



## RESEARCH PAPER

# Effects of Structural Refuge and Density on Foraging Behaviour and Mortality of Hungry Tadpoles Subject to Predation Risk

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**Abstract**

Theoretical models of prey behaviour predict that food-limited prey engage in risk-prone foraging and thereby succumb to increased mortality from predation. However, predation risk also may be influenced by factors including prey density and structural cover, such that the presumed role of prey hunger on predation risk may be obfuscated in many complex predator–prey systems. Using a tadpole (prey) – dragonfly larva (predator) system, we determined relative risk posed to hungry vs. sated prey when both density and structural cover were varied experimentally. Overall, prey response to perceived predation risk was primarily restricted to increased cover use, and hungry prey did not exhibit risk-prone foraging. Surprisingly, hungry prey showed lower activity than sated prey when exposed to predation risk, perhaps indicating increased effort in search of refuge or spatial avoidance of predator cues among sated animals. An interaction between hunger level and predation risk treatments indicated that prey state affected sensitivity to perceived risk. We also examined the lethal implications of prey hunger by allowing predators to select directly between hungry and sated prey. Although predators qualitatively favoured hungry prey when density was elevated and structural cover was sparse, the overall low observed variation in mortality risk between hunger treatments suggests that preferential selection of hungry prey was weak. This implies that hunger effects on prey mortality risk may not be readily observed in complex landscapes with additional factors influencing risk. Thus, current starvation–predation trade-off theory may need to be broadened to account for other mechanisms through which undernourished prey may cope with predation risk.

**Introduction**

Considerable uncertainty exists regarding aspects of the complex relationship between predators and their prey, including the suite of responses potentially underlying trade-offs between prey foraging opportunity vs. predation risk (McPeck 2004; Steiner & Van Buskirk 2009). Previous empirical studies in this general area have helped shape our current understanding of the starvation–predation risk trade-off (e.g. Sih 1987; Sinclair & Arcese 1995; Preisser

et al. 2007); however, several potential mechanisms underlying the balance between risk from starvation vs. risk from predation remain poorly understood. For example, studies show that prey can modulate their exposure to predation risk depending on food availability or quality (e.g. Sih et al. 1988; Holmes 1991; Anholt & Werner 1998), with food-limited individuals exhibiting risk-prone foraging and accepting attendant increase in predation risk to avoid malnutrition (e.g. Lima 1998; Murray 2002). In addition, prey subject to chronic food limitation

may be debilitated and thereby experience impeded predator escape ability, leading to increased predation risk (e.g. FitzGibbon & Fanshawe 1989; Sinclair & Arcese 1995). In contrast, under certain conditions, predators may even select over nourished individuals disproportionately from the prey population (Rohner & Krebs 1996; Murray 2002). Clearly, mechanisms underlying predation risk responses in malnourished prey and their associated consequences remain poorly understood (see also, Steiner & Van Buskirk 2009).

The effect of predation risk may be further masked by other constraints such as escape cover availability, the presence of which should lower risk (Heck & Crowder 1991; Hossie & Murray 2010; but see Schooley et al. 1996; Bro et al. 2004). Yet, given that prey animals live in complex environments, hunger level and cover availability may interact causing the anticipated benefits of cover to differ between hungry and sated prey. One can imagine that undernourished and risk-prone prey will receive fewer benefits from cover compared to sated prey and that additional disparity in responses may emerge depending on whether food limitation elicits short-term hunger vs. chronic malnutrition. Currently, such complex interactions are poorly understood, largely because of difficulties associated with disentangling cause-and-effect relationships between mechanisms affecting nutritional status, cover use and mortality risk (e.g. Murray 2002; Vance-Chalcraft & Soluk 2005).

