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INTERACTION BETWEEN FOOD AVAILABILITY AND
PREDATION MORTALITY MEDIATED BY
ADAPTIVE BEHAVIOR

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Abstract. Increased activity rates in larval anurans are associated with both higher growth rates and higher predation mortality. Models of adaptive foraging behavior in the face of predation risk predict that at higher resource levels, foraging activity should be reduced. Thus, at higher resource levels predation mortality should also be reduced. We manipulated the resources available to Rana catesbeiana tadpoles and then measured the activity of tadpoles in the presence of caged dragonfly larvae and the mortality rate of the tadpoles when the dragonflies were free to forage. At low food levels the tadpoles moved more often and more quickly. Similarly, at low food levels the tadpoles suffered higher predation mortality. The dependence of predation mortality on resources available to prey underlines the futility of characterizing population regulation as being due to predation or resources. Adaptive variation in behavior responds to both pressures simultaneously. These results also suggest the possibility that adaptive variation in behavior may lead to density-dependent population regulation. Density-dependent depletion of resources by prey should lead to increased activity levels, which will result in higher per capita predation rates. The generality of the trade-off between growth rate and mortality rate argues that this mechanism may be widespread. If adaptive variation in behavior is as widespread as it appears, incorporating this variation into population dynamic modelling may improve our ability to predict the outcome of interactions within ecological communities.

Key words: antipredator behavior; behavioral indirect effects; density dependence; growth-rate-mortality-rate trade-offs; interaction modification; population regulation; Rana catesbeiana; Tramea lacerata.

INTRODUCTION

Many animals must actively search for their food. The faster an animal searches, or the more time spent searching, the more likely it is to encounter food items. However, both of these components of activity will also increase an animal’s encounter rate with predators (Gerritsen and Strickler 1977). Prey movement can also enhance prey detection by some predators (Curio 1976, Taylor 1984). Thus acquiring resources to produce additional offspring decreases the probability of surviving long enough to realize the production of those offspring.

This trade-off is particularly clear in larval anurans (tadpoles). Tadpoles feed by scraping attached algae and detritus or filtering suspended particles while swimming (Seale and Wassersug 1979, Wassersug and Hoff 1979). More active tadpoles grow faster and are often better competitors both interspecifically (Woodward 1982, Morin 1983, Lawler 1989, Werner 1991, 1992a) and intraspecifically (Skelly and Werner 1990). However, more active tadpoles also appear to be more vulnerable to their invertebrate predators (interspecific: Lawler 1989, Azevedo-Ramos et al. 1992; intraspecific: Skelly 1994).

Because reproduction and survival, the two components of Darwinian fitness, are both functions of activity, an adaptive resolution of the trade-off can be proposed in terms of activity. Models that incorporate risk of mortality as a trade-off with resource acquisition (McNamara and Houston 1987, 1994, Abrams 1993, Werner and Anholt 1993) predict reduced activity when mortality risk increases. Considerable empirical evidence exists to support this prediction (reviewed in Sih 1987, Lima and Dill 1990). Rarely tested, though, is the prediction that foraging activity should also be lower at high food levels (McNamara and Houston 1987, 1994, Abrams 1993, Werner and Anholt 1993) when high food levels are not transient (McNamara and Houston 1994). There is considerable empirical evidence for this prediction as well (reviewed in Werner and Anholt 1993). This prediction stands in contrast to the case where mortality risk is independent of foraging activity. When this is the case, foraging effort should increase at higher resource levels (Norberg 1981, Dunbrack and Giguere 1987, McNamara and Houston 1994a).
Therefore, changes in behavior with food level provide a critical test between situations where mortality risk is a function of foraging effort and those where it is not.

If the trade-off between food acquisition and mortality is indeed mediated by foraging activity, we should also be able to demonstrate that increased food level leads to a decreased predation mortality rate because activity has been reduced at the higher resource level.

In this study we measured the activity of larval anurans (bullfrog tadpoles, *Rana catesbeiana*) at different resource levels when caged larval dragonflies (*Tramea lacerata*) were present. In a parallel experiment we tested whether these changes in behavior affected the tadpoles’ mortality rate when the predators were not caged. We predicted that experimentally decreasing food levels would cause bullfrog tadpoles to increase their foraging activity and, as a consequence, mortality due to predation would also increase.

