

# Hungry predators render predator-avoidance behavior in tadpoles ineffective

Res Altwegg

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Behavioral responses of prey to their predators can critically alter community dynamics. Whether or not a prey responds, clearly depends on the effectiveness of that response. The effectiveness on the other hand is predicted to depend on predator behavior. Actively searching predators can render the behavioral responses in their prey ineffective. Nevertheless, most studies investigating the optimal reaction of prey treated predators as immobile elements of the environment. I experimentally manipulated activity of poolfrog (*Rana lessonae*) tadpoles by keeping them at low and high food levels, and exposed them to three species of invertebrate predators (*Aeshma cyanea*, *Anax imperator*, and *Dytiscus marginalis*), whose activity also was manipulated through different food levels. Satiated, less active predators were more likely to kill hungry, more active tadpoles, but hungry predators killed hungry and satiated tadpoles about equally often. This result suggests that reducing their activity is a more effective strategy for tadpoles if the predators themselves are less active. On the other hand, against hungry, highly motivated predators, the behavioral avoidance strategies were essentially ineffective. Antipredator behavior is generally thought to stabilize the dynamics of predator–prey systems. The results presented here, however, suggest that the community dynamical consequences of antipredator behavior also critically depend on decisions made by predators.

R. Altwegg, *Inst. of Zoology, Univ. of Zürich, Winterthurerstr. 190, CH-8057 Zürich, Switzerland (altweggr@zool.unizh.ch)*. Present address: *Univ. of Victoria, Dept of Biology, Victoria, B.C., V8W 3N5, Canada (altwegg@uvic.ca)*.

Feeding is risky for most animals, because they have to move in order to find food, and in so doing increase their risk of encountering predators and/or being detected by them. Animals have less opportunity to scan their vicinity for predators when they are busy feeding, and often the most profitable areas for feeding are also the most dangerous ones because they attract predators. Therefore, most animals face a trade-off between growth and mortality (Lima and Dill 1990). If this trade-off is the dominant constraint affecting prey animals, they can adjust their behavior to optimize the conflicting tasks. Specifically, they can reduce their activity level in the presence of predators, which leads to lower encounter rates and decreases the likelihood of detection (Lima 1998). Most theory and empirical work on optimal behavior and growth strategies under predation risk have assumed that this is true (reviewed in

Lima and Dill 1990, Lima 1998).

This depiction may, however, be too simplistic, because there are features of the system that lower the degree of control by the prey individual. One example is variation in search behavior and feeding motivation of the predator. The role of variation in predator behavior for predator–prey interactions has received little empirical and theoretical attention so far (Lima 2002). According to a simple model the encounter rates  $Z$  of a prey individual with a predator is

$$Z = 2rN\sqrt{(v^2 + s^2)}$$

where  $r$  is the perceptual radius of the predator,  $N$  is predator density, and  $v$  and  $s$  are average foraging

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speeds of the predator and prey, respectively (Gerritsen and Strickler 1977, Werner and Anholt 1993). The model assumes that both are moving at characteristic speeds, and that the direction of predator movement is randomly and uniformly distributed with respect to prey movement direction. If prey are moving much faster than the predator, the equation simplifies to  $Z = 2rNs$ , and the encounter rate is directly proportional to prey speed. In this situation, which is typical for a sit-and-wait predator and moving prey, the prey individuals can lower their encounter risk by reducing their own velocity. On the other hand, if predator speed is high relative to prey speed, changes in prey speed have little effect on the encounter rate. This argument is valid for speed or general activity levels (Werner and Anholt 1993).

Besides simple encounter probabilities, other mechanisms are likely to change the qualitative nature of predator–prey interactions. A prey individual, trying to escape from a predator after detection, is more likely to succeed when the predator puts less effort into the attack. For example a satiated predator may be more attentive to its own predators when hunting than a hungry one. On the other hand, a prey individual has more difficulties finding a predator-free space if a hungry predator increases its hunting area. Any factor that affects a predator's feeding motivation may modify the effectiveness of prey defense behavior, and therefore feed back on the optimal defense strategies of prey.

