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The dynamics of predation risk assessment: responses of anuran larvae to chemical cues of predators

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Summary

1. While the antipredator behaviour of prey has been well studied, little is known about the rules governing the predation risk assessment of prey. In this study, I measured the activity levels of predator-naive green frog (*Rana clamitans*) tadpoles during and after exposures to the chemical cue of predatory larval dragonflies (*Anax* spp.). I then used the lengths of the time lags from the end of the cue exposures until the tadpoles returned to a control level of activity as an index of the perceived risk of the tadpoles.

2. While tadpoles always responded upon exposure to the *Anax* chemical cue by strongly reducing their activity level, their perceived risk increased asymptotically over time during the initial period of the cue exposure. Tadpoles of all size classes perceived increasing risk in proportion to chemical cue concentration, but the length of time that tadpoles responded during cue exposure and the length of their post-exposure time lags decreased with increasing body mass.

3. The results suggest that the perceived risk of green frog tadpoles varies over time and does not correspond directly to their behavioural response (i.e. activity level). However, their perceived risk does appear to vary in accordance with the predation risk associated with the *Anax* chemical cue and the reliability of the information from the cue, and therefore may be predictable.

Key-words: information use, non-lethal interaction, trait-mediated interaction.

Introduction

Research on antipredator behaviour has shown, that in a wide variety of systems and taxa, prey can perceive differences between levels of predation risk (Lima & Dill 1990; Kats & Dill 1998) and that prey follow basic decision rules in their behavioural responses (e.g. minimize the predation risk-to-foraging gain ratio, Gilliam & Fraser 1987). However, little is known about how prey actually use the information available to them (e.g. predator chemical cue) to assess the level of predation risk (Luttbeg & Schmitz 2000; Lima & Steury 2005). This lack of knowledge has hindered the process of making generalizations from specific examples. Characterizing the information available to prey and identifying the rules that govern their predation risk assessment will help to improve predictions of prey behaviour and its effects (Bolker *et al*. 2003; Lima & Steury 2005).

Describing the rules governing predation risk assessment requires first identifying what prey should be favoured to estimate. Because antipredator defences are plastic at different time-scales, prey should be favoured to estimate the level of predation risk at the time-scale at which they can respond. For example, many prey can change their activity level almost instantly, but can change life history characteristics only over much longer time-scales. While prey may integrate multiple defences (Relyea 2001; Steiner & Pfeiffer 2007), the relative costs and benefits (e.g. in time spent foraging, mating or exposed to predators (Lima & Dill 1990) of a particular defence depend upon how closely the level of defence matches the predation risk at the time-scale at which the defence is plastic. Prey that can adjust their activity level almost instantly should be favoured to estimate the actual predation risk at their location at each moment, referred to hereafter as the momentary predation risk. Across a habitat, the momentary predation risk is high within the attack range of a predator (i.e. the momentary predation risk is equal to the probability of a successful attack by the predator) and zero everywhere else. From the perspective of optimization, selection should favour prey that respond behaviourally to the momentary predation risk. Prey that respond perfectly to the momentary predation risk will both minimize the cost of reduced activity when outside the attack range of a predator, because they will be foraging maximally, and minimize the cost of responding too weakly when within the attack range of a predator, because they will be responding

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maximally. Prey that exhibit fixed activity levels or vary their activity level at a longer time-scale will face comparatively higher costs (but see Bouskila & Blumstein 1992 and Abrams 1994 for discussion on the relative costs of suboptimal responses).

In most systems, prey must estimate the predation risk in a dynamic environment in which the momentary predation risk and the information available to them (e.g. predator chemical cue) vary over time (Sih, Ziemba & Harding 2000). Moreover, the information available to prey is often limited and not completely reliable (i.e. variation in the momentary predation risk may not correspond directly to variation in information sources). As a result, prey must incorporate into their estimate uncertainty of the momentary predation risk. Theory suggests that the perceived risk of prey should depend upon the level of risk associated with an information source and its reliability (Sih 1992; Koops 2004).

