

A test of the risk allocation hypothesis: tadpole responses to temporal change in predation risk

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The risk allocation hypothesis predicts that temporal variation in predation risk can influence how animals allocate feeding behavior among situations that differ in danger. We tested the risk allocation model with tadpoles of the frog *Rana lessonae*, which satisfy the main assumptions of this model because they must feed to reach metamorphosis within a single season, their behavioral defense against predators is costly, and they can respond to changes in risk integrated over time. Our experiment switched tadpoles between artificial ponds with different numbers of caged dragonfly larvae and held them at high and low risk for different portions of their lives. Tadpoles responded strongly to predators, but they did not obey the risk allocation hypothesis: as the high-risk environment became more dangerous, there was no tendency for tadpoles to allocate more feeding to the low-risk environment, and as tadpoles spent more time at risk, they did not increase feeding in both environments. Our results suggest that the model might be more applicable when the time spent under high predation risk is large relative to the time required to collect resources. *Key words*: *Aeshna*, Anura, behavior, predation risk, *Rana lessonae*, tadpoles. [*Behav Ecol* 13: 526–530 (2002)]

Lima and Bednekoff (1999) recently introduced an intuitively appealing refinement to foraging theory. Most models of foraging under predation risk assume that animals are exposed to constant levels of danger or that variation in danger is a feature of the background environment (Clark and Levy, 1988; McNamara and Houston, 1994; Werner and Anholt, 1993). But animals foraging under temporal variation in risk face a problem in allocating costly antipredator behavior across situations of different risk. Lima and Bednekoff examined this problem and arrived at two key predictions. First, if an animal experiences two environments having high and low levels of risk, it will allocate increasing amounts of antipredator behavior to the high-risk environment as the danger in that environment increases relative to that in the low-risk situation (Figure 1A). Intuitively, if one environment is much more dangerous than the other, the animal will choose to collect most of its food requirements during its time in the less dangerous environment. The second prediction is that as the environment with higher danger is encountered more frequently, an animal will exhibit less antipredator behavior in both environments, but especially when in the situation with lower risk (Figure 1B). In other words, if high-risk situations predominate, an animal must take risks to gather enough food to survive, but it will allocate as much risk taking as possible to the less dangerous environment. Thus, the pattern of variation dramatically alters the response to predators. Here we describe an empirical test of this hypothesis.

Early foraging models examined how animals should behave to optimize some measure of resource consumption, without regard to their exposure to predators (Stephens and Krebs, 1986). The inclusion of predation risk within foraging theory has been an improvement, in spite of the more complex theoretical approach that it requires, because it more

accurately predicts the behavior of animals within natural settings. Behavioral responses to predation risk are diverse and ubiquitous in foraging animals, and these often entail a change in foraging rate (Kats and Dill, 1998; Lima, 1998). Lima and Bednekoff's study prompts us to ask whether temporal variation in danger is also a necessary ingredient of foraging models.

We studied the impact of temporal variation in predation risk on tadpoles foraging in ponds that contain chemical cues signaling whether predators are present. Amphibian larvae have had ample opportunity to evolve adaptive responses to temporal variation in predation risk because they encounter changes in predator density over short and long time scales within natural ponds (Van Buskirk, 2002). Further, tadpoles are particularly well suited for testing the risk allocation hypothesis because they often fulfill the conditions under which risk allocation is most likely to operate (Lima and Bednekoff, 1999). For example, the model assumes that an animal must meet its energetic requirements within a fixed time period. Many pond-breeding tadpoles satisfy this assumption because they must attain a minimum size for metamorphosis within the limited time available before their larval habitat degenerates (Wilbur, 1980). The model assumes further that an animal may defend itself against predation but that successful defense can be achieved only at the cost of reduced energy intake. The hiding behavior and reduced feeding activity exhibited by many tadpoles when exposed to predators fulfills this assumption because it protects tadpoles from predation (Skelly, 1994) and yet carries a cost of reduced rates of growth and development (Van Buskirk, 2000, 2002). Finally, the model assumes that an animal can assess current predation risk and remember changes in risk for a meaningful period of time. Tadpoles also meet this assumption: they use chemical cues as a sensitive gauge of short-term changes in predation risk (Stauffer and Semlitsch, 1993), and they behave as if they can "remember" a previously experienced predation environment for several days (Semlitsch and Reyer, 1992; Van Buskirk, 2002). In these respects, then, anuran larvae offer an appropriate system for testing the risk allocation hypothesis.