Anuran larvae are an ideal system to test these ideas, because these animals adjust their activity when exposed to different levels of food and predation risk, and thus precisely balance their growth and mortality (Morin 1983, Lawler 1989, Skelly and Werner 1990, Azevedo-Ramos et al. 1992, Skelly 1992, 1994, Anholt and Werner 1995, 1998, Eklöv and Halvarsson 2000).

I experimentally tested the prediction that highly active predators impose a similar mortality risk to active and inactive prey, while inactive predators represent a higher threat for active prey individuals than for inactive ones. I manipulated activity of poolfrog (*Rana lessonae* Camerano) tadpoles by holding them at two different food levels, and then exposed both kinds of tadpoles to three species of predators whose activity was also manipulated by using hungry and satiated individuals.

## Methods

The *R. lessonae* tadpoles used in this experiment were obtained from seven pairs of adult frogs caught on 16 May 2000 in a bog pond near Hellberg, Switzerland. I added groups of 15 tadpoles to green 80 l plastic tubs, where they were raised outdoors under standard conditions until they had reached stages 31–36 (Gosner 1960), and 400–1000 mg body mass.

Predation trials were conducted between 22 and 30 June. Tadpoles used on a particular day of the experiment all came from the same family and had been raised in four adjacent tubs. I brought those individuals back to the laboratory, divided them into two groups, and held them in 20 × 30 cm plastic tubs filled with 3 l of aged tap water. For 24 h, I subjected them to either no food or a mixture of 1 g finely-ground rabbit chow and green algae collected from the outdoor tubs. The next day, the predation trials took place in white plastic tubs filled with 3 l of aged tap water. Every tub also received a cylindrical structure of mosquito mesh, which served as a perch for the predator, and 500 mg finely ground rabbit chow. The food quickly spread over the whole water volume and was intended to make the tadpoles move if they wanted to feed.

After having stained the hungry or the satiated tadpoles (alternating each day) for 45 min in a solution of neutral red (3 mg/l, SIGMA, N-7005), I added one hungry and one satiated tadpole of matching size to every tub, and let them acclimatize for 30 min. I recorded activity of both tadpoles by taking ten scan samples, at the rate of one sample per minute, both before and 30 min after adding the predator. Activity was defined as the proportion of time in which I observed any kind of movement. To every tub I added one individual of either larval *Anax imperator* dragonfly (last two instars), *Aeshna cyanea* dragonfly (final instar), or third (final) instar *Dytiscus marginalis* beetle, which I obtained from natural ponds near Zürich. Each predator species was presented in two hunger levels. The individuals for the 'satiated predator' treatments were fed one large (ca 800 mg) tadpole 1–2 h before the onset of the experiment, while the other ones had not fed for at least 48 h. Within the first 10 min after adding the predators, I recorded their activity by taking ten scan samples. I only calculated activity for individuals having five or more scan samples (i.e. I omitted individuals that ate a tadpole before five scan samples had been acquired). Every 15–30 min, I slowly approached the tubs to see whether one of the tadpoles had been killed, in which case the trial was terminated and the identity of the survivor recorded. If both tadpoles were still alive after 4 h, I also terminated the trial. All surviving animals were returned to their pond of origin after the experiment was over.

I conducted three replicates of all six treatment combinations (3 predators × 2 hunger levels) every day for eight days. On two occasions I replaced the two *Dytiscus* treatments by an additional replicate of *Anax* or *Aeshna*, because none of the former were available. Table 1 summarizes the sample sizes and outcomes per treatment. Some predators were in short supply and had to be used more than once, but they always underwent the feeding preparation described above. In total, I used 54 *Aeshna*, 29 *Anax*, and 8 *Dytiscus* individuals.

Table 1. Summary of the replications per treatment. Table entries are the number of replicates with the particular outcome.

Predator	Hunger level	Tadpole killed			
		Hungry	Satiated	None	Total
<i>Aeshna cyanea</i>	Hungry	15	12	0	27
	Satiated	9	1	17	27
<i>Anax imperator</i>	Hungry	12	12	3	27
	Satiated	16	4	7	27
<i>Dytiscus marginalis</i>	Hungry	9	7	2	18
	Satiated	9	3	6	18

### Statistical analyses

I performed the analysis in two steps. First, I examined the effect of experimental factors and individual characteristics on the mortality risk of an individual tadpole. Second, I asked whether the experimental factors successfully predicted which of the two tadpoles within one tub was killed. The first analysis yielded survivorship curves for the individuals subjected to the different treatments, but ignored possible dependencies of the fates of the two tadpoles within one tub. The second analysis accounted for this possibility, but ignored the time elapsed until a trial was ended, and excluded trials where no tadpole was killed.

