Temporal variability, threat sensitivity and conflicting information about the nature of risk: understanding the dynamics of tadpole antipredator behaviour

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Abstract

The importance of temporal variability in predation risk has recently come to the forefront of research examining the behavioural ecology of predator–prey relationships. Temporal variability has been known to drive patterns of behavioural responses associated with foraging, reproduction and territorial defence of prey animals. We investigated whether larval woodfrog, *Rana sylvatica*, tadpoles learn to adjust the intensity of their antipredator responses to match (1) the temporal patterns of risk they experience throughout the day and (2) the risk level of a predator. We also examined how tadpoles incorporate temporally conflicting information on the risk posed by the predators. Our results indicate that tadpoles show dynamic adjustments in their behaviour, adjusting their response to predators according to the level of threat associated with the predator and the time of day at which the predator represents the most significant threat. Moreover, tadpoles responded to conflicting information by adjusting their response intensity depending on the nature of the change in vulnerability (whether the risk increased or decreased) and the time that the conflicting information was experienced (whether it was recent or old information). We discuss our results within the context of predator predictability in natural systems and game theory approaches to the behavioural response race between predator and prey.

Keywords: antipredator behaviour, conflicting information, predation risk, predictability, *Rana sylvatica*, safety strategy, temporal learning, woodfrog tadpole

Spatial variability in predation pressure is at the cornerstone of research on predator–prey interactions (Werner et al. 1983). In contrast, temporal variability has received much less attention (Lima & Bednekoff 1999; Sih et al. 2000), but this changed in the last decade, particularly with the publication of Lima & Bednekoff’s (1999) risk allocation model, which attempted to predict the effect of patterns of exposure to risk on the foraging and vigilance behaviours of prey. This model highlighted the need for behavioural ecologists to consider how patterns of risk experienced by prey over ecological timescales influence their behavioural decision making. One shortcoming that experimental tests of risk allocation highlighted was our realization that we do not know how predictable predation is in natural conditions.

Intuitively, ecologists and behavioural ecologists know that predation pressure varies from moment to moment, through diel, lunar and seasonal cycles and over evolutionary time (Sih et al. 2000). A few studies have shown the effects of this risk cycling on the feeding, reproduction and distribution of prey. A classic example is copepods showing diel vertical migration as an antipredator response (Neill 1990). Studies have shown that many rodents adjust their activity levels according to lunar cycles (Kotler et al. 2002), avoiding foraging during periods of full moon light, presumably to avoid nocturnal predators (Clarke 1983; Bowers 1988). Little blue herons, *Egretta caerulea*, switch their foraging to safer times, such as rainfalls or dusk, when under intense hawk predation (Caldwell 1986). Sullivan et al. (2005) found that red-backed salamanders, *Plethodon cinereus*, show a stronger response to the odour of garter snakes, *Thamnophis sirtalis*, early in the evening than they do late at night, probably because thermal constraints restrict the activity of predatory snakes later at night, making them less of a threat for salamanders. Thus, we have indications that in some systems at least, predation risk may be predictable enough to allow prey to adaptively adjust their behaviours and habitat choice to decrease their vulnerability to predators and thus optimize their trade-offs between predator avoidance and foraging (Lima & Dill 1990). Whether these adjustments are learned or are the result of selective predation is unknown.

Temporal learning by prey species has been investigated in only a few studies. Reebbs (1999) showed that *Galaxias maculatus* fish can learn to be at a specific place at a specific time (time–place learning) to obtain a food reward, but cannot learn to avoid a specific place at a specific time to escape predation. Do these results imply that the lack of predictability of predation over evolutionary time precludes time–place learning of predators? What evidence do we have that
prey can learn the temporal patterns of risk to which they are exposed? Ferrari et al. (2008b) provided the first preliminary evidence that prey (woodfrog tadpole, *Rana sylvatica*) are able to learn to match the intensity of their antipredator response to the time of day at which they experienced predation risk, in this case, cues of tiger salamanders, *Ambystoma tigrinum*. As highlighted by Sullivan et al. (2005), salamanders are ectotherms and thus, may follow a predictable diel activity schedule that prey could learn to recognize (Holomuzki & Collins 1983). These studies raise several interesting questions that deserve both theoretical and empirical considerations. How much predictability is needed for prey to learn the temporal patterns of their predators? What happens if the schedule of predictability is broken? That is, how do prey deal with conflicting information? Are there evolutionary predispositions for prey with different experience with predators to have the ability to adjust their behaviour to match the predictability of their predators? It is possible that prey species that did not evolve with predictable predators may lack the ability to temporally adjust their antipredator responses, while those prey that have evolved with predictable predators do make temporal adjustments.

