Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources

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I contrasted the short-term and long-term effects of predation risk on snail habitat use and resource dynamics. Pulmonate snails (Physella gyrina) were placed into experimental pools and exposed to four levels of predation risk while holding their density constant. Periphyton resources were made available in two habitats: open and covered. I hypothesized that a behavioral response by snails to predation risk would influence periphyton standing crop in the open and covered habitats. Snails responded to increasing predation risk by moving into safer (covered) habitats, and the magnitude of their response was sensitive to the actual level of risk. Intermediate levels of risk resulted in intermediate habitat use. However, use of the risky (open) habitat by snails was time dependent. Snails initially responded strongly to predation risk, but they exhibited similar patterns of habitat use at all risk levels by the end of the experiment. Periphyton standing crop was positively related to predation risk. In contrast to snail habitat use, this response was initially weak and became stronger as the experiment progressed. Thus, the short- and long-term responses of snail habitat use and periphyton standing crop contrasted sharply. I suggest that the changing patterns of snail habitat use over time are consistent with the idea that snails balance predation risk against foraging gains when selecting habitats and that the manner in which they balance foraging gains and predation risk determines the pattern of periphyton standing crops across habitats. Key words: habitat selection, indirect effects, induced defenses, periphyton, Physella, predation risk, refuge, trade-offs, trophic cascades. (Behav Ecol 8:120–125 (1997))

Animals often respond to increased predation risk by moving into safer habitats (reviews in Dill, 1987; Lima and Dill, 1990; Sih, 1987). Ecological theory suggests that if animals regulate resource levels within habitats, then predator-mediated habitat selection will eventually result in higher resource levels in more dangerous habitats relative to safer ones (Abrams, 1984; Covich, 1976; Gilliam and Fraser, 1988). These sorts of behavioral indirect effects may be widespread and common (e.g., Koder, 1984; Power, 1984, 1987; Power et al., 1985; Turner and Mittelbach, 1990), but the data to assess their importance in ecological communities are meager (Werner, 1992).

The freshwater snail, Physella gyrina, is usually found under cover in lakes containing the molluscivorous pumpkinseed sunfish (Lepomis gibbosus), whereas in lakes lacking pumpkinseeds, Physella use exposed substrates (Turner, 1996). Experiments showed that Physella offered covered substrates are safer from pumpkinseed predation than are Physella offered only exposed substrates, and the presence of pumpkinseeds causes Physella to move into safer (covered) habitats (Turner, 1996). Because Physella are known to depress resource levels in habitats in which they graze (Lowe and Hunter, 1988), I hypothesized that the predator-induced habitat shift will allow periphyton to increase in abundance in dangerous habitats (Turner, 1996). Here I present the results of an experiment in which I tested this prediction by stocking Physella into experimental pools containing periphyton resources in dangerous and safe habitats. I then imposed four levels of simulated mortality and monitored both the habitat use of the snails and the response of periphyton.

Predictions regarding the short-term effects of predation risk on the habitat use of foragers are clear: if habitats are otherwise of equal value, foragers should use the safest habitats available. Over time, however, foragers may deplete resources in safe habitats, they may deplete their energy reserves (McNamara and Houston, 1987), or they may face time constraints (Ludwig and Rowe, 1990; Werner and Anholt, 1993). The forager may then choose to use more dangerous habitats containing abundant resources (Gilliam and Fraser, 1987, 1988; McNamara and Houston, 1994). Thus, optimal habitat use can change over time (Mangel and Clark, 1988). There have been few experimental manipulations of predation risk on foragers dynamically interacting with their resources. A goal of this study was to contrast the short-term and long-term effects of predation risk on forager habitat use and resource dynamics.

METHODS

I carried out this experiment in 16 circular polyethylene wading pools, each containing 270 l of water (20 cm deep × 1.5 m diam). In late July the pools were placed outdoors at the Kellogg Biological Station in a 4 × 4 grid and filled with unchlorinated well water (alkalinity equivalent to CaCO₃ concentration > 100 mg/l). Each pool contained a 31 × 31 cm unglazed ceramic tile raised off the bottom by four legs 5.5 cm tall. These tiles were designed to mimic natural refuges from predators and were placed into the middle of the pools, where they covered 4% of the 2.15 m² of substrate available to the snails. Thus, each pool was composed of two habitats: a small refuge and a large, dangerous area. Twelve adult Physella gyrina were stocked into each pool on 27 July (mean shell length = 9.9 mm, mean dry mass excluding shell material = 10.06 mg). I collected the snails from dense aggregations (>100/m²) in shallow littoral areas (<10 cm deep) of nearby
Middle Crooked Lake and selected them to be similar in size (coefficient of variation in length = 5%).