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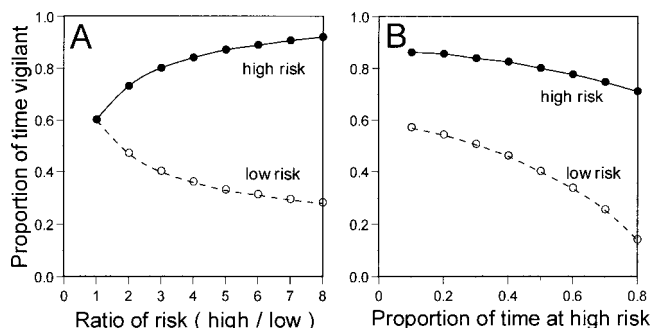


Figure 1 Predicted responses (Lima and Bednekoff, 1999) of an animal exposed to two kinds of environments (high and low risk of predation) under (A) different ratios of risk between environments and (B) different frequencies of the two environments. Filled circles represent the animal's antipredator behavior when in the more risky environment; open circles show antipredator behavior in the less risky environment. Panel A illustrates that as the more risky environment increases in danger, the animal should exhibit increased antipredator behavior when at higher risk and decreased antipredator behavior at lower risk. The proportion of time at high risk in A is 0.5. Panel B shows that as the animal finds itself within the higher risk environment more frequently, it should decrease investment in antipredator behavior in both environments, but especially in the low-risk situation.

METHODS

The two main predictions of the risk allocation hypothesis (Figure 1) can be tested by experimentally manipulating two features of the predation environment perceived by an animal: the relative predation risks experienced within two or more environments, and the amount of time spent in the more risky environment. We tested the two predictions by manipulating both features simultaneously in an experiment with tadpoles of the pool frog, *Rana lessonae*.

Experimental design and implementation

The experiment was conducted in plastic tubs holding 80 l of water (0.27 m²) placed outdoors in a field on the campus of the University of Zürich. The large size of these tubs and their exposure to prevailing outdoor conditions provided a favorable environment for tadpoles, which seemed to grow and behave normally in the experiment. We added 2 g rabbit food to each tub on the first day of the experiment; thereafter, the tadpoles consumed this food and the algae growing naturally on the walls of the tubs. To facilitate behavioral observations, we left tubs free of litter or structures under which tadpoles might take refuge. The conditions in our experimental tubs did not simulate those prevailing in natural ponds, but this does not compromise a test of Lima and Bednekoff's hypothesis. Risk allocation behavior emerges as the solution of an optimality model and therefore presumably is maintained by optimizing selection under conditions specified by the model. As long as these conditions and assumptions are satisfied by our experimental system, as we assert that they are, then tadpoles should obey the model if it incorporates all biologically important processes.

The experiment had the five treatments depicted in Figure 2, plus a control treatment not shown in the figure. For five treatments, tadpoles were captured and transferred between tubs every day, so that they were exposed over time to two distinct environments with potentially different predation risks. We manipulated the perceived danger by confining different numbers of predatory dragonfly larvae (*Aeshna cyanea*)