**METHODS**

We conducted separate experiments to measure (1) the effect of resource levels on tadpole activity and (2) the mortality due to predators at these food levels. Ideally, we would have preferred to measure activity in the containers where predators were actively foraging, because activity level might be influenced by the size of the container (e.g., Tang and Boisclair 1993, McLaughlin et al. 1994). However, because of the number of tanks, the disturbance inherent in moving the cameras between tanks, and the structure in the tanks obscuring animals from view, this was not logistically possible.

**Measurement of activity**

We recorded the activity of tadpoles on videotape in the laboratory. Eight plastic containers (37.5 cm x 24.1 cm) were filled to 7 cm depth with well water. Each container had 12 bullfrog tadpoles (\(\bar{X} \pm 1\) std: 14.6 ± 2.4 mg; Gosner [1960] stage 25) and one caged dragonfly larvae (instar F-2) that had recently eaten a bullfrog tadpole. Cylindrical dragonfly cages (7.5 cm long \(\times\) 2.8 cm wide) were made of aluminum wire and plastic mesh with an inner sleeve of fiberglass window screening. It was essential to have dragonflies present because bullfrog tadpoles reduce their activity in the presence of predators (Werner 1991). We provided the tadpoles pulverized Purina Rabbit Chow at either low (0.68 g/m\(^2\)) or high (13.7 g/m\(^2\)) food rations at the beginning of the experiment. Each treatment had four replicates.

After allowing 24 h acclimation to the experimental conditions, the containers were filmed on 5 August 1992 using four cameras on rotating timers which were permanently fixed in position. Cameras were turned on remotely 30 min after starting the videotape in order to reduce the effect of any disturbance that might occur by initiating the filming sequence. Containers were filmed in pairs for 10 min at a time, in four bouts equally spaced over 135 min. Cameras were turned on and off using automatic timers. The containers were undisturbed is a closed room during the entire filming sequence. There were no detectable differences in behavior between the beginning and end of the filming.

Proportion of time active and movement speed in each container were estimated from pairs of digitized video images separated by 2 s. If the difference in location between images was within the ability of the operator to relocate a stationary point (<0.175 cm/s), the animal was deemed to have not moved. This accounts for the vast majority of feeding movements, as well as for all of the other movements in the containers. More than 80 changes in location were measured for each container by a technician unaware of the hypotheses being tested. This was enough to stabilize the mean and variance of the estimates of the proportion of animals swimming and the speed of swimming animals within each tank. Measurements of displacement from the entire 40 min of filming were combined for a single estimate of the proportion of time animals spent moving and the mean speed of movement in each experimental container. Thus, the sample size was four for each treatment. Proportion of time active was analyzed using GLIM (version 3.77) with binomial errors and the logit link function. Changes in deviance (analogous to sums of squares) in this analysis are approximately chi-square distributed with degrees of freedom equal to treatment degrees of freedom (McCullagh and Nelder 1983, Crawley 1993). The mean speed while swimming was analyzed using GLIM with normally distributed errors and the identity link.

**Mortality costs**

The effect of food level on predation mortality was measured in covered circular wading pools (0.73 m\(^2\)) \(\approx 8\) times the size of the containers where behavior of the tadpoles was filmed. Each wading pool was filled with 75 L of untreated well water and contained 48 m of weighted polypropylene rope for additional surface area. Ten randomly chosen wading pools received the same low food level (0.68 g/m\(^2\)) as in the filming experiment, and 10 wading pools received the high food level (13.7 g/m\(^2\)). One hundred bullfrog larvae and five caged dragonfly larvae of the same size as that used in the activity experiments were added to each pool with the food on 22 July 1992. The density of bullfrog larvae was the same as that in the filming experiment, while the density of dragonfly larvae was slightly lower than that in the filming experiment. After 24 h of acclimation to the experimental conditions, dragonfly larvae were released from their cages to begin foraging. Dragonfly larvae were removed from the wading pools 48 h later, and surviving bullfrog larvae counted. All of the mortality was ascribed to predation because no mortality occurred under identical resource levels in
FIG. 1. (A) Percentage (± 1 se, n = 4 for each treatment) of observations where animals were active in the presence of caged predators at high and low food levels. (B) The mean speed of movement (± 1 se, n = 4 for each treatment) of active animals in the presence of caged predators at high and low food levels. (C) Percentage (± 1 se, n = 20 for each treatment) predation mortality in the presence of uncaged predators at high and low food levels.

the filming experiment when caged predators were present. Proportion of animals disappearing was analyzed in GLIM using binomial errors and the logit link function.