I simulated four levels of mortality on snails in the experimental pools by adding four doses of crushed conspecifics: 0, 0.25, 1, or 4 snails daily. Physalla responds behaviorally to chemical cues released into the environment by crushed conspecifics, regardless of whether the snails are crushed by a natural predator (a pumpkinseed sunfish) or by the experimenter (Turner, 1996). The appropriate number of snails were placed into each pool and immediately crushed by hand. The crushed snails were of the same size and from the same population as the resident snails. I employed this design, rather than imposing mortality on a given number of snails in each pool and then replacing them with similar-sized conspecifics, because it maintained a constant level of experience among the snails in a pool. The 0.25/day mortality treatment was accomplished by adding a single crushed snail on day 1 and every 4 days thereafter. The mortality treatments were imposed daily in mid-afternoon.

I evaluated the effect of variation in snail habitat use on resources by measuring periphyton standing crop on a pair of ceramic tiles in each pool: one under the refuge and one in the open. Small tiles (15.2 cm on a side) were first incubated for 10 days in an outdoor recirculating artificial stream system. Periphyton quickly grew on tiles in the stream, reaching a mean standing crop of 3.75 ± 1.55 mg/cm² (mean ash-free dry weight ± SE, n = 4 samples) after 10 days. Two randomly selected tiles were transferred to each experimental pool (one in each habitat) on 28 July, one day after the introduction of snails. The periphyton community on the tiles was dominated by highly edible taxa: the filamentous overstorey was primarily composed of Oedogonium spp., and common prostrate forms were the chlorophytes Ankistrodesmus, Chlorella, and Cyclotella, and the diatom Navicula. I estimated periphyton standing crop on each tile over the course of the experiment by measuring ash-free dry weight (AFDW) 2, 4, and 14 days after the tiles were introduced to the pools. Periphyton was scraped from a strip 8.75 cm wide, and running the width of the tile (13.5 cm²), rinsed onto a Whatman GF/F glass fiber filter, was dried at 60°C for 24 h, weighed, ashed at 500°C, and reweighed.

Snail habitat use was censused in the mid-afternoon of each day, immediately before the daily mortality treatments were imposed. I recorded the number of snails under the refuge, the number in the open, and the number feeding on periphyton on the small ceramic tiles in each habitat. For each pool I estimated the probability that an individual snail would use the open habitat (hereafter referred to as, "open habitat use") by dividing the number of snails observed in the open by the total number censused. At the end of 14 days I collected, counted, and measured the shell length of the surviving snails. Lengths were converted into dry masses, excluding shell material, using the following length-weight relation: Physalla dry mass (mg) = 0.014 (shell length (mm))².46 (p < .06, N < .01, n = 191).

I analyzed the effect of simulated mortality on snail habitat use and periphyton abundance using linear regression analyses (n = 16 points for all analyses). I applied a log (x + 0.1) transformation to the four levels of mortality (0, 0.25, 1, and 4 snails/pool/day) to linearize the relationships and to equalize the influence of all four levels. Inspection of the residuals confirmed that there was no apparent curvilinearity. This analysis tests the hypothesis that there is a monotonic relationship between simulated mortality and the dependent variable under consideration (slope equal to zero was used as the null hypothesis of no treatment effect). For clarity of presentation, figures show mortality as categorical data.

RESULTS

Snail survivorship averaged 91% and was not related to the level of simulated mortality (p > .10). Because there were no treatment effects on snail densities, I was able to examine the consequences of variation in snail habitat use without any confounding differences in snail density (i.e., behavioral indirect effects, Miller and Kerfoot, 1987).

Predation risk had a negative effect on the growth of Physalla (Figure 1). Growth of Physalla declined with increasing mortality rate (p < .01). There were no effects of mortality rate on the within-pool variance in snail size at the end of the experiment (p > .10).

When averaged over the entire experiment, increasing predation risk had a negative effect on use of the open habitat by Physalla and a positive effect on periphyton abundance in the open habitat (Figure 2; open habitat use p < .05, periphyton standing crop p < .01). Periphyton standing crop in the refuge was much lower than in the open, and there was no effect of mortality on periphyton in the refuge (Figure 2; p > .10). Snail habitat use did not show a threshold response to increasing predation. Instead, each successively higher level of mortality resulted in a correspondingly lower use of the open habitat (Figure 2).