Larval amphibians provide great models to understand risk assessment and the evolution of prey defence mechanisms. Several studies have shown that tadpoles show alterations in body morphology (e.g. increase in tail depth) that reduces their risk of being captured during encounters with predators (Van Buskirk & Arioli 2002; Relyea 2003b). Many other studies have documented sophisticated behavioural responses to predation risk. A common finding is that tadpoles show graded behavioural responses with increasing levels of risk (Van Buskirk et al. 2002; Relyea 2003a; Laurila et al. 2004; Hammond et al. 2007).

In this study, we tested whether woodfrog tadpoles (1) learn to adjust the intensity of their antipredator responses to match the temporal patterns of risk they experience throughout the day, (2) learn to adjust the intensity of their response based on the danger level of a predator and (3) incorporate temporally conflicting information on the risk posed by a predator. Tadpoles can learn to recognize a novel predator through the pairing of injured conspecific cues and the odour of the novel predator (Woody & Mathis 1998; Mirza et al. 2006). Using this methodology, we performed two experiments. The first experiment focused on threat-sensitive and temporal-sensitive adjustments in the behaviour of tadpoles to risk posed by predators. Tadpoles were exposed to four treatments: groups of tadpoles received cues from predators representing either a medium threat or a high threat in the morning and a low threat in the evening, while the other two groups received cues from a predator representing a low threat in the morning and either a medium or a high threat in the evening. In the second experiment, we investigated the dynamic adjustments of tadpole antipredator behaviour to conflicting information. Two groups received consistent information throughout the conditioning period; one group was exposed to cues from a predator representing a medium threat in the morning and a low threat in the evening, while the second group received opposite treatments. In addition, two other groups received temporally inconsistent information, varying in the nature of change in vulnerability (increase or decrease in the threat level of the predator) and the time at which the conflicting information was experienced (new or old information). We tested animals from the four risk regimes in both the morning and the evening.

**METHODS**

**Water, Test Subjects and Predator**

Two weeks prior to starting the experiments, we filled a 1900-litre plastic water trough with well water and left it outdoors. We seeded the water with zooplankton and phytoplankton from a local pond (central Alberta) using a fine mesh dip net (hereafter ‘well water’), which ensured that the water used for holding and testing contained a full array of algae and plankton but no amphibian cues.

We collected eight woodfrog egg clutches in early May from a local pond and transferred them into a pool (60 cm diameter) containing pond water and aquatic plants. The pool was positioned on the pond to equalize the temperature of the pool water with that of the pond water. After hatching, the tadpoles were reared for 2 weeks. Rabbit food was provided to supplement the algae already present in the pool. Several studies have documented that tadpoles from this pond do not have innate recognition of tiger salamanders (Ferrari & Chivers 2008; Ferrari et al. 2007b), the focal predator used in our experiments.

An adult tiger salamander (snout–vent length: 14.1 cm) was obtained from a commercial supplier and housed in the Biology Department Animal Care Unit at the University of Saskatchewan. The salamander was maintained on a diet of live crickets and earthworms. While a single salamander was used in the present experiment, previous work suggests that the defensive response elicited in tadpoles by salamander predators is not unique to the individual predator being examined (Ferrari et al. 2007b; Ferrari & Chivers 2008, 2009).

**Experiment 1: Threat- and Temporal-sensitive Predator Recognition**

To examine whether tadpoles can integrate both temporal and threat level information about their predators within a brief period, we exposed groups of 10 tadpoles to various levels of risk (low, L; medium, M; high, H) for 7 consecutive days using four regimes. The first group of tadpoles was exposed to medium risk in the morning and low risk in the evening (M/L: the first letter indicates the risk level received in the morning and the second letter indicates the risk level received in the evening). The second group received the opposite treatment (L/M). The third group received high risk in the morning and low risk in the evening (H/L) and the last group received the opposite treatment (L/H). The three levels of risk simulated three situations in which the predator was (1) present but not feeding (low risk), (2) present and feeding on a few tadpoles (medium risk) and (3) present and feeding on many tadpoles (high risk).

