

Effects of predators on prey growth rate: relative contributions of thinning and reduced activity

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Predators affect individual growth rates of surviving prey in two conflicting ways. First, predation acts to increase growth rate by thinning the density of prey populations, which releases survivors from competition. At the same time, predators intimidate prey into decreasing their feeding activity and increasing refuge use, causing prey to grow more slowly. Both processes are known to affect individual growth rates in many systems, but their relative importances and interactive effects have not been measured. We designed an experiment to estimate the separate and joint effects of thinning and activity suppression, using *Rana sylvatica* tadpoles reared in 1100-L outdoor artificial ponds. The experiment manipulated the perceived risk of predation (using caged *Anax* dragonfly larvae) independently from the loss rate (by manually removing tadpoles every other day according to a predetermined "mortality schedule"). The presence of predators caused tadpoles to decrease time spent feeding and swimming, verifying that the conditions for behaviorally-mediated growth suppression were satisfied. During the first half of the experiment, when tadpoles were small and not yet competing for food, growth declined sharply with predation risk but was unaffected by thinning. During the second half of the experiment, when tadpoles were much larger and had presumably depleted food resources, growth rate increased under thinning but was unaffected by predation risk. Overall, there was an interaction among treatments because activity suppression was only important at low density, while thinning was especially important in the absence of predation risk. Our results suggest that the numerical effects of predators on prey will predominate in communities composed of strongly interacting species with resource depletion (e.g., communities with clear keystone predator effects), whereas growth costs of predator avoidance may quantitatively affect species interactions in communities with less severe exploitative competition.

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Ecological studies of predation usually focus on direct numerical impacts of predators on prey species, because it has long been recognized that predators can shift community composition by selectively targeting particular prey (Paine 1966, Morin 1983, Hurd and Eisenberg 1990, Wooster 1994). But the community response to predators is not always clear from species differences in vulnerability, due to several processes with potentially conflicting influences, including indirect effects propa-

gated through the foodweb, costly behavioral responses of prey to predators, and direct numerical effects of mortality. One way to address this problem is to first develop a framework for understanding the different mechanisms by which predation affects individuals within a single prey population, and then apply that framework to the performance of species within communities. Here we report an experiment that addresses the first stage of this approach, and we argue that the

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results will be applicable within multi-species communities.

Without question, the impact of predators on the fitness of victims that are killed is catastrophic, but their influence on the performance of individuals that survive is less clear. Predators lower prey density by killing members of the prey population, which can improve the growth rate of survivors by reducing competition (Ullyett 1950, Slobodkin 1962, Morin 1983, Wilbur 1988). At the same time, predators decrease the foraging activity or increase refuge use of surviving prey, which has the effect of reducing their growth (Sih 1987, Lima and Dill 1990, Kotler et al. 1991, Diehl and Eklöv 1995). These two mechanisms, which we will refer to as thinning and activity suppression, potentially act in opposite directions on the growth rate of individuals within a single prey population.

Single-species models of foraging under predation risk indicate that both mechanisms could be quantitatively important, and could influence life history evolution and population dynamics (Ives and Dobson 1987, Abrams 1992, Abrams and Rowe 1996, Abrams et al. 1996). For example, Abrams and Rowe (1996) have shown that the optimal growth rates of prey can either increase or decrease when the threat of predators and predator-induced mortality rates increase. The uncertain impact of predation results from conditions that are widespread within animal predator-prey systems: enhanced growth by the prey is obtained at the price of increased mortality, and there is density-dependent feedback between the prey and its food supply. Abrams and Rowe note that the relative importance of the two mechanisms probably varies among systems and is not easily generalizable. What is needed are empirical studies that measure separately the growth responses of prey to thinning and activity suppression, in order to estimate their relative magnitudes under well-defined conditions.