In aquatic systems, many prey assess predation risk indirectly through chemical cues released by predators and prey during and after predation events (Kats & Dill 1998). Prey may use chemical cues to gain information on both what species of predator consumed a prey and which species of prey was consumed (Schoeppner & Relyea 2005). Because stronger cue concentrations are related generally to a higher density of predators, more voracious predators or closer predators (Chivers & Smith 1998; Kats *et al.* 1998; Dupuch, Magnan & Dill 2004), prey should perceive increasing risk with increasing cue concentration (e.g. Van Buskirk & Arioli 2002). The predator chemical cue, however, may not always be a reliable indicator of the momentary predation risk. The chemical cue of predators can diffuse out from the site of predation events and decompose over several days after being released (Turner & Montgomery 2003; Peacor 2006). Because of this and because predators move, cue concentration will generally become a poorer indicator of the location of predators over time. Additionally, the cue produced during each new predation event will not be related to the location of other predators at all. Consequently, while the predator chemical cue provides some information on the level of the momentary predation risk, its reliability may be limited at that time-scale.

As a result, the risk perception of prey that depend on the predator chemical cue should not remain constant during cue exposure; prey should perceive chemical cue exposures as declining in reliability over time. The rate of decrease in risk that prey perceive over time may be affected by the initial concentration of the chemical cue. For example, weaker cue concentrations may be less reliable initially because they can be produced by a recent small predation event or be decomposing cue from a larger past event (i.e. a group of predators or a voracious individual predator), while strong cue concentrations may be present only soon after or near a large predation event. As a result, the risk that prey perceive from stronger cue concentrations may decline more slowly than the risk perceived from weaker cues. Additionally, while prey should generally perceive declining predation risk over time, during the first part of a cue exposure prey may actually perceive increasing risk as exposure length increases. If prey face sit-and-wait predators (e.g. the larval dragonflies used in this experiment), a persistent, new cue exposure may indicate that a predator is nearby. In contrast, prey that face actively hunting predators should perceive a consistently declining risk as exposure length increases. This difference should occur because the predator chemical cue will generally remain correlated with the location of a sit-and-wait predator for a longer time compared to a more active predator.

In this study, I estimated indirectly the level of risk that tadpoles perceive over time during an exposure to a predator chemical cue. I measured the behavioural responses (activity level reductions) of green frog (*Rana clamitans* Latreille 1801) tadpoles during and after exposures of varying length to a range of concentrations of the chemical cue of predatory larval dragonflies (*Anax longipes* Drury 1770 and *A. junius* Hagen 1861). By ending the cue exposures artificially, the perceived predation risk at that point in the exposure can be estimated indirectly by measuring the length of time lags in returning to a control level of activity.

Longer post-exposure time lags indicate a greater perceived risk (Sih 1992), assuming that perceived risk declines continuously after a cue exposure (i.e. when tadpoles are no longer exposed to a predation stimulus). Because neurological data are not available, the particular decay curve that describes the pattern by which the perceived risk of tadpoles declines is unknown. However, as long as their perceived risk does not increase after they are no longer exposed to the predator chemical cue, the lengths of time lags will provide an index for their perceived risk levels. Not knowing the shape of the decay curve precludes quantifying differences directly in perceived risk levels (i.e. if tadpoles exhibit longer time lags after one cue exposure compared to a second cue exposure, the magnitude of the difference in their perceived risk levels cannot be calculated – only that tadpoles perceived a higher risk from the first cue exposure can be supported). Additionally, the use of time lags to estimate perceived risk assumes that other factors that may influence prey behaviour, such as a prey's energetic state, remain similar among treatments. For example, if a prey's energetic state declines during a cue exposure due to its antipredator behaviour, comparisons among different exposure length treatments may be limited because of differing energetic states.

I also used three size classes of tadpoles to determine if tadpoles perceive risk similarly as their body mass increases. I hypothesized that larger tadpoles should respond less strongly to the same concentration of predator cue (i.e. because they should perceive less risk) because they are generally less vulnerable to predation (Eklov & Werner 2000), but the pattern of the perceived risk across treatments should remain similar among size classes because the informational value of the chemical cue will not change.