We arbitrarily selected tadpoles from our holding pool, which originally contained the eight egg clutches, and randomly assigned them to 40 groups of 10. We placed each group into a 3.7-litre plastic pail filled with 3 litres of well water and provided them with rabbit chow. Ten pails were then randomly assigned to each of the four treatment groups. The low-risk treatment consisted of injecting 20 ml of salamander odour and 9 ml of well water in the buckets containing tadpoles. The medium-risk treatment consisted of injecting 20 ml of salamander odour paired with 9 ml of a low concentration of injured conspecific cues. The high-risk treatment consisted of injecting 20 ml of salamander odour paired 9 ml of a high concentration of injured cues. Woodfrog tadpoles show an antipredator response to cues of injured conspecifics (e.g. Ferrari et al. 2008c) and the intensity of their responses increases when exposed to increasing concentration of cues (M. C. O. Ferrari, C. E. Brown, F. Messier & D. P. Chivers, unpublished data). The injured conspecific cues were obtained by crushing the equivalent of 1.5 (medium risk) or 4.5 (high risk) tadpoles per bucket in 9 ml of well water using a mortar and pestle. The salamander odour was obtained by soaking one tiger salamander in 2 litres of well water for 12 h.

Conditioning took place in the morning (0800–1000 hours) and in the evening (2000–2200 hours). Because recent histories of predation risk differed between groups (some received high risk and some received low risk as their last information), we had to tease apart the effects of learning from those of behavioural risk.
Experiment 2: Dealing with Conflicting Information Within and Across Days

To determine the effects of exposure to conflicting information in the short term (within a day) and in the long term (between days) on tadpoles’ ability to assess the risk associated with their predators, we exposed groups of 10 tadpoles to four risk regimes for 7 consecutive days. In the first treatment, we exposed tadpoles to medium (M) risk in the morning and low (L) risk in the evening (7M/7L), and in the second treatment, we exposed tadpoles to the opposite treatment (7L/7M). Thus, these two groups of tadpoles received consistent information during the 7-day conditioning period. In the third treatment, we exposed tadpoles to medium risk in the morning and low risk in the evening for 6 days, then we exposed them to low risk in the morning and medium risk in the evening on the last day of the conditioning period (6M1L/6L1M). In the fourth treatment, we exposed tadpoles to the opposite treatment: tadpoles were exposed to low risk in the morning and medium risk in the evening for 1 day, then exposed them to medium risk in the morning and low risk in the evening for 6 days (1L6M/1M6L). The last two treatments provided conflicting information to the tadpoles regarding the risk associated with the predator at a given time of day.

The set-up was identical to that of experiment 1. Each of 40 groups of 10 tadpoles was randomly assigned to a 3.7-litre plastic pail filled with 3 litres of well water and provided with rabbit chow. Ten pails were then randomly assigned to each of the four treatment groups. The medium-risk exposures consisted of injecting 20 ml of salamander odour paired with injured conspecific cues (predator present and feeding). The low-risk exposures consisted of injecting 20 ml of salamander odour only (predator present but not feeding). The salamander odour was prepared using the same procedure as that of experiment 1. For the injured conspecific cue, we injected the equivalent of 1.5 tadpoles per bucket, following the same protocol as that used for experiment 1. Following the conditioning period, tadpoles were left undisturbed for 3 days, and were tested for their response to salamander odour in the morning and in the evening of the testing period, as defined for experiment 1.

While conceptually different, experiments 1 and 2 were conducted simultaneously (1) because of temporal constraints existing on tadpole life history and (2) to reduce the number of animals used in the experiment. Accordingly, tadpoles from M/L and L/M treatments from experiment 1 were the same tadpoles that served for the 7M/7L and 7L/7M treatments in experiment 2.

