The effects of temporal variation in predation risk on anti-predator behaviour: an empirical test using marine snails

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Foraging animals must often balance the conflicting demands of finding food and avoiding predators. Temporal variation in predation risk is expected to influence how animals allocate time to these behaviours. Counterintuitively, the proportion of time spent foraging during both high- and low-risk periods should increase with increasing time exposed to high risk. We tested this prediction using intertidal marine snails (*Littorina* spp.) that were exposed to temporal variation in perceived predation risk from crabs (*Cancer productus* and *Cancer magister*). Our results were consistent with those predicted for high-risk, but not low-risk, periods. During high-risk periods, a greater number of snails foraged (versus those that left the water or remained in their shells) as time at high perceived risk increased. For low-risk periods, there was no relationship between the number of snails foraging and time at high risk. This might be due to snails in all treatments foraging maximally in the low-risk periods. As a consequence, the difference in the number of snails foraging between high- and low-risk periods decreased with increasing time subject to high risk. These results indicate that the commonly used protocol of exposing foragers to a single pulse of heightened risk might tend to overestimate their typical investment in anti-predator behaviour.

Keywords: foraging; vigilance; predation-risk allocation hypothesis

1. INTRODUCTION

The behavioural decisions of organisms often reflect a compromise between avoiding predators and obtaining the resources necessary for survival and reproduction. Frequently, behaviours that reduce the risk of predation also reduce opportunities to forage or find mates (Dill 1987; Lima & Dill 1990; Sih 1994; Lima 1998). In general, organisms show an increased tendency to give up risky feeding opportunities as their perception of risk increases. For example, Dill & Fraser (1984) and Metcalfe *et al.* (1987) found that juvenile salmonids reduced their foraging effort after exposure to a predator. Male tungara frogs increased their escape response to predators—thus, forgoing mating opportunities—as the risk from predatory bats increased (Ryan 1985).

Most previous studies of behavioural decisions under the risk of predation have focused on the behavioural responses to changes in risk that are independent of the time spent at different levels of risk. However, the overall time available for foraging can greatly influence the allocation of effort to foraging and avoiding predators, with greater foraging effort during periods of high risk when the overall time available for foraging is low (McNamara *et al.* 1994). Such an effect has been shown for wintering yellowhammers (Van der Veen 2000). In addition, it has recently been argued that, for a given time period, the proportion of that time in which an organism is subjected to periods of high and low risk is itself an integral factor

influencing its decisions (the ‘predation-risk allocation hypothesis’, Lima & Bednekoff 1999).

Lima & Bednekoff (1999) addressed this issue with a model of an organism’s allocation of time between foraging and anti-predator behaviours that preclude foraging. This decision depends on both the relative levels of risk and the proportion of time the forager is subjected to high-risk situations. The resulting predation-risk allocation hypothesis predicts that when the proportion of time subjected to high predation risk increases, foragers should decrease the proportions of both high- and low-risk periods allocated to anti-predator behaviours. Thus, there should be an increase in the proportions of both high- and low-risk periods spent foraging. Also, unless foragers are already foraging at their maximum effort in low-risk situations, they should decrease their allocation of time to anti-predator behaviours more in those situations than in high-risk situations.

Many tests of the effects of predation risk on behaviour involve animals kept in low (or no)-risk environments that are then exposed to a single pulse of high risk (Abrahams & Dill 1989; Kennedy *et al.* 1994; Grand & Dill 1997). The predation-risk allocation hypothesis predicts that organisms exposed to a single pulse of high risk will show more extreme anti-predator responses than they would under many natural conditions. Therefore, the predation-risk allocation hypothesis is an important, but as yet empirically untested, contribution to the study of decision-making under the risk of predation.

In this study, we tested the predictions of the predation-risk allocation hypothesis using intertidal marine snails (*Littorina* spp.) that were exposed to predation risk in the form of crabs (*Cancer productus* and *Cancer magister*). These snails can avoid predators by leaving the water (Kats &

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Dill 1998) or, possibly, by remaining in their shells. Both of these prevent them from foraging on epilithic algae. The distribution of these snails is possibly influenced by the distribution of *Cancer* spp. crabs, particularly *C. productus* (Behrens Yamada & Boulding 1996). Risk from *Cancer* spp. crabs is spatially and temporally variable because of variation in tide height and movement of crabs among patches (Behrens Yamada & Boulding 1996). Therefore, littorinid snails would be expected to respond flexibly to the risk of predation from crabs, and are suitable organisms for testing this hypothesis.