I used Cox proportional hazard regression models (Cox 1972) to analyze the effects of tadpole hunger level, predator species and hunger level, tadpole color marking, and tadpole weight on the risk of mortality. The analysis was run in procedure PHREG in SAS (Allison 1995, SAS Institute Inc. 1996), and included both complete observations and right-censored data. A tadpole that was killed during the trial represented a complete observation, whereas a surviving tadpole yielded a right-censored observation. The latter contributed information to all earlier estimates, because I know that it survived at least until the end of the trial. Tied mortality events were resolved using the 'exact' method, which explores all possible orderings under the assumption that ties result from imprecise measurement (Allison 1995).

I used a logistic regression analysis, run in procedure GENMOD in SAS (SAS Institute Inc. 1996), to assess the effect of predator species and predator hunger level on the outcome of the trial. The two possible outcomes (death of the hungry or the satiated tadpole) can be viewed as a choice made by the predator.

## Results

### Effect of starvation on predator and prey activity

The three predator species strongly differed in their general activity, as well as in their reaction to starvation (Fig. 1, predator main effect:  $F_{2,87} = 13.5$ ,  $P < 0.001$ ; hunger level main effect:  $F_{1,87} = 6.7$ ,  $P = 0.012$ ; interac-

tion:  $F_{2,87} = 9.8$ ,  $P < 0.001$ ). *Aeshna* and *Anax* both were more active when hungry than when satiated, but *Anax* was generally less active than *Aeshna*. *Dytiscus* was the most active predator, and its activity was unaffected by the hunger level.

In the absence of predators, hungry tadpoles were not more active than satiated ones (Fig. 2, mean difference within trial  $-0.8\%$ ,  $se = 2.0$ ,  $n = 144$ ,  $P = 0.7$ ). Thirty minutes after the predator had been added to the

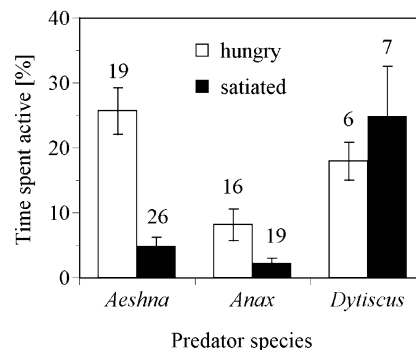


Fig. 1. Activity of hungry and satiated predator individuals. Error bars are standard errors. The numbers show sample sizes. Note that sample sizes differ from the number of replicates given in Table 1 because this figure pools repeated measurements of the same predator individual for each state.

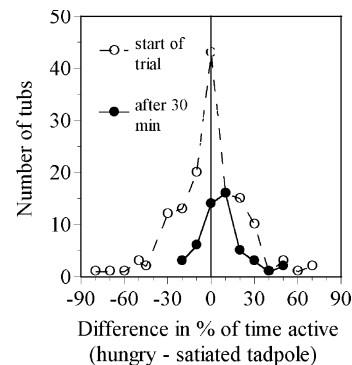


Fig. 2. Frequency distribution of the difference in activity between the hungry and the satiated tadpoles within each tub. Open symbols show estimates before the predator was added to the tub, filled symbols show estimates 30 min after predator addition.

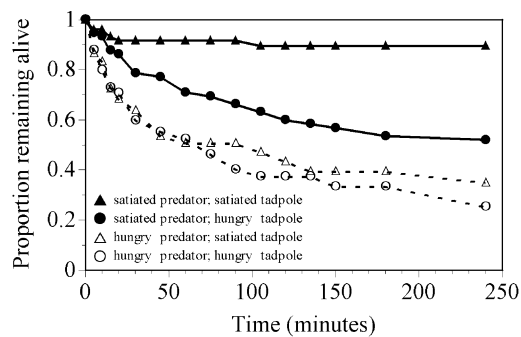


Fig. 3. Survivorship curves for hungry and satiated *Rana lessonae* tadpoles when exposed to hungry and satiated predators. Solid lines correspond to treatments with satiated predators, whereas broken lines correspond to treatments with hungry predators.