Experimental Procedures

The conditioning procedures were similar for both experiments. The stimuli were gently injected on the side of the pails, to minimize disturbance to the tadpoles. We treated the pails between 0800 and 1000 hours each morning and 2000 and 2200 hours each evening for the duration of the conditioning phase. The sun rose at approximately 0515 hours and set at approximately 2145 hours at our field site during this period. After treating the tadpoles for 7 days, we performed a 100% water change on all the pails and provided the tadpoles with rabbit chow. The tadpoles were then left undisturbed for 3 days prior to testing.

The testing procedures were similar for both experiments. Tadpoles were treated for their response to salamander odour during both morning and evening. Activity of woodfrog tadpoles is severely restricted by low temperatures (Ferrari et al. 2008a). Consequently, the morning testing period was shifted to allow the water to warm up, increasing the movement of the tadpoles to match that of tadpoles tested in the evening. Hence, the tadpoles were tested between 1030 and 1200 hours in the morning and between 2000 and 2130 hours in the evening. Testing trials took place over a 3-day period. We randomly selected four tadpoles from each pail, then exposed two of the tadpoles to salamander odour and two of the tadpoles to a control of well water, and recorded their behaviour. The order of treatments was randomized.

Twenty minutes prior to testing, we placed individual tadpoles in plastic cups (0.5 litre, 10 cm diameter, 12 cm high) filled with well water. We recorded tadpole behaviour for 4 min before and 4 min after injection of the stimulus in the cup. The results of experiment 1 were the same bucket. The salamander odour was prepared using the same methodology used for the conditioning phase.

We used a well-established behavioural protocol to quantify the antipredator responses of the tadpoles (Ferrari et al. 2007b; Ferrari & Chivers 2008). The typical antipredator response of larval amphibians, including woodfrog tadpoles, is to decrease activity upon detection of predation cues. Thus, we drew a line on the bottom of the testing cups and recorded the number of lines crossed during the pre- and poststimulus periods. We considered a line was crossed when the entire body of the tadpole was on the other side of the line.

Statistical Analysis

Statistical comparisons were performed on the percentage change in line crosses from the prestimulus baseline (number of line crosses in the prestimulus period minus number of line crosses in the prestimulus period/number of line crosses in the prestimulus period). The values for the two tadpoles conditioned in the same bucket and receiving the same treatment were averaged to reflect that ‘bucket’ was our replicate, not tadpoles. In addition, tadpoles from the same bucket tested for different cues were not considered independent, and ‘bucket’ was introduced as a nesting factor. All data met assumptions of normality and homoscedasticity. For experiment 1, the results of conditioning time (morning or evening), predator risk during conditioning (medium or high) and testing time (morning or evening) were assessed on the responses of tadpoles to water (first analysis) and salamander odour (second analysis) using a four-way nested ANOVA in which testing time was nested within bucket. Subsequent post hoc tests were performed on the responses of tadpoles to salamander odour only in the morning and evening. For experiment 2, the effects of treatment, cue (water or salamander odour), testing time (morning or evening) were assessed using a four-way nested ANOVA in which cue and testing time were nested within buckets. Subsequent post hoc comparisons on the responses of tadpoles to salamander odour at both times of day were performed. All analyses were performed using SPSS 16 (SPSS, Chicago, IL, U.S.A.).

RESULTS

Experiment 1

The ANOVA revealed that the tadpoles’ response to water was not affected by any of the factors examined (Fig. 1a, b; Table 1).
However, tadpoles’ response to salamander odour was affected by risk, and there was a significant interaction between conditioning time and testing time (Table 1). Post hoc comparisons revealed that tadpoles showed a stronger response to the salamander odour under medium or high threat (i.e. when the salamander was actively feeding) than under low threat (i.e. non-feeding salamander; Table 2). When tested in the evening, tadpoles that had experienced the high-risk predator responded to salamander odour with a significantly stronger intensity of response than tadpoles that had experienced the medium-risk predator, regardless of the conditioning time (Fig. 1b). However, there was no such effect in the morning (e.g. morning: M/L versus H/L: P = 0.09; Table 2, Fig. 1a).