The empirical separation of thinning and activity suppression is problematic because the two operate simultaneously in most natural situations. Predators that impose mortality upon prey are usually detectable to prey individuals and stimulate predator-avoidance behavior in the survivors. This is particularly true for aquatic habitats in which chemical cues signal the proximity of predators (Dodson 1989), but behavioral avoidance of predators is widespread in terrestrial habitats as well (Lima and Dill 1990, Kotler et al. 1991). Likewise, chemical or visual signals indicating the proximity of predators are very often accompanied by actual predation, so individuals that behaviorally respond to predators also experience declining densities of competitors (Wilbur 1988). Good examples in which both processes operate at once are known in freshwater fish: small species or size classes invariably decrease activity or switch to less risky habitats in the presence of piscivorous species, and at the same time predators

decrease the densities of small species (Werner et al. 1983, Fraser and Gilliam 1992, Tonn et al. 1992, Diehl and Eklöv 1995). The fact that predators do not consistently either enhance or suppress growth rates of small fish (Diehl and Eklöv 1995) suggests that the net effect of thinning and feeding suppression may be variable in this system.

Our study was designed to manipulate the perception of predation risk independently from mortality rate, to estimate their separate and combined influences on the growth of surviving individuals. We chose to study tadpole populations in experimental ponds because we could easily manipulate both perception of risk and loss rate. The system captures some general features of predator-prey systems, including behavioral avoidance of predators by prey (McCollum and Van Buskirk 1996), density dependence in prey (Wilbur 1987), and feedback between prey and their resources (Leibold and Wilbur 1992). We controlled the loss rate by manually removing individuals from certain treatments according to a pre-determined "mortality schedule". Perception of risk was evoked without permitting predators to kill prey by presenting prey populations with chemical stimuli associated with caged dragonfly larvae, which have been shown previously to reduce anuran activity (Skelly and Werner 1990, McCollum and Van Buskirk 1996). In this way, we estimated the directions and relative magnitudes of the effects of thinning and activity suppression on prey growth, with a focus on determining whether the two processes act independently.

We predict that the impacts of thinning and activity suppression on growth rate will depend on the degree and kind of competition within the prey population. For example, if the prey do not engage in competition (i.e., they have no impact on their food supply and do not interact with one another), then the rate of food consumption will depend only on the amount of time spent foraging. If predation risk causes a fixed reduction in foraging activity, then food intake (and hence growth rate) will decrease with perceived predation risk. Growth will not respond to thinning in the absence of competition because food availability and intake rate are not influenced by density.

If prey engage in pure interference competition, we expect both thinning and activity suppression to influence growth rate, with no interaction between the two. The effect of density arises because crowded individuals reduce the amount of time they can devote to feeding (e.g., due to distraction, increased time spent avoiding conspecifics, or increased investment in territory defense), although they do not appreciably affect food availability. The effect of activity suppression arises, as before, because inactive prey spend less time feeding and therefore grow more slowly. Since resources are not depleted by pure interference competition, there is no possibility for density-mediated and activity-mediated responses to influence one another through their joint

impacts on food level. Under interference, then, we predict that the proportional effects of thinning and perceived risk on growth will be independent (i.e., they combine multiplicatively).

In the case of pure exploitative competition (prey compete only by depleting the food supply), we expect that activity suppression and thinning will interact in their effects on growth. Under exploitation the rate of food intake does not always increase with increasing foraging effort, especially at high density. This is because resources become depleted at high levels of either feeding activity or density, so an individual's foraging time is increasingly expended locating scarce resources or grazing on sites that have recently been exploited. In this case a behavioral response to predators entails a high growth cost at low density when resources are abundant, but not at high density when few resources are available anyway. Under this scenario, the behavioral and numerical effects of predators can influence each other because they both impact food availability, and so are indirectly connected. With pure exploitative competition, therefore, we expect an interaction between perceived predation risk and thinning. The models mentioned above (e.g., Ives and Dobson 1987, Abrams and Rowe 1996) assume that prey engage in exploitative competition.