Prey density is another factor that may affect predation risk either directly or indirectly through food and cover. Predators generally become more selective as prey density and associated encounter rates increase (Krebs et al. 1977; Werner & Hall 1979). However, the presence of finite hiding cover may complicate predator-prey relationships by limiting the number of individuals able to effectively seek refuge from predation risk. When prey numbers are low, vacant refuge should limit predation risk among all prey (whether risk-prone or not) by increasing both randomness of prey encounters by searching predator and the ability for prey to escape to predator-free space (Heck & Crowder 1991). In contrast, if prey density is high and cover availability is limited, risk-prone (i.e. hungry) individuals should be increasingly exposed to predation risk (Sih et al. 1988; Lima & Dill 1990). Finally, abundant structural cover may prompt the use of hiding cover as a primary means to avoid predator detection, as opposed to strict reductions in activity (e.g. Sih & Kats 1991). We can therefore surmise that as prey may respond in a variety of ways to the conflicting

demands of predation and starvation, anti-predator behaviour and mortality risk also may vary with other factors in the environment. Notwithstanding challenges in addressing such questions empirically, to broaden our general understanding of predator-prey relationships, there, clearly, is a need to further elucidate how prey respond to risk in variable and complex environments.

Using a tadpole (prey) – dragonfly larva (predator) system, we quantified anti-predator behaviour and mortality risk relative to prey hunger levels, the availability of hiding cover and prey density. We predicted that: (1) proportionally more hungry (i.e. risk-prone) prey should be consumed as prey density increases; (2) risk-prone prey should suffer greater mortality if structural cover is saturated at high prey density; and (3) greater than proportional consumption of hungry prey should be dampened when structural cover remains unsaturated.

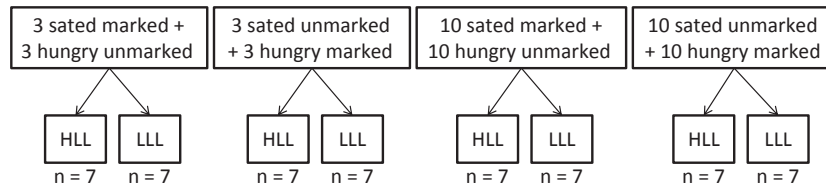
## Methods

### Husbandry and Maintenance

Six *Rana catesbeiana* egg broods were collected in June 2008 from a semi-permanent pond near Peterborough, Ontario, Canada (44° 16' N 78° 37' W). Tadpoles were raised to Gosner stage 25 (Gosner 1960) following the methods outlined in Hossie & Murray (2010), at which point they were used for the experiments outlined later. *Anax junius* dragonfly larvae were collected from temporary and semi-permanent ponds in the surrounding area and were maintained in plastic dishes filled with aged tap water. Dragonfly larvae were fed 1–2 tadpoles daily, but were not fed 24 h before use in the experiment outlined later. This work was approved by the animal care committee of Trent University and conforms to all relevant legal and ethical protocols.

### Structure, Density and Hunger Effects on Tadpole Behaviour and Mortality

To assess interactive effects of structural cover, conspecific density and hunger on tadpole anti-predator behaviour, we used a factorial design with two levels of prey hunger within each experimental tank and two between-tank levels of both habitat structure and overall prey density (see Fig. 1). We filled 28 aquaria (30 × 20 × 20 cm) with 10 l of aged tap water and applied one of the two cover treatments: low leaf litter (LLL) or high leaf litter (HLL). The LLL treatment received sufficient leaf litter to provide a



**Fig. 1:** Graphical representation of experimental design. Experimental tanks were composed of equal densities of hungry and sated tadpoles at both absolute densities (i.e. six or 20 tadpoles), and tanks with hungry-marked as well as tanks with sated-marked tadpoles were divided evenly between cover treatments. HLL = high leaf litter and LLL = low leaf litter cover treatments. Sample sizes indicate the total number of replicate tanks.