Experiment 2

The ANOVA revealed a significant effect of cue and an interaction between treatment and time of testing (Table 3). Tadpoles showed a stronger response to salamander odour than to water. In addition, post hoc comparisons (Table 2) revealed that, in the morning, tadpoles from the 7M/7L, 6M1L/6L1M and 1L6M/1M6L treatments responded with the same intensity of antipredator behaviour when exposed to salamander odour than did tadpoles from the other treatments (Fig. 2a). In the evening, however, tadpoles from the 7M/7L and 1L6M/1M6L treatments showed lower antipredator responses to the salamander odour than did tadpoles from the 7L/7M and 6M1L/6L1M treatments (Fig. 2b).

DISCUSSION

The importance of temporal predictability in driving behavioural decision making has recently come to the forefront of behavioural ecology. Much of this work has focused on testing Lima & Bednekoff’s (1999) risk allocation hypothesis. Studies on a variety of prey animals, including amphibians, have provided mixed support for predictions of the risk allocation model (Van Buskirk et al. 2002; Laurila et al. 2004). One of the major impacts of this work was to highlight our need to understand how predictable risk is under natural conditions and whether prey can learn to respond to temporal patterns of risk. Moreover, we need to understand how prey respond to conflicting information about temporal patterns of risk.

Our work represents a comprehensive study examining the role of learning in determining temporal responses of prey to predators.

Table 2

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Morning</th>
<th>Evening</th>
</tr>
</thead>
<tbody>
<tr>
<td>M/L</td>
<td>0.012</td>
<td>0.012</td>
</tr>
<tr>
<td>H/L</td>
<td>0.093</td>
<td>0.020</td>
</tr>
<tr>
<td>L/M</td>
<td>&lt;0.001</td>
<td>0.829</td>
</tr>
<tr>
<td>L/H</td>
<td>0.943</td>
<td>0.025</td>
</tr>
<tr>
<td>H/L</td>
<td>&lt;0.001</td>
<td>0.015</td>
</tr>
</tbody>
</table>

Values in bold denote a significant difference (P < 0.05).

Table 3

ANOVA of tadpoles’ responses to the sequence of exposure (treatment, see text), testing time (TT: morning or evening), cue exposure (water or salamander odour) and bucket (random factor) in experiment 2

<table>
<thead>
<tr>
<th>Treatment</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>TT</td>
<td>3, 36</td>
<td>1.47</td>
<td>0.240</td>
</tr>
<tr>
<td>Cue</td>
<td>1, 36</td>
<td>11.7</td>
<td>0.002</td>
</tr>
<tr>
<td>Treatment</td>
<td>3, 36</td>
<td>4.91</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TT &amp; cue</td>
<td>3, 36</td>
<td>0.73</td>
<td>0.538</td>
</tr>
<tr>
<td>Bucket</td>
<td>3, 36</td>
<td>0.82</td>
<td>0.725</td>
</tr>
</tbody>
</table>

Values in bold denote a significant difference (P < 0.05).
In experiment 1, tadpoles that received temporally opposite treatments displayed opposite response patterns to the predator, showing that they have the ability to learn to respond to predation risk according to the time of day that they perceive the risk. When tested in the evening under high risk (i.e. when a predatory salamander was feeding), tadpoles that had experienced the high-risk treatment showed a stronger response to salamander odour than did tadpoles that had experienced the medium-risk treatment. Interestingly, when tested at the times of day when the salamander was not feeding, tadpoles that had experienced the high-risk treatment showed a stronger response to salamander odour than did tadpoles that had experienced the medium-risk treatment. These results indicate that tadpoles simultaneously adjusted the intensity of their response to the risk associated with the predator and to the times of day at which they had experienced different patterns of risk. This pattern was not observed during the morning, probably because of the temporal shift in testing. The distribution of tadpoles' temporal response to salamander cues is probably bimodal, with two peaks of different amplitudes at the two times of day, during which tadpoles experience salamanders. Delaying the testing time in the morning might have lowered the tadpoles' response to the salamander, hence obscuring subtle differences that we had observed in the evening patterns.