These alternative scenarios represent extreme characterizations, of course, whereas real systems might exhibit different degrees and combinations of interaction. But they do provide a set of contrasting predictions with which our results can be compared. Independently manipulating prey thinning rate and perceived predation risk enables us to assess several of the relationships described above. First, we ask whether the activity of prey declines in response to predation threat, and whether the response is independent of density. Second, we ask whether individual growth rate increases in response to thinning, as occurs under both kinds of competition. We also focus on how predation risk and thinning regime combine to determine growth rate, to gain insight into mechanisms of interaction among individuals. Finally, our results allow us to predict what conditions tend to influence the net outcome of thinning and activity suppression, and anticipate the kinds of communities in which one or the other effect will predominate.

Methods

The experimental design included two levels of predation risk crossed with three levels of thinning, in a 2×3 complete factorial design with four replicates. We included three thinning regimes in order to bracket a range of mortality rates that could be imposed by predators, and we used a factorial design because we

were interested in the interaction between predation risk and thinning. Experimental units were black polyethylene stock tanks filled with well water to a depth of 41 cm (1100 L volume, 2.6 m² surface area). Each tank contained 0.5 kg oak leaf litter and 25 g commercial rabbit chow to provide structural heterogeneity and nutrients to support the growth of bacteria and algae. We introduced pelagic phytoplankton and herbivores to the tanks with a 2.0-L inoculation of water and two well-randomized collections of zooplankton taken from nearby ponds. The tanks were fitted with screen lids constructed of 60% shade cloth to prevent unwanted colonization by insects and amphibians, and arranged 0.8 m apart in a hexagonal array at the University of Michigan's E.S. George Reserve in southeastern Michigan, USA. The four experimental blocks were assigned on the basis of spatial proximity within this array.

Perceived predation risk was manipulated by introducing 0 or 3 larval *Anax junius* or *A. longipes* dragonflies within cages suspended in each tank: the *Anax* treatment contained three dragonflies in the final two instars, and the no-*Anax* treatment contained three empty cages. Cages were constructed of plastic drain pipe (11 cm long by 12 cm in diameter) with fiberglass window screening over the ends to permit movement of water and chemical signals. Dragonflies were fed 6–10 *R. sylvatica* tadpoles every other day throughout the experiment, the number depending on the size of the tadpoles. Tadpoles in tanks with caged *Anax* probably could not see the predators but they could detect the chemical signals produced by dragonflies capturing and consuming prey, and they responded by decreasing their activity (see Results).

We simulated the thinning effect of predation by removing tadpoles from the tanks according to three predetermined "mortality schedules". We assumed there would be 90% survival in the absence of predation (which was not quite correct: survival in the no-removal treatment averaged 95%), and we targeted the low- and high-removal treatments to yield final survivorships of 50% and 10%, respectively. The removals were performed with small aquarium nets every other day, and we gently stirred tanks in the no-removal treatment to control for the disturbance created by performing removals. We produced an exponentially declining survivorship curve (type II), which ensured that the proportion of the population removed remained constant while the number of individuals removed declined through time. In nature, predation risk often declines with increasing body size of the prey (Werner 1974, Paine 1976, Zaret 1980, Travis et al. 1985), although *Anax* is capable of killing *Rana sylvatica* tadpoles up to metamorphosis (Van Buskirk and Yurewicz pers. obs.).

In each of four additional tanks we introduced three free-ranging *Anax* to estimate the actual mortality imposed by predators on *R. sylvatica* under the conditions

of the experiment. One of these tanks was destructively sampled every five days during the experiment, giving us four unreplicated points along a survival curve. A shortage of tanks prevented us from replicating each of the samples along the curve, and we began sampling the four tanks before the conclusion of the experiment because we were unsure how rapidly the predators would kill tadpoles. The free-*Anax* treatment was not included within the spatial array of four blocks that contained the other treatments.