Materials and methods

Green frog egg masses were collected on 3 June 2004 from the experimental ponds on the University of Michigan's E. S. George Reserve near Pinckney, Michigan. The eggs were cultured in covered 300-L wading pools filled with well water and inoculated

with phytoplankton and zooplankton. After hatching, the tadpoles were fed rabbit chow (Purina, St Louis, MO, USA) *ad libitum* until the beginning of the experiment. The tadpoles were raised predator-naive in order to control for the effects of prior predator exposures and learning on current behaviour. Late-instar *Anax* spp. (*A. longipes* and *A. junius*) were collected from the same ponds between 1 and 3 weeks prior to the experiment. Both species of *Anax* co-occur commonly with green frog tadpoles and pose similar risk (S. J. McCauley, personal communication). The *Anax* were raised in plastic cups filled with well water, and were fed ~100 mg of green frog tadpoles three times per week.

The experiment was conducted indoors in 37 cm × 24 cm plastic containers filled with 8 L of aged well water. The side and bottom panels were cut out of a second set of plastic containers (33 cm × 20 cm) and replaced by a 1-mm fibreglass screen. The screened containers fitted inside the outer containers and allowed the tadpoles to be transferred from treatment to treatment during the experiment while minimizing disturbance. The sets of containers were placed in randomized blocks on shelves under fluorescent lights set to a 14 : 10 light : dark schedule.

The experiment was a 3 × 3 × 4 factorial design consisting of three size-classes of green frog tadpoles (20 mg, 100 mg and 200 mg), three lengths of *Anax* chemical cue exposure (10 min, 1 h and 2 h) and four concentrations of *Anax* chemical cue (no cue, 100 mg, 200 mg and 300 mg; hereafter: no cue, 1×, 2× and 3×). The cue concentrations refer to the mass of tadpoles consumed by the *Anax* to produce the chemical cue (see below). The no-cue treatment was used as a control. Each combination was replicated four times. The tadpole masses used represent a range from small and highly vulnerable to large and approaching invulnerability to predation by *Anax* (Eklov *et al*. 2000). The lengths of exposure and chemical cue concentrations used were chosen to provide a range of short-term exposure lengths to a range of concentrations, as the temporal variation and strength of chemical cue concentrations in natural ponds and how tadpoles experience this variation are unknown. However, in preliminary experiments, penultimate-instar *Anax* (4–5 cm in length) consumed a mean of 50 mg [standard error (SE) ± 10 mg] of green frog tadpoles per h, with a maximum of 425 mg. Earlier-instar *Anax* (2 cm in length) consumed a mean of 20 mg (SE ± 6 mg) per h, with a maximum of 175 mg. Preliminary experiments also indicated that tadpoles of all size classes responded by decreasing their activity level to a 2× *Anax* chemical cue up to 72 h old.

Experimental trials were conducted separately for each size class. Because of the large number of tadpoles needed, tadpoles from different egg masses were used for each size class, with all tadpoles within a size class coming from the same egg mass. As a result, comparisons between size classes may be confounded with genetic differences between tadpoles, although the activity-level response of green frog tadpoles during predator chemical cue exposures may have a low heritability (Watkins & McPeek 2006). The behavioural trials were conducted on 22–24 June (20 mg size class), 12–14 July (100 mg) and 2–4 August (200 mg). In each set of trials, the first day consisted of the 10-min exposure length to each of the four cue concentrations. The 1-h and 2-h exposure length treatments were run on the second and third days, respectively, each using a new set of tadpoles. All trials were conducted between 0800 h and 1700 h eastern daylight time.

For each 3-day set of trials, on the day before each exposure length treatment the outer containers were filled with well water containing no chemical cue and the screened containers were placed inside. Tadpoles were sorted into the appropriate size class, then allocated haphazardly into sets of 10. The range of tadpole masses in each size class were: 20-mg size class to 18–22 mg; 100-mg size class to 95–105 mg; and 200-mg size class to 190–220 mg. After sorting, the tadpoles were added to the containers along with 10% of the total mass of each set of tadpoles in ground rabbit chow.