The overall effects of increasing mortality were to decrease open habitat use and increase periphyton standing crop, but these responses were time dependent. Physalla habitat use initially responded strongly to the mortality treatments but was indifferent to mortality at the end of the experiment (Figure 3; early mortality effect p < .01, late mortality effect p > .10). Conversely, periphyton standing crop in the open habitat initially showed no treatment effects but showed a strong, positive relationship with mortality at the end of the experiment (Figure 3; early mortality effect p > .10, late mortality effect p < .01). Periphyton standing crop in the refuge did not show any treatment effects either early or late in the experiment.
relationship between mortality and "snapshots" of habitat use. I used the F ratio of regression analyses (F, slope = 0) performed on the relationship between mortality and "snapshot" of habitat use (2-day means, n = 7) and open-water periphyton (n = 3 sample dates) as an index of the strength of response (Cohen, 1988). Figure 4 shows that while both habitat use and periphyton responded to predation risk, their responses differed through time. In fact, at no point during the experiment did both habitat use and periphyton simultaneously show significant responses to predation risk. Instead, the responses mirror one another (Figure 4). Thus, snail habitat use and periphyton standing crop responded in opposite directions and at different times to the risk of mortality.

DISCUSSION

This experiment demonstrates that predation risk can change Physella refuge use as well as periphyton standing crop. Physella refuge use and periphyton standing crop were positively related to the level of risk. However, the effects of predation risk on Physella habitat use and periphyton standing crop were not concurrent: behavioral effects were strongest early in the experiment, and the periphyton abundance effects were strongest later in the experiment.

The strong interactions among snails, their predators, and their resources have been documented by several investigators (Brönmark et al., 1992; Lodge et al., 1994; Osenberg, 1988, 1989), but these studies focused on the numerical interactions among trophic levels. Here I have shown that predators can have the same effect by changing prey behavior. The overall pattern of predator density (risk), Physella habitat use, and periphyton standing crop showed the pattern of negative correlations between adjacent trophic levels typical of consumer control; however, this pattern was mediated completely by behavior. These results have important implications for the interpretation of predator manipulations: behavioral mechanisms may be as important or more important than mortality mechanisms in mediating the effects of top predators on lower trophic levels.

Physella increased their use of dangerous habitats as the experiment progressed, demonstrating that habitat use can be a dynamic process. Various adaptive and nonadaptive processes could conceivably generate dynamic habitat use patterns. Perhaps the most straightforward explanation for increased risk-taking over time is that changes in the state of the snails lead to altered decisions rules (Ludwig and Rowe, 1990; Mangel and Clark, 1986, 1988; McFarland, 1977; McNamara and Houston, 1986). For example, large Physella have thicker shells and are less vulnerable to predators than small Physella (Turner A, unpublished data). Because Physella grow substantially in the present experiment (Figure 1), their increased use of open habitats over time (Figure 3, early versus late) may reflect their lower vulnerability to predators (Werner and Anholt, 1993). Alternatively, Physella may have depleted their energy reserves during the initial move into the refuge (e.g., Lima, 1985, 1986), or they may face seasonal constraints on the time available to grow and reproduce (e.g., Murie and Boag, 1984; Semlitsch et al., 1988; Tauber et al., 1986). In either case, theory predicts increased use of risky habitats and the higher resources levels found there (Ludwig and Rowe, 1990, McNamara and Houston, 1987; Werner and Anholt, 1995). Clearly, experimental manipulations of the various aspects of an animal’s state are necessary to determine which factors influence behavioral strategies.