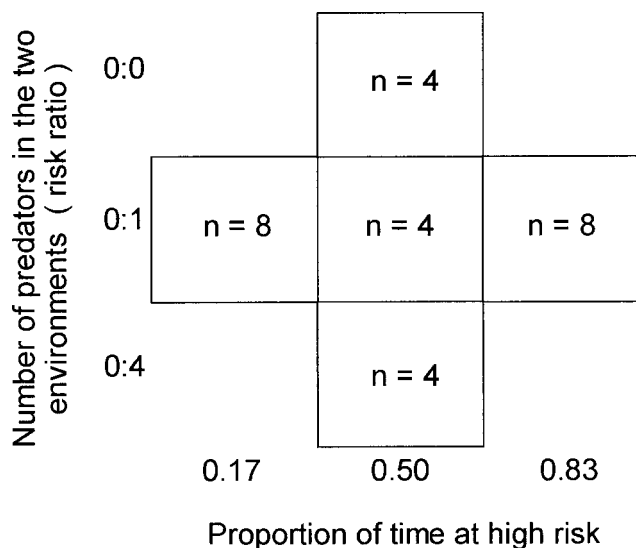


Figure 2 Experimental design used to test the two predictions of the risk allocation hypothesis depicted in Figure 1. All tadpoles except for those in a control treatment (not shown) were transferred between two environments (experimental tubs) at regular intervals. The three levels of risk ratio corresponded to different numbers of caged *Aeshna* within the two tubs. Three levels of time at high risk determined the proportion of each 48-h period spent in the tub with higher risk. The number of replicates is listed within each cell. All treatments were conducted within eight tubs, but for three treatments the independent experimental units were pairs of tubs, resulting in four replicates.

within four cages floating in every tub. Cages were constructed of a 10-cm length of plastic tube (11 cm diam, covered at the ends with fiberglass window screen), and depending on the treatment they were either left empty or they contained a single *Aeshna*. We fed each dragonfly 300 mg *R. lessonae* tadpoles on every third day, to ensure that chemical signals of predation were present in the pools.

Three treatments included different ratios of risk between the high- and low-risk situations (vertical column in Figure 2). In the first treatment, tadpoles were transferred regularly between two tubs that had no dragonflies. This represents the case in which the risk in the two environments is identical. In the second and third treatments, tadpoles spent half the time in tubs that had no predators and half the time in tubs that had either one or four caged *Aeshna* larvae. These treatments represented increasing ratios of risk between the high- and low-risk situations. In all three cases, tadpoles were switched between tubs every 24 h, at 1100 h each day, so they spent 50% of the time in each environment over every 48-h period.

These treatments allowed us to test the prediction shown in Figure 1A. The risk allocation hypothesis will be supported if tadpoles respond to increasing ratio of risk by becoming increasingly inactive when at high risk and increasingly active at low risk. An underlying premise of our design is that a tub with no predators was not perceived by tadpoles as a completely danger-free situation. Although we cannot gauge the risk assigned by tadpoles to a tub having no dragonflies, we do know that a tub with four *Aeshna* is perceived as riskier than a tub with one *Aeshna*, which in turn is more dangerous than a zero-predator tub. A separate experiment confirmed that *R. lessonae* tadpoles respond with increasing strength along a gradient in risk from tubs with 0–4 caged *Aeshna* (Van Buskirk and Arioli, 2002).

Three treatments manipulated the proportion of time spent

in situations with high and low risk (horizontal row in Figure 2). In the first treatment, tadpoles spent 4 h out of every 24-h period in a tub with one caged *Aeshna* and spent the other 20 h in a tub with no predators. In the second treatment, tadpoles spent 24 h in the *Aeshna* tub and 24 h in the predator-free tub. (The data from this same treatment were also used to assess tadpole responses to changes in the ratio of risk, as explained above.) In the third treatment, tadpoles were exposed to one *Aeshna* for 20 h before being transferred to a predator-free tub for the remaining 4 h. Thus, the proportions of time spent at higher risk, over every 48-h period, were 0.17, 0.5, and 0.83 in the three treatments. All tadpoles were captured twice per day: in the 0.17 and 0.83 treatments they were switched between caged *Aeshna* and predator-free tubs; in the 0.5 treatment they were switched between tubs at 1100 h, but 4 h later they were simply recaptured and returned immediately to the same tub.

These three treatments allowed us to test the prediction shown in Figure 1B. Support for the risk allocation hypothesis will be obtained if, within both the caged *Aeshna* tubs and the predator-free tubs, activity increases with increasing time spent at high risk, and the increase should be more obvious in tadpoles within the low-risk environment.

In a sixth "control" treatment, there were no predators and the tadpoles were never captured or transferred between tubs. Comparison between the control and the treatment with a risk ratio of 0:0 estimates the behavioral consequences of transferring tadpoles.