On the day of each exposure length treatment, the *Anax* were placed into new cups filled with 400 mL of well water. Thirty min before the beginning of the trials, the *Anax* were fed the appropriate number of 100-mg green frog tadpoles to generate the cue (i.e. for the 300-mg cue concentration, three 100-mg tadpoles were fed to each *Anax*). Immediately before the trials, the water and chemical cue from each cup were poured through a fine-meshed net into a larger container to mix the chemical cue and standardize it. At the beginning of the trials, one cup (400 mL) of the mixed chemical cue was added to each replicate by pouring it slowly through a fine-meshed net into the centre of each container. This minimized the disturbance to the water. The no-cue treatments received one cup (400 mL) of well water.

To record the activity response of the tadpoles, each container was approached slowly and the number of tadpoles swimming or feeding during a 5-s observation interval was counted. This approach did not appear to disturb the tadpoles. The first observation was made 15 min after the chemical cue addition and observations were made every 15 min thereafter until the end of the exposure period. In the trials with a 10-min exposure length, the first and only observation was made 10 min after the chemical cue was added. At the end of the exposure period, the sets of tadpoles (including the no-cue control treatments) were moved by lifting the screened container gently out of the outer container and transferring them into new outer containers filled with well water. During the transfer, the water was allowed to drain out of the screened bottoms of the inner containers, so that little of the chemical cue (i.e. no pooled water) remained. Preliminary experiments indicated that the amount of predator chemical cue transferred to the new containers was insufficient to elicit an observable behavioural response in the tadpoles. Observations were then made every 15 min until the mean activity level of the tadpoles appeared to reach the activity level of the no-cue control treatments on at least two consecutive observations. The time between the end of the chemical cue exposure and the first observation in which the mean activity was within the 95% confidence interval of the control at that time-point was defined as the post-exposure time lag of that treatment combination.

The activity levels during cue exposure (in the 1-h and 2-h exposure length treatments) and the post-exposure time lags in activity for each size class–exposure length combination were analysed using repeated-measures analysis of variance (ANOVA) with cue concentration as the between-treatment factor. The last observation in the cue exposure treatment was included in the analysis of the post-exposure time lags. Post-exposure time lags were analysed as long as the mean activity levels of tadpoles remained lower than the control at the end of the cue exposure (i.e. if tadpoles had returned to a control level of activity in the first observation after the cue exposure, the time lag was considered to be 15 min). Differences in the time lags with differences in cue concentration were indicated by a significant time–concentration interaction, as tested by Wilks' λ. The Huynh–Feldt correction was applied if data did not meet the assumption of sphericity. When a significant time–concentration interaction was found, the Bonferroni test was used to make *post-hoc* pairwise multiple comparisons among cue concentration treatments. Activity levels during cue exposure in the 10-min exposure length treatments were analysed using one-way ANOVA and Bonferroni *post-hoc* tests. All analyses were conducted using SPSS version 13·0 (SPSS Inc., Chicago, IL, USA).