2. METHODS

We collected snails and crabs from Belcarra Regional Park, British Columbia, on 11 November 2000. Most snails collected were of the *Littorina scutulata* species complex, with smaller numbers from the *Littorina sitkana* species complex. Because of the relatively small number of *L. sitkana*-complex snails, the presence of a number of individuals for which the species complex could not be determined and the existence of cryptic species in each species complex (Mastro *et al.* 1982; Boulding *et al.* 1993), we pooled all snail species for analyses. We do not expect pooling snail species to influence analyses as species complexes were distributed randomly among experimental treatments. Snails were held in a large aquarium until they were used in trials. Before experimental trials, snails were individually marked with either a small, coloured plastic bead attached to their shell by clear fingernail polish (week 1) or with only coloured fingernail polish (weeks 2–4). Crabs were housed individually and separate from the snails.

The experimental chambers consisted of three 120 cm × 20 cm × 20 cm Plexiglas tanks, sectioned by Plexiglas dividers into eight chambers (six of which were used in experiments), measuring 15 cm × 20 cm × 20 cm. There was no water flow between chambers. During experimental trials, six chambers in each tank were filled with seawater to a depth of 16 cm. At the beginning of the trials, crabs were placed into small mesh cages that fitted snugly into the bottom of the chamber. Therefore, crabs were unable to catch snails outside the cage, but snails would nonetheless be exposed to their chemical cues. *Littorina* spp. have been shown to respond to the chemical cues of predators, including crabs (Kats & Dill 1998). An algae-covered rock and a mesh cage, with or without a crab inside, were then placed in each chamber. Crab species and treatment were cross-factored in this experiment.

On the first day of the experiment, 10 individually marked snails were added to each tank by placing them on a Petri dish and gently lowering it onto the mesh cage, with the edge of the dish touching two sides of the chamber. Snails were assigned to dishes randomly with respect to species. We sought to compare the behaviours of snails that spend most of their time in high-risk environments, punctuated by short periods of low risk, with those in the opposite regime. Therefore, snails in three of the chambers were not exposed to crabs for the first 24 h after being placed in the chamber, whereas those in the other treatments were constantly exposed to crabs.

In each tank, chambers were randomly assigned to one of six treatments that varied in the number of hours per day during which snails were exposed to crabs: 0, 2, 6, 18, 22 or 24. Each tank included one chamber of each of these treatments. One tank was used three times, and the others twice, for a total of seven replicates of each treatment over a total of four consecu-

tive weeks. The 2 and 22 h treatments, and 6 and 18 h treatments, were paired such that the empty mesh cage and crab were exchanged twice per day. Starting on the second day of trials, at 10.00 we recorded the location and activity of each snail. All snails, crabs and empty cages were then removed and the chambers drained. Chambers were immediately refilled with seawater, and the cages and crabs for the 0 and 24 h treatments returned to the same chambers. For the other treatments, empty cages and crabs were switched as described above. Snails were then returned to the chambers. The same procedure was repeated at 12.00 for 0, 2, 22 and 24 h treatments. The location of snails in all treatments was also recorded at this time. At 16.00, crabs and water were changed in the 6 and 18 h treatments, and the location of snails in all treatments recorded again. These procedures were repeated for a total of four days. Snails were observed to move out of the dish within several minutes of being returned to the chambers. Therefore, there was equal opportunity for snails to move regardless of the time between observations.

We recorded the number of snails moving (and thus potentially foraging) in each chamber during each observation period, immediately before removing cages in any tank. Each observation period was classified as either 'high risk' or 'low risk' depending on the presence or absence of a crab. For statistical analyses, we only used data from the last two days, after snails had been exposed to temporal variation in risk for two full days.