The experiment began on 26 May 2000, when we added to every tub 10 tadpoles (37/m²), drawn equally from two clutches produced from crosses between adult frogs collected at a pond that naturally contains *Aeshna*, 22 km SE of Zürich. When we started the experiment, the tadpoles were 6 days old (stage 25; Gosner, 1960) with an average weight of 21 mg (SE = 2.8). We replaced dead tadpoles in a number of tubs on two occasions early in the experiment, after 4 and 6 days. The behavioral observations began on 13 June, after tadpoles had been exposed to the predation treatments for 18 days. By the end of the experiment, the tadpoles averaged 500 mg and were at about Gosner stage 34.

The numbers of predators and tadpoles used in the experiment were realistic in comparison with natural densities observed in a sample of 40 ponds near Zürich between 1997 and 2000 (Van Buskirk, unpublished data). The experimental treatment with four caged predators was similar to the ponds with highest aeshnid densities in nature (14/m²), while the one-predator treatment had a lower *Aeshna* density than 21% of the ponds. Fourteen percent of all ponds supported higher densities of *R. lessonae* tadpoles than we used in the experiment, 61% of ponds had lower densities of tadpoles, and 25% contained no *R. lessonae*. The pond sampling data also illustrate that large temporal changes in predator density, occurring over a period of weeks, are very common in natural ponds (Van Buskirk, 2002). Sudden changes in predator composition, such as we imposed here, probably occur only when tadpoles move through different microhabitats within ponds.

Behavioral observations

Activity data were collected on 13–14 June and 16–17 June. Over these 4 days we made 18 observations of every group of tadpoles in both high- and low-risk tubs. The control tadpoles were never transferred between tubs and therefore were observed 36 times within the same tubs. Observations were spaced at least 10 min apart and consisted of a count of the number of tadpoles active (swimming or feeding) and resting inactively. We began collecting data at least 90 min after tadpoles were transferred into a new tub, and for each group of

tadpoles we averaged the observations within each of the two tubs separately to obtain measures of behavior in the high- and low-risk environments.

We interpret the proportion of tadpoles that are inactive as a measure of cautiousness, corresponding to vigilance in Lima and Bednekoff's (1999) formulation (see Figure 1). This interpretation is justified by two features of the tadpole activity response. First, reduced activity protects tadpoles from dragonfly predation (Skelly, 1994) in the same way that vigilance acts to decrease vulnerability in the Lima and Bednekoff model. Second, tadpoles often suffer a growth cost of their response to predators (Van Buskirk, 2000), just as vigilance is assumed by Lima and Bednekoff to carry the cost of reduced food consumption. Our analysis therefore asked whether tadpole inactivity responded to the experimental treatments in the manner predicted in Figure 1.

Analyses

The treatments were replicated eight times, but our transferring procedure destroyed independence between some experimental units. For the three treatments used to test the response to increasing risk ratio, the eight separate groups of tadpoles were arranged into four pairs that were switched back and forth between matched pairs of tubs, one of which contained no predator and the other of which had a caged *Aeshna*. The independent experimental units for this comparison were the pairs of tubs, so we began by calculating the mean response for each paired group of tadpoles. The tadpoles used to assess the impact of increasing proportion of time at high risk were also switched between matched pairs of tubs, but here we did not combine results from the two sets of non-independent tadpoles because they belonged to different treatments. We therefore performed analyses and prepared figures as if the eight replicates were independent for these two treatments, which increased the apparent power of the experiment. The extent to which our data fit the pattern depicted in Figure 1B does not depend on the replication of these two treatments, so we suspect that this was not a cause for concern. The eight replicates of the control treatment were completely independent, as were the four replicates of the manipulation of risk ratio.

In the absence of information about all its parameters, the risk allocation hypothesis cannot make quantitative predictions. We therefore assessed the degree of support offered by the data for statistical outcomes predicted by the model, rather than testing for significant departure from specific null hypotheses. For example, when the ratio of risk between high- and low-risk situations is manipulated, we expect to observe a main effect of predation risk and a predation-by-risk ratio interaction (Figure 1A). When the proportion of time at risk is manipulated, the risk allocation hypothesis predicts effects of both predation risk and time at risk, as well as an interaction between the two (Figure 1B). We used model selection techniques to ask how much support these predicted outcomes obtain from the data, relative to alternative outcomes in which other combinations of the manipulated factors are important. Our approach used a small-sample version of Akaike's Information Criterion (AICc) to identify the statistical model that best represents the data using the fewest parameters (lowest AICc value). We evaluated the overall weight of evidence favoring each model according to its Akaike weight. Burnham and Anderson (1998) provide a complete description of model selection methods.