thin layer across the entire bottom of the tank only [dry mass:  $7.07 \text{ g} \pm 0.39$  (SE)], which was suitable to allow dragonfly larva locomotion across the tank without providing a refuge for prey. The HLL treatment received litter covering the bottom 3 cm of the tank [dry mass:  $34.4 \text{ g} \pm 1.32$  (SE)]. Before use in our experiment, leaves (*Quercus rubra* L.) serving as structural cover were soaked and homogenized to  $\sim 1 \text{ cm}^2$  pieces following methods outlined in Hossie & Murray (2010). By the end of this process, tank water had comparable pH ( $\bar{x}$ : LLL =  $7.2 \pm 0.2$ , HLL =  $7.5 \pm 0.2$ ;  $t_4 = -2.0$ ,  $p = 0.12$ ,  $n = 6$ ) and clarity was visually indistinguishable between treatments. We provided oxygen to all tanks via continuous-flow aeration. Tadpole feeding on leaf litter was not observed, and leaf litter is known to be unprofitable forage for tadpoles (Iwai & Kagaya 2005; Williams et al. 2008).

We used two broods for the experiment detailed later; remaining broods were used to maintain predators until tadpoles had developed to stage 25 (Gosner 1960) for the experiment. Tadpoles within a tank were all from a single brood; however, the two broods were divided evenly among treatments to avoid genetic confounds. This approach has the further benefit of reducing within-treatment variability and should increase our ability to detect fine-scale responses to predation risk. Twenty-four hours before the experiment, tadpoles were divided into two groups: sated and hungry. The sated treatment was fed shredded boiled spinach *ad libitum*, whereas the 'hungry' treatment was deprived of food for 24 h. This treatment sought to elicit symptoms of acute hunger, including risk-prone foraging, while avoiding responses characteristic of tadpoles experiencing chronic malnutrition (e.g. Altwegg 2003; Fraker 2008). The following day, we dyed half of the tadpoles in each food level treatment (i.e. 91 tadpoles each) with 0.02 g/l neutral red (Herreid & Kinney 1966; Guttman & Creasey 1973). This dose was sufficient to distinguish tadpoles for 24 h without

causing mortality or other discernible secondary effects (T.J. Hossie, unpubl. data). Porous predator cages ( $7.5 \times 13 \times 7.5 \text{ cm}$ ) were affixed to each tank and partially submerged in the water (Ferland-Raymond & Murray 2008). Predator cages allowed the transfer of chemical cues to the tanks without allowing direct contact between dragonfly larvae and tadpoles. We combined tadpoles in the centre of experimental tanks such that each tank achieved a final density of 6 or 20 tadpoles, contained equal proportions of sated and hungry tadpoles, and tanks with either hungry or sated tadpoles marked were divided evenly between cover treatments (Fig. 1). After a 20 min acclimation period, two behaviour tests were conducted (1300 and 1320 h) and included recording number of tadpoles active (i.e. movement of any kind) and number of tadpoles visible for each dye treatment. Note that tadpoles were considered inactive when not visible. Following the second behaviour test, larval *Anax junius* predators were placed in predator cages and two additional behaviour tests were conducted at 1340 and 1400 h. This design allowed us to quantify interactive effects of food deprivation, conspecific density, and cover on tadpole anti-predator behaviour, while blocking for effects of dye. Individual tadpoles were used a single time throughout this experiment.

Following the behaviour test, dragonfly larvae were released from cages and allowed to consume tadpoles for 4 h, at which point they were removed and tadpoles were enumerated by colour. During the lethal predation trial, we recorded predator activity level by assessing which side of the tank the larva was on to quantify the degree of active search across tanks. Forty-nine predator observations were recorded over 4 h (i.e.  $\sim 1 \text{ scan} \cdot 5/\text{min}$ ); to achieve this level of replication, we focused our observations on a subset of 16 tanks (four per treatment group). Predator observations allowed us to quantify any treatment-related differences in predator activity, and tadpole enumeration determined if predators selected

prey based on hunger condition and if this selection pattern differed with prey density and cover availability. Trials were repeated 2 d following completion of initial trials to achieve a final sample size of 56 tanks, (i.e.  $n = 14$  tanks per cover–density treatment) and 32 tanks with predator observations. Note that previous studies have: (1) matched or exceeded the degree of food deprivation experienced by tadpoles in our experiments (e.g. Horat & Semlitsch 1994 Fraker 2008); and (2) subjected tadpoles to direct predation by dragonfly nymphs (e.g. Altwegg 2003).