We introduced 200 *R. sylvatica* tadpoles into each tank (76/m²) in the experiment on 8 May (blocks I and II) and 12 May (blocks III and IV) 1995, when the tadpoles were approximately 3 weeks old and weighed 24–34 mg. The two sets of blocks differed in precise timing, as well as the date on which we filled the tanks and the population from which the eggs had originally been collected. We estimated growth 10 d after the experiment was begun by capturing a sample of 15 tadpoles from each tank, weighing them, and returning them unharmed. At this point the tadpoles were between 60 and 300 mg. All tanks were drained after 22 d, when we counted and weighed the survivors, which weighed 300–1200 mg.

We measured the impact of predation risk and thinning on tadpole behavior by recording the time spent inactive, swimming, or feeding by five haphazardly chosen tadpoles in each tank. Focal tadpoles were observed for 1 minute each, by an observer sitting beside the tank with a laptop computer programmed to convert sequences of keystrokes into the total time spent in each activity. We made the observations on sunny days about halfway through the experiment. Observations were restricted to the subset of tadpoles not hidden by leaf litter, which introduced a potential bias of undersampling inactive individuals. This may be a minor problem since estimates of activity made in cattle tanks are similar to those from simple laboratory containers in which all individuals can be observed (e.g., compare Skelly 1992 and McCollum and Van Buskirk 1996).

We analyzed the results using mixed model analysis of variance in which caged *Anax* and tadpole-removal were classed and treated as fixed effects and block was a random effect. The main effects and the two-way interaction were tested over their interaction with block. Activity (angular transformation of the proportion of time spent inactive, feeding, or swimming) was analyzed using multivariate ANOVA on two of the three behaviors, since the three sum to 1 and are thus linearly dependent. The multivariate analysis was used first to determine the significance of the behavioral response, but we subsequently employed univariate analyses to determine which activities accounted for significant effects in the MANOVA (Littell et al. 1991). Growth was the average daily proportional increase in mass. We analyzed the log-transformation of growth

rate calculated over three time intervals: first half (days 0 to 10), second half (days 10 to 22), and the entire experiment (days 0 to 22). Log-transformation made explicit the hypothesis that the proportional effects of thinning and risk are independent, as expected if resources are not limiting.

Results

Mortality in the free-*Anax* treatment

Results from the four free-*Anax* tanks, taken down at five-d intervals during the experiment, indicated that the two removal treatments encompassed the range of mortality actually imposed by dragonflies (Table 1). Under an exponential mortality model, in which the daily per capita risk of death remains constant through time, mortality rates for the four tanks ranged from 0.055/d to 0.23/d. The removal rates used in our experiment (0.034/d and 0.109/d) were similar to the rates measured in three of the four tanks, but were lower than the highest mortality rate in the free-*Anax* treatment. Although we do not know if the exponential model adequately describes tadpole mortality imposed by *Anax*, the result suggests that our experimentally imposed removal rates were not extremely different from predation rates of dragonflies on tadpoles.

Tadpole activity

Both perceived predation risk and thinning strongly affected the behavior of *R. sylvatica* (Fig. 1). Tadpoles exposed to dragonflies spent proportionally more time inactive, and less time swimming or feeding, than tadpoles in tanks without predators (Wilks' $\lambda = 0.005$, $F_{2,2} = 207.5$, $P = 0.0048$). The univariate analyses demonstrated that this result arose from significant responses to caged *Anax* in all three activities (Table 2). Tadpoles in tanks containing free-ranging *Anax* showed an activity level similar to that in the caged-*Anax* treatment (Fig. 1), which confirms that caged dragonflies were clearly perceived by the tadpoles.

Table 1. Survival results and estimates of daily mortality risk for *Rana sylvatica* tadpoles exposed to three free-ranging *Anax* dragonflies in four experimental ponds. Under an exponential model of mortality the daily risk of death remains constant through time, which would be appropriate if the number killed depends only on predator-prey encounter rate.