In analyses, we used the means of the number of snails moving during periods of high and low risk for each chamber. Therefore, each chamber that experienced variation in risk contributed two values (one at high risk and one at low risk). These values were square-root transformed to normalize the distributions (Zar 1984) and were tested with separate general linear models in SAS/STAT (SAS Institute, Inc, Cary, NC, USA). Week and tank were combined into a blocking variable, replicate, which was treated as a random effect. The species of crab was included as a fixed effect, and hours per day spent in the presence of a crab as the covariate. All interactions among these were included in the model and removed if not significant. The differences between low- and high-risk periods were also compared with a similar model. To test for changes in the responses of snails over time, we compared the number of snails moving during high- and low-risk periods between the last two days of the experiment with repeated-measures ANCOVAs.

3. RESULTS

During periods of high risk, there was a significant increase in the mean number of snails moving per observation as the proportion of time they spent in the presence of a crab increased (figure 1a; $F_{1,27}=15.32$, $p < 0.001$). During low-risk periods (i.e. no crab present), this measure was not significantly influenced by the proportion of time spent in the presence of crabs (figure 1b; $F_{1,27}=0.06$, $p > 0.8$). We found the same results if the treatments in which risk was not varied (i.e. 0 and 24 h per day at high risk) were excluded (high risk: $F_{1,19}=12.01$, $p < 0.005$; low risk: $F_{1,19}=1.33$, $p > 0.26$). The difference in the mean number of snails moving in the tank between low- and high-risk periods decreased with increasing time spent in the presence of crabs ($F_{1,19}=8.77$, $p < 0.01$). The species of crab did not significantly influence the number of snails moving in either risk environment (high risk: $F_{1,19}=1.22$, $p > 0.28$; low risk:

Figure 1. Influence of the proportion of time exposed to high risk of predation on the mean number of snails observed moving in the tank during (a) periods of high predation risk, and (b) periods of low predation risk.

$F_{1,19} = 0.001$, $p > 0.98$; difference between high and low risk: $F_{1,19} = 0.87$, $p > 0.36$).

Separating results for the two days, there was not a significant difference between days in the number of snails moving (repeated-measures ANCOVA; low risk: $F_{1,28} = 0.13$, $p > 0.72$; high risk: $F_{1,28} = 0.01$, $p > 0.92$), or the effect of time spent in the presence of crabs on the movement of snails (low risk: $F_{1,28} = 0.2$, $p > 0.66$; high risk: $F_{1,28} = 0.17$, $p > 0.68$).

4. DISCUSSION

To the best of our knowledge, this study provides the first experimental support of Lima & Bednekoff's (1999) prediction that foragers should increase the proportion of time allocated to foraging (versus anti-predator behaviours) in high-risk situations when a greater proportion of time is subject to those situations. There was no influence of the time subjected to high predation risk on the number of snails moving during periods of low risk, leading to a decrease in the difference in response between high- and low-risk periods with increasing time subject to high risk. This is contrary to the predictions of the predation-risk allocation hypothesis if snails can adjust their foraging efforts in both high- and low-risk periods (Lima & Bednekoff 1999). However, if snails always allocated maximum foraging effort in low-risk environments (which would be predicted if the 'attack

ratio' or ratio of risks in high-risk to low-risk treatments were very high), this result conforms to the predation-risk allocation hypothesis (Lima & Bednekoff 1999).

A possible proximate explanation for this result is habituation of snails to the presence of crabs. If this was the case, snails might be expected to move more later in the experiment. Also, the effect of time exposed to high risk should have increased later in the experiment, as the difference in cumulative time spent at high risk increased. However, we did not find a significant effect of observation day on the number of snails moving, or of time spent in the presence of crabs on the number of snails moving.

Many studies of anti-predator behaviour examine the responses of animals to a single pulse of high risk (e.g. Abrahams & Dill 1989; Kennedy *et al.* 1994; Grand & Dill 1997). Lima & Bednekoff (1999) suggested that this protocol would lead to an overestimate of typical investment in anti-predator behaviour. Animals in these situations are able to invest heavily in anti-predator behaviour during rare periods of high risk, whereas animals that are typically exposed to high risk in natural situations cannot afford to do so. Our results provide empirical support for this contention.

In summary, to the best of our knowledge, this study provides the first empirical support for the counterintuitive prediction that foraging will occupy a larger proportion of high-risk periods as the proportion of time subjected to high predation risk increases. We did not find a difference during low-risk periods. Experiments to confirm that the snails could not increase their foraging effort in low-risk periods, as well as with organisms that can adjust their foraging effort in both high- and low-risk periods would further strengthen support for this hypothesis.

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