Our second experiment was the first to consider how conflicting information influences the ability of prey to learn to recognize temporal patterns of risk posed by predators. We found that tadpoles continually readjusted their response intensity to reflect the change in vulnerability they had experienced when faced with conflicting information and seemed to use a safety strategy to do so. The adjustment appeared to be dependent on the nature of change in vulnerability (whether the risk increased or decreased) and the time at which the conflicting information was experienced (whether it was recent or old information). When the conflicting information was followed by six pieces of consistent information, the tadpoles responded with an intensity that matched the consistent information (i.e. the conflicting information was ignored, regardless of the nature of the information). When the conflicting information was recent, the tadpoles' responses depended on the nature of the information. When the conflicting information represented an increase in risk (e.g. 6L1M), the tadpoles' response intensity matched the risk associated with the last piece of information. When the conflicting information represented a decrease in risk (e.g. 6M1L), one piece of information was not enough to elicit a decrease in antipredator responses. These response patterns are probably adaptive, as it would seem safer to over-respond to a predator (and potentially waste feeding opportunities) than under-respond and be eaten. These results support the findings of Ferrari & Chivers (2006), who tested the effect of conflicting information on the ability of naïve fathead minnows, Pimephales promelas, to learn to recognize an unknown predator. That study did not consider temporal aspects of learning but rather the danger levels associated with the predator. Minnows exposed to two pieces of conflicting information about risk did not adjust their responses when the day before the feeding of a novel predator adjusted their responses to the predator primarily using the most recent pieces of information. In addition, when minnows received two recent pieces of conflicting information, the intensity of their response matched the higher-intensity (i.e. most conservative) information.

Prey that are able to adjust the intensity of their antipredator behaviour to match the level of risk posed by the predator, a phenomenon known as threat-sensitive predator avoidance, should be at a selective advantage, as they optimize the trade-off between costly but necessary predator avoidance and fitness-related activities such as foraging (Helfman 1989; Ferrari et al. 2007a, 2008a). The ability of prey to learn to display such adjustments specifically in response to temporal variation in predation risk has been tested in one species of fish, Galaxias maculatus (Reebs 1999), and one larval amphibian (Ferrari et al. 2008b; this study). Reebs (1999) found that G. maculatus do not match temporal patterns of risk with a specific location. Although our results indicate that tadpoles show temporal learning of predators, it is unknown whether they can also match temporal learning of predators with location. Does the lack of the ability to learn a time associated with predation by galaxids indicate that they were never under predictable predation pressure? The present results indicate that a single conflicting event is enough to cancel the predictable schedule of the prey's response. Hence, the question that arises from this is whether or not such predictability exists in nature. This is a vital question if we are to expand our understanding of the influence of temporal variation in predation risk on behavioural decision making by prey.

To determine the likelihood that predators will predictably forage at certain spots, we need to enter the dynamic matrix of predator–prey interactions. The distribution of predators in relation to their prey is not a well-understood aspect of predator–prey relationships. Some models predict that predators should always forage in patches where prey density is high (Stephens & Krebs 1986), and such optimal foraging theory usually holds when the prey are behaviourally inert (like plants or benthic animals). When prey have an opportunity to adjust their behaviours or locations, the behavioural response race between prey and predator will lead to dynamic game theory models, where predator distributions should match their prey's resources while prey distributions should reflect habitat riskiness (Hugie & Dill 1994; Sih 2005). Some predators, like hawks, revisit the same area with a temporal
schedule that does not differ from random (e.g. Roth & Lima 2007). Hence, the spatial and temporal unpredictability provides predators with the ‘surprise attack’ advantage, as prey are unable to predict when to display strong behavioural responses. There exists, however, some predatory species that may be constrained in their ability to display unpredictable attacks. Ectotherm predators do not have the ability to display their maximal foraging behaviour during the cooler times of the day. Hence, their physiology forces them to be somewhat predictable, as is the case for tiger salamanders (Holomuzki & Collins 1983). Similarly, the hunting strategy of some predators may force them to forage during the day or the night. We strongly encourage studies that attempt to determine the predictability of predator attacks in natural systems.

Amphibians provide a great system to test different aspects of predator predictability on the evolution of prey behaviour. A pre-exposure of only 7 days is enough to obtain prey responding to temporal patterns of risk. While this response pattern comes quickly, it also goes quickly, as one mismatch in the schedule results in the loss of the response pattern. This highlights the importance of predation pressure on shaping prey behaviours. While temporal aspects of predation risk are difficult to investigate, additional efforts are required to include these factors in behavioural predation experiments. Ultimately, we should move towards meshing spatial and temporal predictability into studies of decision making.

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