Tank emptied on day	Proportion remaining	Exponential mortality rate
5	0.735	0.0597
10	0.43	0.0809
15	0.02	0.2296
20	0.32	0.0554

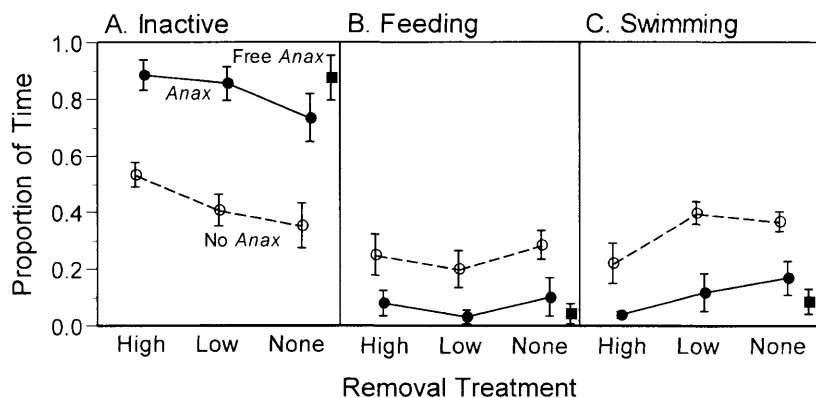


Fig. 1. Behavior of *Rana sylvatica* tadpoles after 10 days exposure to *Anax* predators and the removal treatments. The three panels depict the average (± 1 SE) proportion of time spent inactive (A), feeding (B), and swimming (C) by tadpoles in the seven treatments. Results for the free-*Anax* treatment are shown separately on the right side of each panel. Caged and free-ranging predators caused tadpoles to spend more time inactive and less time feeding and swimming.

In tanks from which tadpoles were removed, there was an increase in the proportion of time spent inactive and a decrease in time spent swimming (Fig. 1, Wilks' $\lambda = 0.048$, $F_{4,10} = 8.91$, $P = 0.0025$). Most of the effect of thinning stemmed from increased inactive time (Table 2), which may reflect decreased hunger levels in tadpoles within the high-removal treatment.

There was no interaction between the *Anax* and removal treatments (Wilks' $\lambda = 0.913$, $F_{4,10} = 0.12$, $P = 0.974$), indicating that they have independent effects on tadpole activity.

Tadpole growth

Tadpole growth rate showed an early decline in response to the presence of caged dragonflies, and a delayed positive response to thinning (Fig. 2). In the sample collected after ten days, tadpoles from the caged-*Anax* treatment were significantly smaller than those from tanks with no predators (Fig. 2A, Table 3A). There was no effect of the removal treatment at this time. The block effect was significant in this analysis, as in some others, probably reflecting variation in initial conditions, timing, and genetic composition of the tadpoles.

Growth rate during the second half of the experiment (between days 10 and 22) was primarily affected by the removal treatment: tadpoles grew faster when density was thinned (Fig. 2B, Table 3B). The thinning effect was more pronounced in the absence of *Anax* than when caged *Anax* was present, and this was reflected in the significant interaction between removal and predation risk.

Averaged across the entire experiment, there were significant effects of thinning, predation risk, and their interaction on the daily growth rate of tadpoles (Fig. 2C, Table 3C). The strong interaction indicates that the proportional effects of risk and removal each depended on the level of the other. Exposure to caged *Anax* reduced tadpole growth rate by 18% under the high

thinning regime, but only by 1.6% when no tadpoles were removed. Reduced density under the high removal regime caused a 33% increase in growth rate when predators were absent, but only a 10% increase when *Anax* was present.

Discussion

This experiment illustrates how predators exert two simultaneous but distinct impacts on the growth rates of prey individuals, by reducing both the population density of prey and the time that individuals spend actively gathering food. Under the conditions of the experiment both impacts were quantitatively important and of similar magnitude, but they acted in opposite directions. The results suggest that activity suppression is the more important effect of predators when resources are not limiting (in our case, early in the larval period), whereas thinning is the more significant effect when resources are scarce (late in the larval period). Resource availability therefore plays a critical role in determining the balance between conflicting effects on prey growth, and we will argue that the implications of this result are important for understanding the impact of predators on the relative abundances of species in communities.

