduce their activity (time spent walking, distance traveled, and speed) in response to hunger level of *H. helluo* from the cues alone (Table 1). Studies have shown that the probability of lycosids lunging at prey is directly related to the time the prey spend moving (Persons & Uetz 1997). Our results suggest that there is a difference in the quality of the cues produced that varies with hunger level and is independent of the quantity of silk and excreta produced.

Non-forward motion was not found to be significantly different among treatments in this study. This behavior consists of slow leg waving and tapping, pedipalp rotation for chemoexploring, and pivoting in place. These behaviors probably serve a function in gathering sensory information. Findings from other studies with *P. milvina* suggest that these less overt behaviors may not significantly draw the attention of a predator or induce predatory behavior (Persons & Uetz 1997; Barnes et al. 2002) and therefore may be less important than rapid movement with high acceleration, or directed horizontal movements characteristic of lycosid courtship displays (Pruden & Uetz 2004).

The mechanism by which *P. milvina* can discriminate between cues from hungry or satiated predators is unknown. We hypothesized that a hungry spider would not produce as much excreta as a fully satiated spider. Silk production is likely to vary with hunger state as well. Silk proteins are highly conserved and recycled among some web-building spiders, which suggest that they are metabolically expensive to produce (Tanaka 1989; Foelix 1996). A study found that orb weavers deprived of food actually increased the amount of silk used in web production (Tso 1998). Increased silk production may continue until energetic constraints prohibit the production of large webs (Sherman 1994). It is unknown if wolf spiders shift the amount of silk deposited as a function of hunger state. Wolf spiders do not depend on their silk for prey capture, so it is likely that hungry *H. helluo* will not invest energy in silk production if there is no energetic payoff, particularly as such cues alert potential prey of their presence. If the quantity of both silk and excreta produced by *H. helluo* does not drop with hunger, then the observed strong antipredator behaviors of *P. milvina* are in response to qualitative rather than quantitative properties of the chemical cues.

Hogna helluo activity level is known to increase with hunger level (Walker et al. 1999b), which may have played a role in how active *H. helluo* were while laying down chemical cues. Hungry individuals have higher energetic requirements and must feed at an increased rate to meet these needs (Lima 1998), presumably resulting in the increased movement reported by Walker et al. (1999b). Increased predator activity could result in the deposition of cues relatively evenly throughout the container, while a satiated predator may tend to localize silk and excreta deposition resulting in earlier and more frequent encounters by *P. milvina* with predator cues from the hungry predator. Walker et al. (1999a) found that satiated *H. helluo* are significantly more likely to build silk-lined burrows and forage from these sites than hungry individuals, suggesting that silk and excreta distributions between hungry and satiated *H. helluo* may be quite different. Quantitative data were not recorded on the distribution of silk in the container, but anecdotally we observed more excreta deposited by satiated predators.

In expt 2, we found that hungry *H. helluo* are significantly more dangerous predators to *P. milvina* than satiated ones. However, the significant difference in activity between cues from hungry vs. satiated predators did not translate into significant differences in survival among the two hunger level treatments of the predator. Variation in *P. milvina* survival among treatments was largely attributable to the presence or absence of predator silk and excreta and the hunger state of the predator rather than the source of the chemical cues (hungry or satiated *H. helluo*). When placed on a natural substrate (moist peat moss) with a live predator, *P. milvina* showed significantly greater survival in the presence of *H. helluo* cues compared with blank substrates (Fig. 1). *Pardosa milvina* also survived significantly longer in the presence of satiated *H. helluo* compared with hungry *H. helluo* on blank substrates (Fig. 1). This finding confirms our assumption that the hunger level of the predator does change the risk of predation for *P. milvina*. In general, the type of chemical cue (from a hungry or satiated predator) had a relatively minor impact on *P. milvina* survival compared with the presence or absence of the cue.

The results for hungry *H. helluo* on blank substrate and hungry *H. helluo* on satiated cues do support the findings from the first experiment that *P. milvina* responds less strongly to satiated predator cues. Survival of *P. milvina* in the presence of hungry *H. helluo* with no initial predator cues is

extremely low, and shows a statistical difference relative to all of the other treatments except the one containing satiated predator cues with a hungry live *H. helluo*. This indicates a response consistent with appropriate antipredator behavior. *Pardosa milvina* tended to match its activity level with the perceived predation threat based on silk and excreta information. We suggest that other sensory information about the predator (e.g. visual cues, vibrations, etc.) coupled with differences in live predator behavior among hungry and satiated *H. helluo* may have further modified *P. milvina* behavior and mitigated the reaction of *P. milvina* to chemical cues alone. As such, predator chemical cues are likely to be used in conjunction with other sources of information to assess overall risk.

The information gleaned from chemical cues is of the greatest benefit to *P. milvina* in the initial encounter. Silk and excreta may serve to increase vigilance or serve as a priming cue that reduces the overall reaction time of prey when visual or seismic information about the predator is gained. The adjustment in antipredator response to sensory information that is received secondarily is likely to have played a role in the experiment, especially in the survival of *P. milvina* that lasted beyond the initial encounter.

There were a number of methodological differences between expts 1 and 2 that may have contributed to finding significant differences in the ability of *P. milvina* to discriminate between cues from hungry and satiated predators, but not to exhibit significant survival differences because of these behaviors. The use of moist peat moss substrates for expt 2 but not expt 1 may have had an important effect on the quality of the cues that were deposited as well as the way it was deposited. Water is known to degrade some of the cues used to detect *H. helluo* by *P. milvina* (Wilder et al. 2005) and therefore, *P. milvina* on these substrates may have had less information available to them about *H. helluo*. Further, the critical chemical information necessary to discriminate between hungry and satiated *H. helluo* may have been removed or degraded by moisture in the second experiment.

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