### Data Analysis

To determine whether prey selection deviated from random, we calculated the number of hungry vs. sated tadpoles consumed per tank (i.e. number of hungry tadpoles consumed divided by number of sated tadpoles consumed); the selection index was  $>1$  when hungry tadpoles were selected. This method yields a metric that facilitates comparison of prey selection between density and cover treatments. Single sample unpaired *t*-tests evaluated patterns of non-random prey selection against a reference constant of 1 (i.e. no selection). Late instar dragonfly larvae only stop attacking prey when preparing to moult, so we removed from analysis tanks where no tadpoles were consumed ( $n = 5$ ). To determine the effects of cover and density, total number of tadpoles consumed was log transformed and analysed via two-way factorial ANOVA.

Tadpole behaviour measurements were converted to proportions for each hunger treatment group, and proportion visible was converted to proportion present in refuge for each hunger treatment (i.e.  $1 -$  proportion observed per hunger treatment). To simplify the analysis, we restricted our behavioural measures to two values for each behaviour (i.e. a single value for both before and after exposure to a caged predator) by using the average values recorded before vs. after exposure. Proportions were arcsine-square root transformed and analysed by repeated measures ANOVAs. We set cover and density as between-tank factors and blocked between trial effects (i.e. random factor, Zar 1999). Before vs. after predator exposure and satiated vs. starved were set as repeated measures (i.e. within-tank factors) to allow testing of predation risk against tadpole activity and refuge use as well as any interaction between prey hunger and density, while controlling for within-tank variation.

The number of times a dragonfly larva switched sides was summed across one of four time periods (i.e. grouped by hour, yielding  $n = 12$ – $13$  observations

per time period) and analysed by repeated measures ANOVA. Independent factors included cover and tadpole density. All tests were conducted in Statistica 7 (StatSoft, Inc. 2004), and we considered  $0.5 < p < 0.10$  as marginally significant.

## Results

### Prey Selection and Mortality Risk

Predators did not show strong selective predation on hungry prey, regardless of prey density or abundance of structural cover (Table 2). Interestingly, despite the lack of strong evidence for prey selection, all but one of the four density–cover treatment groups tended qualitatively toward greater consumption of hungry prey, and this trend was most apparent when cover was low and tadpole density was high (Table 2). Overall, consumption of tadpoles increased with tadpole density (six tadpoles:  $1.55 \pm 0.10$ ; 20 tadpoles:  $5.46 \pm 0.10$ ;  $F_{1,51} = 12.02$ ,  $p < 0.001$ ), but was not significantly influenced by the main effect of cover ( $\bar{x} \pm$  SE: low cover:  $3.58 \pm 0.10$ , high cover:  $2.58 \pm 0.10$ ;  $F_{1,51} = 3.43$ ,  $p = 0.07$ ). The cover  $\times$  density interaction was marginally significant, but overall fewer tadpoles were consumed in the cover treatment at the 20 but not six tadpole density (six tadpoles:  $1.55 \pm 0.14$  (low cover),  $1.52 \pm 0.14$  (high cover); 20 tadpoles:  $7.21 \pm 0.14$  (low cover),  $4.08 \pm 0.14$  (high cover);  $F_{1,51} = 3.08$ ,  $p = 0.09$ ).