RESULTS

When faced with increasing ratios of danger between high- and low-risk situations, *R. lessonae* tadpoles spent more time

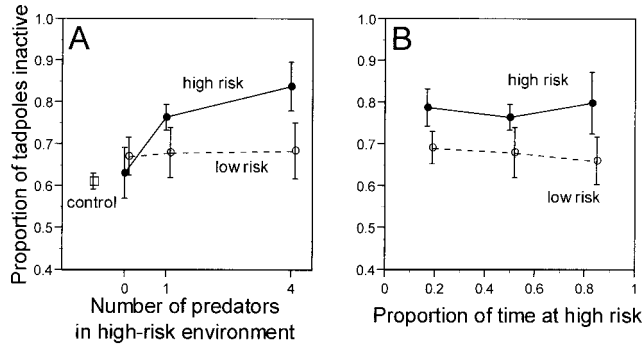


Figure 3 Proportion of *Rana lessonae* tadpoles that were inactive within environments having high or low risk, under (A) different levels of risk ratio between the two environments and (B) different frequencies of the more dangerous environment. Filled circles represent tadpole behavior while in the situation with higher risk; open circles show behavior for the same tadpoles when in the lower risk environment (means ± 1 SE). Results for the handling control, shown at the left side of panel A, suggest that repeatedly catching the tadpoles had little effect on their behavior.

inactive in the high-risk environment (Figure 3A). There was good support for the statistical model predicted by the risk allocation hypothesis, containing the predator effect and its interaction with risk ratio (Table 1), but the observed pattern clearly conflicted with the predicted outcome because tadpoles did not show the expected increase in activity within the low-risk environment (Figure 3A).

We observed no change in cautious behavior as the proportion of time spent in the high-risk environment increased (Figure 3B). Here there was little support for the outcome predicted by the risk allocation hypothesis, and most support went instead to the two models that did not include an effect of the proportion of time at risk (Table 1).

Across the entire experiment, tadpoles responded appropriately to the presence of predators (21% decline in activity in tubs with at least one predator; contrast between predator presence and absence: $F_{1,22} = 41.6, p < .001$). However, the patterns of response to change in risk ratio and proportion

of time at risk did not agree with those predicted by the risk allocation hypothesis (Figure 1).

Behavior in the control treatment was not very different from that in the treatment involving daily transfers between predator-free tubs (contrast between the two treatments: $F_{1,10} = 3.29, p = .10$; Figure 3A). This suggests that repeatedly capturing the tadpoles increased their time spent inactive by only a small amount.

Tadpole growth during the experiment declined with increasing predation risk, although the effect was significant only for the proportion of time spent at risk (effect of time at risk: $F_{1,26} = 5.48, p = .027$; effect of risk ratio: $F_{1,18} = 2.64, p = .12$). Final mass was 568 ± 32 mg (mean \pm SE) in the control treatment, where tadpoles were never exposed to predators, and declined to 434 ± 43 mg in the treatment with the highest proportion of time at risk and 438 ± 62 mg in the treatment with four *Aeshna* in the high-risk environment. These results, in combination with the behavioral data in Figure 3, suggest that inactivity was associated with a cost of reduced growth rate, as assumed by the risk allocation hypothesis.

DISCUSSION

Our findings do not support the predation risk allocation hypothesis (compare Figure 3 with Figure 1). *R. lessonae* responded to predators, as expected, but the pattern of temporal variation in risk had no influence on antipredator behavior. Disagreements such as this between predictions of theory and results of experiments may originate from three general causes: the biological system may not fulfill assumptions underlying the theory, the experiment may not include appropriate conditions or treatments, or the theory may not incorporate processes that have biological importance. We believe that the tadpole system and our experimental design were appropriate for testing Lima and Bednekoff's (1999) model and therefore suggest that the hypothesis can be rejected for this particular situation. Of course, no model can be globally discounted on the basis of a single experimental test, and our results suggest conditions under which variation in predation risk is likely to influence antipredator behavior in animals.