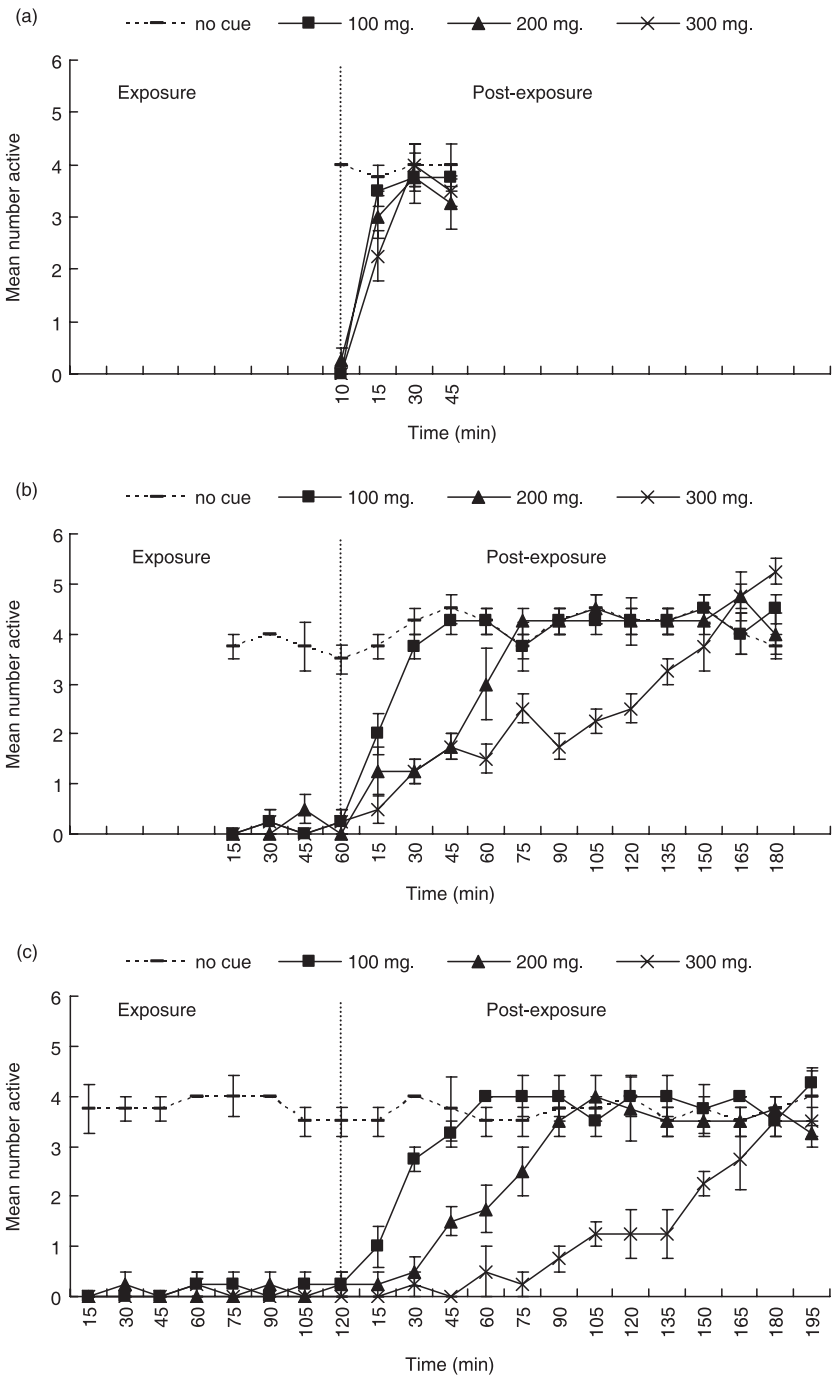

Fig. 1. Mean swimming activity of 20-mg green frog (*Rana clamitans*) tadpoles during and after exposure to the *Anax* chemical cue. The vertical line marks the end of the cue exposure; (a) 10 min exposure, (b) 1 h exposure, (c) 2 h exposure. Note that the times marked on the *x*-axis are reset to zero at the vertical line.

Results

ACTIVITY DURING EXPOSURE TO THE ANAX CHEMICAL CUE

In all treatments, the green frog tadpoles responded instantaneously to exposure to the *Anax* chemical cue by ceasing their activity (Fig. 1; Supplementary material, Figs S1 and S2). Mean activity remained < 0·5 tadpole active (of 10) during cue exposure in most treatment combinations. Activity levels began to increase during the exposure period for the larger tadpoles during longer exposures to weaker cue concentrations, but did not reach control levels of activity (all comparisons between controls and cue concentration treatments, $P < 0{\cdot}001$). The 100-mg tadpoles during the 2-h exposure at the 1× cue concentration (Fig. S1c, Supplementary material), the 200-mg tadpoles during the 1-h exposure at the 1× cue concentration (Fig. S2b, Supplementary material) and the 200-mg tadpoles during the 2-h exposure at the 1× and 2× cue levels (Fig. S2c, Supplementary material) had mean activity increase to > 1·0 tadpole active during the exposure period (comparisons between 1× and 3× cue concentration treatments in these treatment combinations, $P < 0{\cdot}05$).