### Structure, Density and Hunger Effects on Tadpole Behaviour

Analysis of tadpole activity revealed that overall, fewer hungry tadpoles were active compared to sated tadpoles ( $\bar{x}$  proportion  $\pm$  SE; hungry:  $0.19 \pm 0.13$ , sated:  $0.28 \pm 0.14$ ; Table 1); this was opposite to our first prediction. We did not find a significant main effect of cover, density or predation risk on tadpole activity (Table 1). However, a food  $\times$  predation risk interaction revealed that although food deprivation did not alter activity in the absence of predation risk (Tukey's *post hoc*  $p = 0.86$ ), hungry and sated tadpoles responded differently to the onset of such risk (Tukey's *post hoc*  $p = 0.005$ , Table 1). Indeed, hungry tadpoles showed a slight decrease in activity, whereas sated animals slightly increased activity (Fig. 2a). Similarly, the significant density  $\times$  food interaction revealed that overall food deprivation did not affect activity at the six tadpole density (Tukey's *post hoc*  $p = 0.79$ ), but that sated

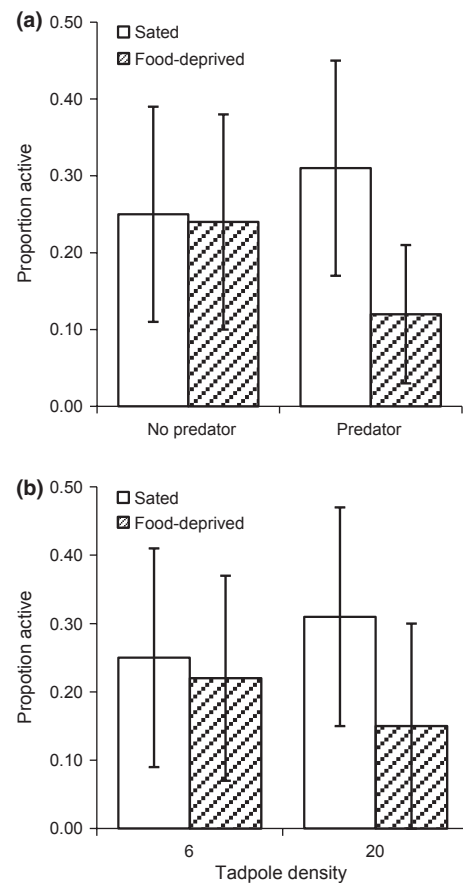
**Table 1:** Repeated measures ANOVAs on the proportion of tadpole active and using structural refuge. Predation risk was analysed as the repeated measure and only three-way interactions with  $p < 0.10$  are reported for brevity

Term	df	F-value	p-value
<b>Activity</b>			
Cover abundance (C)	1	3.49	0.07
Prey density (D)	1	0.15	0.70
Food treatment (F)	1	9.31	0.004
Predation risk (R)	1	0.06	0.81
C × D	1	0.87	0.36
C × F	1	1.96	0.17
D × F	1	5.39	0.024*
F × R	1	4.59	0.037*
D × F × R	1	3.54	0.07
Error	50		
<b>Refuge use</b>			
Cover abundance (C)	1	1.14	0.29
Prey density (D)	1	0.11	0.74
Food treatment (F)	1	0.12	0.73
Predation risk (R)	1	10.02	0.003*
C × D	1	1.45	0.23
C × F	1	1.00	0.32
D × F	1	3.40	0.07
F × R	1	<0.01	0.99
Error	50		

\*Significance at  $\alpha = 0.05$

and hungry tadpoles displayed opposite responses at the 20 tadpole density (Table 1). Sated tadpoles increased activity with density, while hungry tadpoles reduced their activity (Fig. 2b; all remaining interactions  $p > 0.07$ ). The proportion of tadpoles taking refuge increased  $\sim 10\%$  following exposure to predation risk (no predator =  $0.70 \pm 0.001$ , predator =  $0.80 \pm 0.002$ ; Table 1), but food, cover or density had significant main or interactive effects on tadpole refuge use (Table 1). Non-significant effects of cover and density  $\times$  cover interaction indicated that refuge was not saturated with prey and that cover should thus serve to dampen prey selection patterns. In sum, food deprivation resulted in activity levels below that of well-fed prey when exposed to predation risk, whereas prey responded to predator cues primarily through increased cover use.