Table 1 Results of model selection procedure to assess support for the predicted outcome of the risk allocation hypothesis, in comparison with five alternative models

Factors included in the model	Number of parameters	AICc	Δ AICc	AIC weight
Manipulation of risk ratio				
Predator and interaction ^a	3	-73.85	0.00	0.441
Ratio and interaction	3	-73.80	0.04	0.431
Predator, ratio, and interaction	4	-71.36	2.49	0.127
Ratio and predator	3	-61.07	12.77	0.001
Ratio	2	-56.40	17.44	0.000
Predator	2	-53.18	20.66	0.000
Manipulation of time at risk				
Predator	2	-120.49	0.00	0.426
Predator and interaction	3	-119.90	0.60	0.316
Predator and time at risk	3	-118.44	2.05	0.153
Predator, time, and interaction ^a	4	-117.41	3.08	0.091
Time at risk and interaction	3	-113.58	6.92	0.013
Time at risk	2	-88.31	32.18	0.000

AIC, Akaike's Information Criterion. Response is the proportion of time inactive. Models are sorted by their degree of support from the data, which is indicated by the AIC weight.

^a Models predicted by the risk allocation hypothesis.

We do not believe that the results arose from a violation of assumptions of the Lima and Bednekoff model. For *R. lessonae* and many other anurans, sufficient food must be gathered to reach metamorphosis within a limited period of time, with fitness declining precipitously for individuals that fail to escape a drying pond or delay metamorphosis until late in the season (Altwegg, 2001; Smith, 1987; Wilbur, 1980). Thus, tadpoles probably meet the assumption of a fixed time horizon better than most other animals. Fitness costs of avoiding predators, involving reduced growth and development rates, are well established for many anurans (Van Buskirk, 2000). Finally, *R. lessonae* and other tadpoles behave as if they can integrate predation risk over time, although this may simply involve monitoring instantaneous hunger level or physiological conditions that result from previous environments rather than an active memory of earlier predation levels (Semlitsch and Reyer, 1992; Van Buskirk, 2002). The three main assumptions described in the Introduction are therefore fulfilled by this system.

We also believe that our experimental design produced a valid test of the risk allocation hypothesis because we directly manipulated the two main parameters explored by Lima and Bednekoff. The outcome was not a consequence of using predator-free tubs to represent the low-risk environment, although that decision makes it impossible to calculate an exact ratio of predation risk between the high- and low-risk situations. The expected outcomes are not altered by recalculating optimal vigilance values under the condition that the threat of predation in the low-risk environment approaches zero. For example, as the number of predators in the high-risk environment increases (Figure 1A), the model always predicts symmetrical and compensatory behavioral responses in the two environments, even when one environment is nearly risk free. Thus, the differences between our results and those predicted under the risk allocation hypothesis cannot be blamed on this aspect of our design.

We are thus forced to reject the risk allocation hypothesis for the tadpole system and to conclude that this model is not universally upheld in real animals. Are animals other than tadpoles more likely to support predictions of the Lima and Bednekoff model? Allocation of risky behavior to the more dangerous environment should be especially clear when the time spent within the dangerous environment is high relative to the time needed to collect resources. Our experiment showed that tadpoles can maintain high individual growth rates even when exposed to high risk for 83% of their lives, suggesting that they acquire sufficient food without having to increase their allocation of feeding behavior to the high-risk periods. However, a few other well-studied animals may be unable to avoid risk allocation. Some desert rodents and insectivorous birds, for example, must devote large fractions of their time to gathering food (Ekman, 1987; Kotler et al., 1994; Mitchell et al., 1990; Van Buskirk and Smith, 1989), and high-risk predation environments for these animals may be fairly frequent in nature (Bouskila, 1995; Kotler et al., 1993). If we assume that foraging time is related to the minimum required rate of energy intake and that animals must gather resources within a limited period of time, then these observations suggest that the risk allocation hypothesis can be relevant in natural settings. For both desert rodents and insectivorous birds, the proportion of time at high risk may be large relative to the food supply in nature, and as a consequence changes in time at risk are expected to impinge upon time necessary for gathering food. The results of our experiment, although not supporting Lima and Bednekoff's (1999) model, nevertheless point toward conditions under which the hypothesis is more likely to apply.

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