Table 1. Statistically significant time–cue concentration interactions in each size class–exposure length combination as indicated by repeated-measures analysis of variance

Exposure length	*F*	d.f.	*P*
Size class: 20 mg			
10 min	8·46	9, 24·5	< 0·001
1 h	6·86	21, 17·8	< 0·001
2 h	5·94	36, 3·7	< 0·001
Size class: 100 mg			
10 min	17·23	9, 24·3	< 0·001
1 h	10·75	9·5, 30	< 0·001
2 h	3·27	15, 22·5	0·006
Size class: 200 mg			
10 min	12·97	6, 22	< 0·001
1 h	3·83	9, 24·9	0·004
2 h	3·6	9, 24·5	0·006

POST-EXPOSURE TIME LAGS

Post-exposure time lags in returning to the no-cue control level of activity generally decreased with increasing tadpole mass and increased with increasing cue concentration and length of exposure (Fig. 1; Supplementary material, Figs S1 and S2). Significant time–cue concentration interactions were found in all exposure length treatments in all size classes (Table 1). *Post-hoc* analyses indicated that post-exposure time lags occurred in all treatments, with the exception of those treatments noted above in which tadpoles did not respond for the full exposure period (Table 2). Differentiation between cue concentration treatments tended to occur in the longer exposure length treatments in the 20-mg size class, throughout in the 100-mg size class, and not at all in the 200-mg size class (Table 2).

While the post-exposure time lags in all size class–cue concentration combinations continued to increase with exposure length in most treatment combinations, they did appear to begin to asymptote (Fig. 2). However, with only three data points, statistical analysis is difficult. Increases in the length of time lags between the 10-min exposure lengths and the 1-h exposure lengths tended to be larger than the increases between the 1-h and 2-h exposure lengths. In the 100-mg tadpoles exposed to the 1× cue concentration, the length of the time lag decreased slightly from the 1-h exposure period to the 2-h exposure period.

Discussion

The results of this study provide a first step in identifying some of the rules that govern the predation risk assessment of tadpoles, and prey in general. Additionally, the results begin to show how perceived risk will influence prey behaviour over time. Green frog tadpoles always reduced their activity strongly during cue exposure, but exhibited time lags in returning to a no-cue control level of activity that increased in length with stronger *Anax* chemical cue concentrations and increased in length asymptotically with longer cue exposure lengths (Fig. 1; Supplementary material, Figs S1 and S2). While time lags increased asymptotically with exposure length, the maximum time lag length seemed to be determined by the cue concentration (Fig. 2). These basic patterns were followed by tadpoles of all size classes, but larger tadpoles exhibited shorter time lags. There are two general implications of these results: (1) prey that use a predator chemical cue to assess predation risk will perceive a risk level that varies over a cue exposure; and (2) perceived risk does, however, appear to be related to specific aspects of a chemical cue exposure, such as cue concentration, and should be predictable once further

Table 2. Statistically significant differences in post-cue exposure time lags among cue concentration treatments in each size class–exposure length combination as indicated by Bonferroni *post-hoc* multiple comparisons

Exposure length		Exposure length		Exposure length	
10 min	*P*	1 h	*P*	2 h	*P*
Size class: 20 mg					
Control–1×	< 0·001	Control–1×	0·002	Control–1×	< 0·001
Control–2×	< 0·001	Control–2×	< 0·001	Control–2×	< 0·001
Control–3×	< 0·001	Control–3×	< 0·001	Control–3×	< 0·001
		1×–2×	0·001	1×–2×	< 0·001
		1×–3×	< 0·001	1×–3×	< 0·001
		2×–3×	< 0·001	2×–3×	< 0·001
Size class: 100 mg					
Control–1×	0·004	Control–x	0·035	Control–2×	< 0·001
Control–2×	< 0·001	Control–2×	< 0·001	Control–3×	< 0·001
Control–3×	< 0·001	Control–3×	< 0·001	2×–3×	0·017
1×–2×	0·015	1×–2×	0·04		
1×–3×	0·028	1×–3×	< 0·001		
Size class: 200 mg					
Control–1×	0·03	Control–2×	0·029	Control–3×	0·01
Control–2×	0·03	Control–3×	0·014		
Control–3×	0·03				