tub, the hungry tadpoles were more active than the satiated ones in the trials that were still running (mean difference within trial 7.5%,  $se = 2.2$ ,  $n = 50$ ,  $P = 0.002$ ). This figure probably underestimated the true difference because the predators had already made their kill before I collected behavioral observations in tubs with the most active tadpoles. Tadpole activity was not significantly affected by predator species ( $F_{2,44} = 2.5$ ,  $P = 0.1$ ) or predator hunger level ( $F_{1,44} = 0.7$ ,  $P = 0.4$ ).

### Tadpole mortality risk

There was a strong interaction of the effects of predator and prey hunger level on prey survivorship: hungry tadpoles had a higher risk of being killed than satiated ones when exposed to a satiated predator, while the risk was similar for both hungry and satiated tadpoles when the predator was hungry (Fig. 3, Table 2). Apparently, tadpole anti-predator behavior was less effective when the predators made a greater hunting effort. Overall, hungry predators imposed a markedly higher risk on both kinds of tadpoles than satiated predators. Larger tadpoles experienced a lower risk, but tadpole mortality did not differ significantly between the predator species, and the color marking treatment with 'neutral red' had no measurable effect on mortality (Table 2).

Table 2. Cox Proportional Hazards model testing for effects of experimental treatments on mortality risk in *Rana lessonae* tadpoles exposed to predators *Anax imperator*, *Aeshna cyanea* and *Dytiscus marginalis*.

Variable	d.f.	Wald $\chi^2$	<i>P</i>	Hazard ratio*
Tadpole hunger level (T)	1	13.56	0.0002	4.657
Predator hunger level (P)	1	25.35	0.0001	8.412
P × T	1	9.02	0.0027	0.232
Predator species	2	1.40	0.5000	
Tadpole weight	1	6.27	0.0123	0.999
Neutral red	1	1.94	0.1639	0.759

The overall model was significant (likelihood ratio  $\chi^2_7 = 56.75$ ,  $P < 0.0001$ ).

\* The Hazard ratio estimates the magnitude of the effect. Hungry tadpoles, for example, were 4.657 times more likely to be killed than satiated ones.

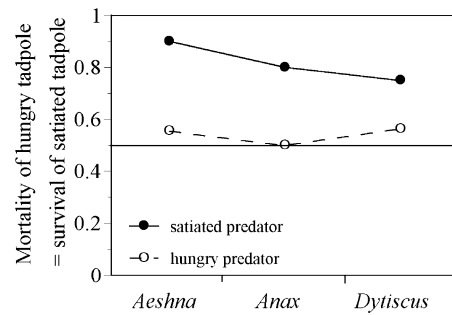


Fig. 4. Relative mortality of the two tadpoles within one tub when exposed to satiated or hungry predators of three different species. The line at 0.5 marks equal survival of both tadpoles.

The logistic regression analysis confirmed the results of the Cox proportional hazards regression: satiated predators killed mostly hungry tadpoles, while hungry predators killed both about equally often (Fig. 4,  $\chi^2_1 = 8.82$ ,  $P = 0.003$ ). There was no significant effect of the predator species on the outcome of the experiment ( $\chi^2_2 = 1.16$ ,  $P = 0.56$ ), and the predator hunger treatment had similar effects on prey selection in all predator species ( $\chi^2_1 = 0.73$ ,  $P = 0.70$ ). A linear contrast, ranking the predators according to their average activity, showed that predator activity was not significantly negatively related to hungry tadpole mortality ( $\chi^2_1 = 1.37$ ,  $P = 0.24$ ).

### Discussion

The main contribution of this study was to manipulate activity of prey and predators independently, and to examine interactions that would have been concealed if predator behavior was assumed constant. The experiment showed that mortality risk of tadpoles was affected by their own state, and also by characteristics of the predators. Satiated predators killed hungry, more active prey individuals more often than the less active satiated prey individuals. Hungry predators on the other hand inflicted the same mortality on both kinds of prey. Essentially, hungry predators rendered behavioral reactions of their prey ineffective.