Dragonfly larvae did not show notable locomotory response, suggesting that they largely employed a sit-and-wait hunting strategy and that movement within tanks occurred primarily from stalking prey before an ambush. Overall, the number of times larvae switched sides of the tank dropped slightly after the first hour and then slowly increased up to the fourth hour of observation (1st h:  $3.4 \pm 0.35$ , 2nd h:  $1.7 \pm 0.26$ , 3rd h:  $2.1 \pm 0.32$ , 4th h:  $3.0 \pm 0.41$ ;  $F_{3,102} = 21.30$ ,



**Fig. 2:**  $\bar{x} \pm SE$  proportion of sated (open bars) or hungry (hatched bars) tadpoles active (a) in the presence or absence of predation risk, and (b) at densities of six or 20 conspecifics.

$p < 0.001$ ). Dragonfly larva movement was not affected by prey density ( $F_{1,28} = 1.11$ ,  $p = 0.30$ ), cover ( $F_{1,28} = 0.02$ ,  $p = 0.88$ ) or their interaction ( $F_{1,28} = 0.28$ ,  $p = 0.60$ ). Moreover, the selection index was not correlated with total number of times a dragonfly larva switched sides (Pearson's  $r = -0.18$ ,  $p = 0.31$ ,  $n = 32$ ), suggesting that the extent of predator movement in the tanks did not influence prey selection patterns.

## Discussion

Our experiment tested specifically whether predation mortality risk induced by short-term food deprivation could be altered by variation in structural cover and prey density. The food treatment affected prey activity, although food deprivation did not elicit risk-prone behaviour as predicted and did not strongly alter mortality patterns caused by predation. Instead, prey consumption was elevated by prey density

**Table 2:** Single sample t-tests assessing non-random prey selection on sated vs. hungry prey. Selection index is >1 if predators select hungry tadpoles. Significance at  $\alpha = 0.05$

Treatment	$\bar{x}$ selection		n	t-value	p-value
	index	SE			
All	1.14	0.12	50	1.13	0.27
Low cover	1.11	0.18	27	0.59	0.56
High cover	1.17	0.17	23	1.05	0.30
Six tadpoles	1.05	0.18	24	0.28	0.78
20 tadpoles	1.22	0.16	26	1.33	0.20
Low cover – six tadpoles	0.94	0.23	13	-0.25	0.81
Low cover – 20 tadpoles	1.26	0.27	14	0.95	0.36
High cover – six tadpoles	1.18	0.30	11	0.60	0.56
High cover – 20 tadpoles	1.17	0.17	12	1.01	0.34

and marginally depressed by addition of structure. Food manipulations did, however, cause important behavioural changes among treatments. We observed prey selection patterns that qualitatively followed our predictions: (1) Increased mortality among risk-prone prey at higher prey density (prediction a); and (2) dampening of mortality among risk-prone individuals when exposed to unsaturated structural cover (prediction c; Table 2). Disentangling such complex and interactive effects in ecology has proved challenging for empiricists; however, clarifying the relative importance of factors which affect prey survival is important for providing a thorough understanding of predation risk and prey selection patterns in complex environments. To our knowledge, ours is the first experiment of this type.

A key distinction from previous experimental work (e.g. Horat & Semlitsch 1994; Anholt & Werner 1995, 1998) is that each predator was exposed to food deprived and sated prey simultaneously, implying that our tests were perhaps better designed to detect differences in predation risk specifically associated with selective predation. Our results also deviate from previous work, because we did not observe a strong increase in mortality risk from food deprivation. Although duration of the lethal predation experiment was relatively short (i.e. 4 h), predators still consumed 20–36% of prey in tanks, which should be sufficient to detect strong differential predation were such a phenomenon present. Strong selective predation of hungry prey was not generally observed in our experiment, although predation on hungry prey tended to be stronger when refuge was low or density was high. Thus, the results suggest that an experimental design involving concurrent availability of hungry and healthy prey tends to dampen predation on hungry prey, although pre-

dition risk for hungry prey may increase with prey density or reduced abundance of hiding cover.