Responses to both manipulations were consistent with theory and earlier empirical work, suggesting that the removal and caged-predator treatments were successful in simulating the effects of predators killing and suppressing the activity of their prey. For example, the removal treatment was intended to imitate only the direct numerical impact on prey; in our experiment it caused improved growth of the survivors, as expected if tadpoles are released from competition at low density (Wilbur 1988). Likewise, the caged-*Anax* treatment was intended to provide signals associated with predation, and to induce behavioral responses in the prey, together with associated growth costs (Dixon and Baker 1988, Abrams 1992, Skelly 1992). We observed the expected

Table 2. Results of univariate analyses of variance on the proportion of time spent inactive, feeding, and swimming by *Rana sylvatica* tadpoles in the experimental tanks. Data were angularly transformed before analysis, and fixed effects (both treatments and the *Anax*-by-Removal interaction) were tested over their interaction with Block. The table shows *F* (above) and *P*-value (below).

Response	Source of variation (df)			
	Block (3,15)	<i>Anax</i> (1,3)	Removal (2,6)	<i>Anax</i> -by-Removal (2,6)
Inactive	9.40 0.0010	164.0 0.0010	33.4 0.0006	0.27 0.7724
Feeding	7.77 0.0023	354.62 0.0003	2.41 0.1701	0.06 0.9411
Swimming	1.18 0.3500	23.49 0.0168	7.18 0.0256	0.28 0.7682

decline in time spent feeding and swimming, along with the growth cost under some circumstances.

The net effect of predators depends on resource availability

The relative importances of predation risk and thinning changed during the course of the experiment. Over the first ten days tadpole growth was significantly reduced in the presence of caged predators, but during this period there was no response to a decrease in density caused by removal. In the second half of the experiment there was a pronounced increase in growth in response to thinning, but predation risk affected growth only in the high-removal treatment.

These results, viewed in the context of the predictions discussed in the Introduction, suggest that there was a shift during the experiment from a period when resources were plentiful to a period when they were scarce. The results from the first half of the experiment were similar to the expected outcome when prey are not competing. This outcome depends on high per capita resource availability, so that food intake and growth increase continuously with foraging effort and are not affected by density. These conditions were likely met during the early phase of the experiment, when tadpoles were still too small to deplete the periphyton they feed on.

Results during the second half of the experiment suggest that tadpoles were competing for food at this stage, but that physical or chemical interference may have been occurring as well. The strong removal effect on growth indicates that competition of some form was important because reduced density led to improved individual performance. The *Anax*-by-removal interaction implies that the impacts of the two treatments were connected, most likely through their effects on resource availability, which could only occur under exploitation competition. In the crowded conditions of the low- and no-removal regimes, activity suppression had no effect on growth, presumably because resources were so scarce that food intake was nearly unrelated to foraging

effort. However, predation risk led to reduced growth in the high-removal treatment, where resources were more abundant. This combination of results is expected to occur when prey are both competing for food and adjusting their feeding effort to minimize contact with predators. At the same time, interference is suggested by the fact that thinning affected growth in the two most crowded treatments (low-removal and no-removal), while predation risk had no impact in either treatment. This implies that competition was important, but that it did not involve resource limitation. Tadpoles are known to exhibit interference mediated by growth-inhibiting algae or chemicals in some instances (Rose 1960, Steinwascher 1978, Griffiths et al. 1993).