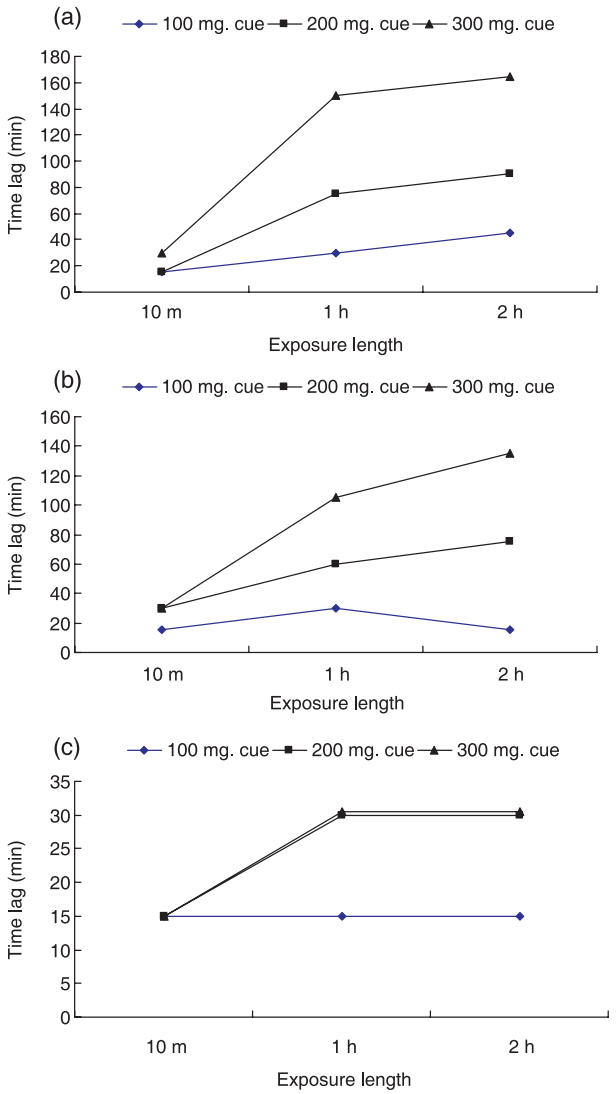

Fig. 2. Post-cue exposure time lags of green frog (*Rana clamitans*) tadpoles. Time lags from the end of cue exposure until the mean activity of the green frog tadpoles returns to the control level of activity in (a) 20 mg, (b) 100 mg and (c) 200 mg tadpoles exposed to the 100-mg cue concentration, 200-mg cue concentration, and 300-mg cue concentration for each exposure length. Note that the *x*-axes are not to scale.

data are gathered (e.g. such as data on the neurological response of tadpoles during cue exposure).

The length of the time lags increased relatively consistently with cue concentration in all size classes (Fig. 1; Supplementary material, Figs S1 and S2). The relationship between the lengths of the post-exposure time lags and cue concentration suggests that tadpoles perceived greater risk with greater cue concentrations. Because the predator chemical cue is related directly to predation, cue concentration is expected to be related directly to the actual predation risk. If the perceived risk of tadpoles declines at a constant rate after the cue exposure ends, the pattern of the time lag lengths is consistent with tadpoles perceiving a risk approximately proportional to the cue concentration.

The asymptotic pattern of the length of the post-exposure time lags with increasing exposure length suggests that tadpoles perceived increasing risk during the initial part of a cue exposure (Fig. 2). Prey may perceive increasing risk during the beginning of a cue exposure because the persistence of a predator chemical cue may be related to a nearby sit-and-wait predator (i.e. the cue may initially increase in reliability over time). Data from other experiments suggest that green frog tadpoles do not begin to perceive decreasing levels of risk until approximately 8 h into a cue exposure (M. E. Fraker, unpublished data). The asymptotic pattern may also reflect the energetic state of the tadpoles decreasing with longer cue exposures and the relative benefit of resuming foraging activity increasing. Although cue concentration appears to set the asymptote, there does not appear to be a further relationship between cue concentration and exposure length on perceived risk during a cue exposure (see Introduction). Perceived risk tended to increase from the 10-min exposure length treatment to the 1-h and 2-h exposure length treatments. It is not clear if there is no relationship because strong chemical cue is not more reliable initially than weak cue or because tadpoles perceive increasing risk over time regardless of the cue concentration (although data from other experiments suggest that weaker cue is less reliable; M. E. Fraker, unpublished data).