Hungry prey did not exhibit compensatory foraging that increased their mortality risk (see also Bridges 2002). Although bullfrog tadpoles generally exhibit a weak response to variation in food abundance (Anholt et al. 2000), our protocol involving food deprivation for 24 h was sufficient to elicit detectable behavioural responses that influenced predation risk (see also Horat & Semlitsch 1994; Fraker 2008). Indeed, the variation in prey activity observed here was related to predation risk via the food  $\times$  predator interaction, contrasting with Horat & Semlitsch (1994) who found no such interaction. Thus, we infer that our experimental treatment had non-trivial effects on behavioural trade-offs of tadpoles. Sated prey in our study behaved similarly to the 'starved' prey in Anholt et al. (2000) who attributed activity reductions in undernourished bullfrog tadpoles to the high energetic cost of actively obtaining food. Well-fed prey that can afford the initial increase in risk of energetic disparity is expected to engage in greater sampling of novel forage sites compared to prey with low energetic reserves (Dall & Johnstone 2002). Reduced activity in hungry prey exposed to predators is consistent with theory that behaviour mediating predation risk in hungry, sick or weak prey will be favoured by natural selection when vulnerability to predation is related to prey health status (e.g. Martín et al. 2006). It follows that strong preferential selection of hungry prey over better-fed prey may not be generally observed because of poorly understood mechanisms through which undernourished prey cope with predation risk.

Because hungry prey were the least active in response to perceived predation risk and high prey density (Fig. 2) but still suffered qualitatively the greatest mortality from predators (Table 2), it seems unlikely that prey activity was the primary driver of food treatment-related predation in our study. Mechanistic explanations for patterns of prey selection include both optimal foraging (i.e. non-random pursuit of prey; Krause & Godin 1996) and increased capture success (i.e. non-random prey capture; Atwood et al. 2007). When the strike success of a predator is high, small variation in prey escape ability may not translate to corresponding changes in prey mortality; however, as strike success declines evasive prey increasingly survive better. In a similar system, we have shown that predator strike success is greatest at low prey density and declines as density increases (Hossie & Murray 2010). The

observed increase in mortality of hungry prey as density increased likely represents increasingly important differences in evading capture between the food treatments as predator strike success declines (see also Altwegg 2003). Yet, we acknowledge that the lack of strong prey selection overall may also relate to moderate differences in evasiveness elicited by short-term food manipulation.

The response of tadpoles to predation risk was primarily restricted to increased refuge use (see also Pearl et al. 2003). Sated and hungry prey lacked a strong differential activity response to predation risk, which is contrary to previous research (e.g. Anholt et al. 2000; Peacor & Werner 2000; Smith et al. 2008) and suggests that activity changes may have been facultative under our experimental regime. We found that sated prey increased activity moderately in response to predation risk, which is consistent with Richardson (2001) and may indicate increased effort in search of refuge (e.g. Sih & Kats 1991; Lima 1998). Alternatively, such a behavioural response may conform to spatial avoidance of predator cues (e.g. Relyea & Werner 1999; Relyea 2001). In nature, leaving an area of perceived risk would reduce the risk of depredation (Helfman 1986; Langerhans 2007); however, confined experimental arenas could have rendered such a response ineffective. If this did explain the observed marginal effects, it would imply that spatial avoidance of predators can act as a primary driver of differential predation among well-fed and hungry prey. Regardless, the spatial aspect of predation risk and prey selection is an exciting dimension for future studies of predator-prey interactions in restricted environments.

## Conclusions

We conclude that the starvation-predation trade-off theory should be cast more broadly to account for the variety of hunger levels and possible responses to reduced food availability, across a variety of environmental conditions. Future efforts should investigate further the association between predation on hungry prey and the abundance of hiding cover, as well as explore more fully physiological and behavioural responses of prey across the full gradient of hunger levels. Doubtless, improved resolution in our understanding of prey responses to different levels of food shortage will facilitate the development of a more synthetic risk-sensitive foraging theory and provide valuable information on how trophic interactions structure complex ecological communities.

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