An alternative explanation for the outcome during the second half of the experiment is that habituation to the proximity of *Anax*, or declining vulnerability to predation with increasing body size, led to weakened behavioral responses and a consequently lower impact of predation risk on growth as the experiment progressed. This mechanism accounts for the weak effect of predation risk at the same time as the strong thinning effect on growth, without invoking reduced resource levels. However, it does not agree with earlier work showing that anuran larvae tend to show consistent or even enhanced behavioral responses to predators with accumulated exposure (Semlitsch and Reyer 1992, McCollum and Van Buskirk 1996), and it ignores the fact that risk did cause reduced growth at the lowest density. Furthermore, earlier studies have shown that grazing tadpoles deplete periphyton, at least when crowded (Dickman 1968, Osborne and McLachlan 1985, Morin et al. 1990, Leibold and Wilbur 1992), and resource depletion seems extremely likely in our experiment as well. Although we have no quantitative data, we noticed that the inside walls of high-removal tanks felt slimy to the touch late in the experiment, in comparison with the no-removal tanks. On balance, then, we suspect that the growth patterns measured during the second half of the experiment resulted from the resource-based mechanism we offer above.

Across the entire experiment there was a strong interaction between activity suppression and thinning

(Fig. 2C), as expected under exploitative competition, although we acknowledge that pure exploitative competition may not have been the only form of interaction taking place. The separate results from early and late in the experiment show that there was little competition during the early stages and that interference may have occurred in crowded treatments late in the experiment. Nevertheless, the overall result strengthens our conclusion that the behavioral response to predators exacts its greatest growth cost when prey are not resource lim-

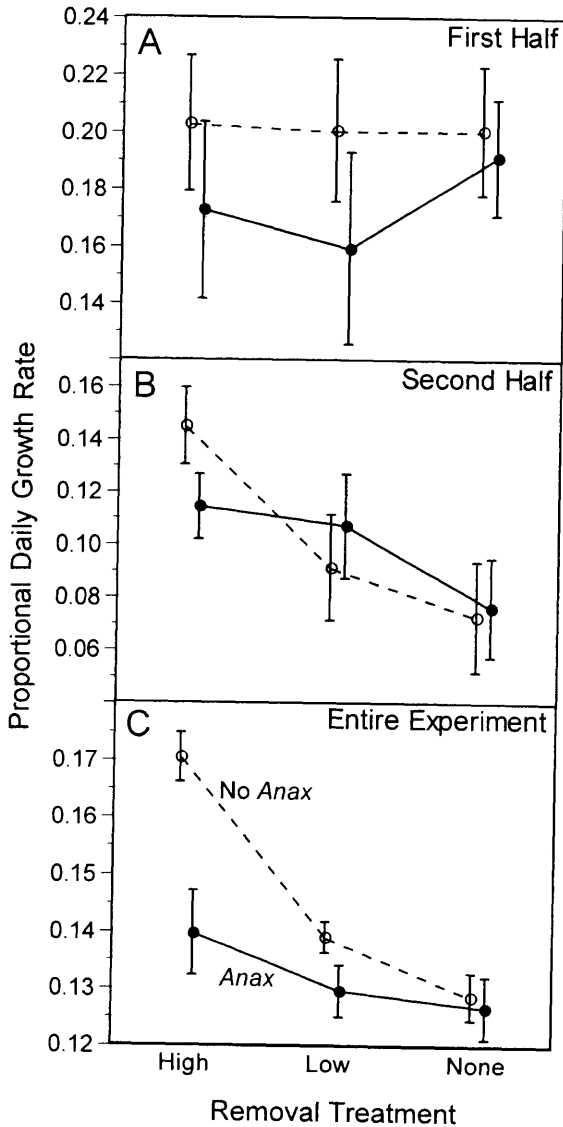


Fig. 2. Proportional daily growth rate (± 1 SE) of *Rana sylvatica* tadpoles over the first 10 days (A), between days 10 and 22 (B), and over the entire experiment (C). Only the caged-*Anax* treatment affected growth after 10 days, the removal treatment was most important late in the experiment, and the presence or absence of predators interacted significantly with thinning over the entire experiment.