This pattern could arise from a simple mechanism, where encounter probabilities between prey and predator individuals determine prey mortality. In this case, prey mortality should depend mainly on prey activity when predators are relatively immobile, whereas it should be largely independent of prey activity when the predators are highly mobile (Gerritsen and Strickler 1977, Werner and Anholt 1993). The results of my experiment support this prediction under the assumption that satiated predators feed less actively.

Within predator species, the results were consistent with the prediction of the activity based model for *Aeshna* and *Anax*, but not for *Dytiscus*. The starvation treatment increased activity in the two odonates, and caused a shift from selectively killing the more active prey to randomly killing one of the two prey individuals. These results are consistent with an earlier study showing that lizard species with a sit-and-wait hunting tactic had higher proportions of active prey species in their diet than widely foraging species, which also ate inactive prey (Huey and Pianka 1981). In my study, *Dytiscus* inflicted the same pattern of mortality on the prey as the other two predator species, even though its activity did not change significantly with the starvation treatment. Overall, the less active predator species/treatment combinations did not significantly prefer the more active one of the two tadpoles, as predicted by the encounter probabilities and under the assumption of equal encounter radii between predator species.

Taken together, these results suggest that predator activity is important for the efficiency of prey defensive behavior, but it cannot alone explain all variation in prey vulnerability. One possible reason is that the relationship between activity and encounter rate varies with the specific predator-prey system. The three predator species, although similar in size, have different hunting strategies. While the dragonfly larvae are visually hunting predators (Folsom and Collins 1984), *Dytiscus* larvae mostly rely on mechanical and chemical cues (Formanowicz 1987). As a consequence, the predator species probably differ in their encounter radius in a way that is unrelated, or only weakly related, to activity.

In contrast to other studies, which have interpreted decreased prey activity in the presence of predators as an adaptive response to enhanced predation risk (Skelly 1994, Van Buskirk and McCollum 2000), my results illustrate that such an activity response is not universally adaptive: when the predators themselves are very active, prey cannot influence the risk by adjusting their own activity. In this case, the optimal strategy for the prey may be to increase their activity in order to maximize growth and to metamorphose as fast as possible. These results imply that any adjustment of the activity level can be the optimal reaction to the presence of predators, depending on how a change in activity affects mortality and growth.

Amphibian larvae, as well as other species, have evolved different responses to different predators (Peckarsky 1996, Van Buskirk 2001). In my experiment, however, the effectiveness of the defense behavior differed more between hungry and satiated predators of the same species than between predator species. It seems unlikely that tadpoles could obtain information on the hunting motivation of the predators in their neighborhood, and therefore an adjusted response is unlikely, even though it would be adaptive.

Hungry predators rendered the behavioral defense reaction of tadpoles virtually ineffective in my experiment. However, the experiment did not account for two features that may reduce the hunting success of both hungry and satiated predators; habitat complexity and induced morphological defenses employed by the prey (McCollum and Van Buskirk 1996). It is difficult to tell whether these features would make the effectiveness of prey defense less dependent on predator strategies under more natural situations. Differential effectiveness of other types of defense, like hiding and morphology, under the threat of predation by hungry or satiated predators has to my knowledge not been investigated so far.

Antipredator behavior in prey individuals tends to stabilize predator-prey dynamics (Fryxell and Lundberg 1997, Ives and Dobson 1987, Brown et al. 1999). In specialized predator-prey systems, where the predator does not switch prey, behavioral reactions of the prey may be less important than suggested by theory. As prey become rare in relation to the predator population size, predators will be hungry more often, make a bigger effort, and so render prey defense less effective. This could feed back on the optimal response of the prey, which should not continue to invest in costly predator avoidance behavior. When modeling the co-evolution between predators and prey, Abrams (1990) concluded that improvements in the predator capture ability often select for a decrease in anti-predator abilities in the prey. If the efficiency of predators increases with decreasing prey population size, the dynamics of the system would be destabilized (Abrams 2000). In the real world, many additional factors, such as the availability of alternative prey and presence of predators on higher trophic levels, affect predator hunting motivation and thus the efficiency of antipredator behavior in the prey. The role of behavior in the dynamics of natural systems is therefore probably variable and dependent on the particular situation.

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