RESULTS

The results were as predicted. Bullfrog tadpoles were active 47.3 ± 7.6% (X ± 1 se) of the time at the low food level but only 30.7 ± 4.7% at the high food level (χ² = 19.9; P < 0.01; Fig. 1A). When active at the low food level, tadpoles swam at 1.77 ± 0.08 cm/s (X ± 1 se) but only 1.21 ± 0.16 cm/s at the high food level (tₙ = 3.63; P = 0.011; Fig. 1B).

Mortality was also higher at the low food level 46.5 ± 2.35% (X ± 1 se) compared to the high food level 29 ± 2.48%, with almost no overlap in the distributions (χ² = 65.6; P < 0.0001; GLIM with binomial errors; Fig. 1C).

DISCUSSION

At high food levels, tadpoles moved less often and when they did move, they moved more slowly than at low food levels. Because the tadpoles were moving more slowly and less frequently they should also be less likely to encounter a predator that would be expected to lead to lower predation mortality. Our observations of reduced mortality at higher food levels is consistent with this interpretation that there is a mortality cost associated with activity. It is also consistent with observations by Skelly (1994) that hyloid tadpoles with pharmacologically reduced activity rates also had reduced mortality rates.

Our results were as predicted by models of adaptive variation of behavior when additional effort expended on resource acquisition increases the probability of predation mortality. Models of resource acquisition where additional effort does not affect predation mortality predict higher activity at higher resource levels (McNamara and Houston 1994). Apparently, the animals are striking some balance between resource gain and the risk of mortality. It is not possible to determine whether the level of activity is consistent with the quantitative predictions of Werner and Anholt (1993) for two reasons. (1) Theory has been restricted to a single antipredator response, either proportion of time active or movement speed. When both responses are present, current theory is inadequate. (2) The exact predictions depend on how resource acquisition and mortality vary with activity (both movement frequency and speed). A strong quantitative test of these models will require measurement of the underlying functions and development of theory that encompasses multiple responses of prey to predators.

Our observation that predation mortality changes as a function of food availability agrees with the suggestion of McNamara and Houston (1987) that it is futile to try to categorize populations as being regulated by predators or food. Animals adjust their behavior to changes in their environment in ways that affect both predation risk and resource acquisition. Werner and Anholt (1995) also found that these two factors could not be separated. In that study, an increased density of caged predators led to higher starvation mortality in vulnerable size classes of tadpoles.

The predicted higher activity rate at lower resource densities (Abrams 1993, Werner and Anholt 1993) demonstrated in this study and the consequent increase in predation rate presents a novel mechanism for density-dependent patterns of mortality. Tadpoles are strong exploitative competitors, and have often been shown to be capable of depleting their food (Woodward 1982, Morin 1983, Wilbur 1987, Lawler 1989, Werner 1991). Our experiments demonstrate that depletion of food will lead to higher activity rates by the tadpoles in their search for food and that higher activity rates can lead to higher mortality due to predation. The fre-
quent observation of a trade-off between growth and mortality (Sih 1987, Lima and Dill 1990) mediated by activity argues strongly that this form of density-dependent population regulation may be widespread.

Much of the history of population ecology has been a search for the causes of density dependence (Sinclair 1989). In predator–prey systems the focus has been on variation in the behavior of the predator. For example, high prey density has been suggested to facilitate learning by the predator, or cause the predator to restrict its search to concentrations of prey (Curio 1976, Taylor 1984). These mechanisms can lead to density-dependent predation, which will tend to stabilize population dynamics. However, none of these mechanisms is as general as adaptive variation of foraging behavior of prey in its ability to generate density-dependent mortality of prey. Changes in activity as a function of food availability applies equally well to situations where the predator cannot learn, or where the predator does not search. Moreover, because adaptive variation in behavior acts without the time delay inherent in many other forms of density dependence, it is likely to be highly stabilizing in its effect (May 1981).

Adaptive variation in behavior has long been thought to affect population dynamics and equilibrium population sizes because, by definition, it affects birth and death rates (Partridge and Green 1985). Theoretical investigations (Abrams 1984, 1991, 1992) have shown that the indirect effects due to adaptive variation in behavior can be stronger than the direct effects of mortality. Models of food-web interactions that do not incorporate this variation may well fail to capture the essential behavior of these systems (Abrams 1991, 1992, Wootton 1992b, Wootton 1993, 1994).

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