Table 3. Analyses of variance on the log-transformed daily proportional growth rate of *Rana sylvatica* tadpoles during the first and second parts of the experiment, and throughout the entire experiment. Fixed effects (both treatments and the *Anax*-by-Removal interaction) were tested over their interaction with Block.

A. Growth during the first 10 days			
Source	df	F	P
Block	3.15	58.74	0.0001
<i>Anax</i>	1.3	20.36	0.0203
Removal	2.6	2.50	0.1626
<i>Anax</i> -by-Removal	2.6	1.65	0.2694
B. Growth between days 10 and 22			
Source	df	F	P
Block	3.17	63.70	0.0001
<i>Anax</i>	1.3	2.15	0.2385
Removal	1.3	31.32	0.0007
<i>Anax</i> -by-Removal	1.3	14.05	0.0054
C. Growth during the entire experiment			
Source	df	F	P
Block	3.15	1.53	0.2472
<i>Anax</i>	1.3	14.16	0.0328
Removal	2.6	10.66	0.0106
<i>Anax</i> -by-Removal	2.6	12.41	0.0074

ited, because the caged-*Anax* treatment led to decreased growth only in the removal treatments.

Behavioral data were generally supportive of the interpretation offered here. Tadpoles dramatically reduced feeding activity when they detected *Anax*, and the magnitude of reduction was independent of the removal rate (Fig. 1). This bolsters the assumption that predation risk causes a fixed reduction in activity level. A second assumption, not entirely supported, is that activity is independent of density. We found that tadpoles in no-removal tanks had slightly increased activity levels, but the change resulted from more time spent swimming rather than feeding. This may mean that crowded tadpoles disturb or interfere with one another, as we suggested above, or spend more time searching for food. In any case, the assumption was not badly violated: the effect of density on activity was rather weak.

Impact of predators on species composition in communities

The role of resource limitation in determining the relative importances of thinning and activity suppression may provide a basis for predicting the balance between these conflicting effects in other systems, and for evaluating the net effect of predators on multi-species communities. Most community-level studies of predation focus on numerical effects on prey, caused by predator foraging preferences or differences among prey in vulnerability (Paine 1966, Morin 1983, Menge et al. 1994). Our results suggest that this perspective will be most

successful in systems where prey strongly deplete resources, so that behavioral responses to predation entail relatively limited growth costs. When prey are not engaged in exploitative competition, activity suppression could be of greater quantitative importance than thinning, and community-level predictions may be more challenging. In this case, one needs to know not only the relative vulnerabilities of the prey species, but also their behavioral responses to predators, the growth costs of those responses, and the relationship between individual growth rate and contribution to population growth.

This appears at first to be a daunting task, but results from a variety of studies show that community models can incorporate numerical and/or behavioral consequences of predation when appropriate. The keystone predator framework, for example, has provided a reasonably successful approach to understanding species composition in strongly interacting prey assemblages (Morin 1983, Menge et al. 1994). In these examples predators were exerting impacts through both the thinning and activity suppression pathways, yet patterns of differential prey vulnerability adequately predicted predator effects on species composition. This suggests that incorporating activity suppression may not be required for accurate community models with strong resource depression by prey species. In some other cases, however, behavioral responses to predators have led to measurable shifts in the performance of coexisting species (Soluk and Collins 1988, Wissinger and McGrady 1993, Werner and Anholt 1996, Peacor and Werner 1997). For example, Werner and Anholt (1996) found that tadpoles in a small, vulnerable size class of *Rana catesbeiana* decreased activity in the presence of an odonate predator, and as a consequence had a reduced competitive impact on a larger size class. That experiment provided no measure of the relative importance of thinning since predators were prevented from killing prey, but the results do illustrate that it is possible to experimentally estimate the magnitudes of behaviorally mediated effects in a community context. When combined with our results, these studies suggest that it will be possible to disentangle the positive and negative effects of predators within multi-species systems, and to extract general conditions that govern when one or the other effect is likely to be most important.

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