The decreasing response strength over time during cue exposure in the larger size classes occurred in the weaker cue concentrations, which is consistent with the hypothesis that weaker cue concentrations are less reliable than stronger concentrations, but does not provide strong support. The rate of change in the large tadpoles' activity level suggests that the larger tadpoles perceived a high risk initially and then adjusted their assessment over time. It is unlikely that the weaker chemical cue decayed significantly in the 2-h exposure period, as other data indicate that the *Anax* chemical cue takes 48–72 h to decay fully (Peacor 2006). Alternatively, larger tadpoles may respond less strongly to a weaker cue after a strong initial response simply because of their lower vulnerability (Eklov & Werner 2000). It is possible that the level of risk that larger tadpoles perceived from a stronger cue also decreased, but did not drop below the inactivity threshold.

The results also suggest that the perceived risk of tadpoles during a cue exposure does not correspond directly to their antipredator response in their activity level. That is, although tadpoles in different treatments perceived different levels of risk during cue exposure, all responded almost instantaneously when exposed initially to the *Anax* chemical cue by reducing their activity level strongly and continuing to remain inactive, although the larger size classes began to respond less strongly during the exposure period at weaker cue concentrations. Initial exposure to a chemical cue may result in a strong response because increases in cue concentration are most frequently the result of a new predation event nearby or a predator encounter (i.e. the information is reliable). Additionally, the strong activity reduction at the initial exposure to the *Anax* chemical cue can be reversed quickly so that the cost of the activity reduction can be limited.

Consequently, measuring a prey's current behaviour alone may not be sufficient to predict its future behaviour. Extrapolating from individual behavioural measurements to predict future behaviour and its effects is likely to be inaccurate. Assuming that the behavioural response of prey remains constant or varies with the rate of decay of the chemical cue is likely to overestimate the strength of the behavioural response over time. If a prey's level of perceived risk interacts with its response to subsequent cue exposures, such that its response to subsequent increases in predation risk depends on its perceived risk at that time, underestimation of the response may result. Rather, identifying how different aspects of a cue exposure, or any information source, relate to perceived risk over time may be necessary. Then, predictions of prey behaviour at any point in time can be based on the levels of the key aspects of the cue exposure at that time and into the past.

In most systems, prey experience repeated increases and decreases in predation risk (Sih *et al*. 2000). Future experiments need to put the present results into this context. Determining how long the risk perceived from one cue exposure (or another information source) interacts with future cue exposures will be necessary to developing predictions about how prey are likely to respond to predation risk in a dynamic environment. Additionally, combining results from studies on temporal variation in risk with studies on spatial variation in predator–prey distributions (Lima 2002; Luttbeg & Sih 2004) will be valuable in determining how predation risk and predator cues are experienced over time. Of course, making predictions about the actual long-term behaviour of prey would need to combine a model of risk perception with models of other factors that influence behaviour, such as energetic state (e.g. McNamara & Houston 1987).

In general, this experiment suggests how the risk perceived by tadpoles from one chemical cue exposure varies over time, independent of any history of cue exposures. Certain aspects of the exposure, such as the cue concentration, appear to interact with other aspects, such as the exposure length, to determine the perceived risk of the tadpoles. Future experiments are needed to determine the relative importance of other aspects and why particular aspects vary in importance. Additionally, the experiments suggest that the perceived risk of prey can be dynamic and can vary differently over time than the concentration of predator chemical cue or the prey's activity level response. To build on the current results, further data are needed on what information is available to prey (e.g. visual cues, Stankowich & Blumstein 2005; combinations of information sources, Mathis & Vincent 2000; Bouwma & Hazlett 2001) and how it influences the level of risk that prey perceive and the degree of uncertainty in their perceived risk.

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Supplementary material

The following supplementary material is available for this article.

Fig. S1. Mean swimming activity of 100-mg green frog tadpoles during and after exposure to the *Anax* chemical cue.

Fig. S2. Mean swimming activity of 200-mg green frog tadpoles during and after exposure to the *Anax* chemical cue.

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