While changes in Physella’s decision rules due to growth, starvation, or time constraints can account for changes in habitat use, these are not the only possible explanations. A time-invariant decision rule can also produce dynamic habitat use if the environment changes. Physella changed their environment by depleting periphyton in the refuge to low levels (Figure 3). High refuge use by Physella early in the experiment was expected because the refuge will initially offer foraging returns equal to the open habitat, as well as a lower risk of predation (Fretwell, 1972; Fretwell and Lucas, 1970). At some
point, however, resources in the dangerous habitat may become sufficiently abundant (relative to resources in the refuge) to offset the higher risk of mortality, and foragers may choose to move back out into the dangerous habitats, trading a higher risk of predation for higher foraging rates (Abrahams and Dill, 1989; Gilliam and Fraser, 1987; Nonacs and Dill, 1990; Todd and Cowie, 1990). Thus, given sufficient divergence of resources and the existence of foraging rate/predation risk trade-offs, static optimization theory predicts that short-term behavioral responses to predation risk will be stronger than long-term behavioral responses. Conversely, the indirect effects of risk on resources would not be immediately manifested, but are predicted to develop as resources are differentially depleted. Resource levels in dangerous and safe habitats should then be maintained at some constant level of difference by foragers, reflecting the relative risk of the two habitats (Abrams, 1984; Gilliam and Fraser, 1988). The temporal pattern of Physella habitat use, the temporal pattern of periphyton abundance, and the relatively high periphyton levels in dangerous habitats are all consistent with these predictions.

The divergence in resource levels between dangerous and safe habitats presumably occurs through the differential grazing and growth of periphyton in risky and safe habitats. Because the length of time needed for resources to diverge sufficiently to offset the higher level of risk in the dangerous habitat depends on the degree of divergence, the length of the transition period (the period during which animals use only the refuge) should be related to the magnitude of danger (McNamara and Houston, 1987). I found that Physella increased their use of the dangerous habitat over time in all treatments, but shifted to using the dangerous habitat sooner

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Figure 3
Snapshots of snail habitat use (top) and periphyton standing crop (bottom) in relation to risk of mortality early and late in the experiment. (Top row) A 2-day-wide window of habitat use immediately before the first and last periphyton sampling dates (days 3 and 14); e.g., “early” is the mean proportion of snails using the open habitat during days 2 and 3. Refuge use is equal to 1 - (open habitat use). (Bottom row) The ash-free dry weight of periphyton on day 3 (early) and on day 14 (late). Circles are the standing crop of periphyton in the open habitat; squares are the standing crop of periphyton in the refuge.
at lower levels of risk (Figure 5). The overall pattern of *Physella* habitat use and periphyton abundance suggests that the snails depleted resources in the two habitats to the point that the dangerous and safe habitats were of equal value to individual foragers, although it took longer for the habitats to equalize at the highest level of risk.

I have argued that the increase in periphyton standing crop in the open habitat in high-mortality treatments is due to a reduction in snail foraging. An alternative explanation is that crushing snails increased nutrient input and thereby increased periphyton abundance. Several lines of evidence argue against this alternative. First, snail growth was negatively related to mortality level (Figure 1), which is consistent with the idea that differences in snail grazing are responsible for the positive relationship between risk of mortality and periphyton abundance in the open habitat. Lower snail growth at high levels of risk reflect lower average feeding rates and coincides with higher periphyton standing crop. Second, several studies have shown that freshwater snails, including *Physella*, control the abundance of their periphyton resources (Brönmark, 1989; Doremus and Harman, 1977; Lowe and Hunter, 1988; Osenberg, 1989). In this experiment, *Physella* spent 45% of their time grazing on the two tile substrates, even though the two tiles made up just 2% of the available substrate. Such an intense concentration of snail foraging activity on the tiles lends support to the notion that *Physella* interacted strongly with their periphyton resources. Finally, if nutrient input and not snail grazing was the predominant factor affecting periphyton standing crop, one might expect to see a positive relationship between mortality level and periphyton abundance in the refuge habitat. I found no relationship between mortality level and periphyton abundance in the refuge, although other factors (e.g., reduced light levels) may have limited periphyton growth in the refuge habitat.

**CONCLUSIONS**

The behavioral decisions made by individual animals may have repercussions that are felt at lower trophic levels and then rebound up the food web and affect future behavioral decisions. *Physella*, like many other animals, readily alter their behavior in response to changing factors in the environment (e.g., predation risk or food availability). Changes in behavior are transmitted to resources, creating the potential for an array of complex, indirect effects. An accumulating body of empirical evidence suggests that induced behavioral responses of animals to food or predators play an important role in determining the nature and strength of species interactions (e.g., Carpenter and Kitchell, 1993; Huang and Sih, 1991; Hundy, 1987; Koder et al., 1991; Power et al., 1988; Turner and Mittelbach, 1990; Werner and Anholt, 1996; Werner et al., 1983). Only further empirical work in which the effects of behavior are clearly isolated from other effects will establish whether induced behavioral responses are of general importance in shaping communities.

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