

## THE GROWTH–PREDATION RISK TRADE-OFF UNDER A GROWING GAPE-LIMITED PREDATION THREAT

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**Abstract.** Growth is a critical ecological trait because it can determine population demography, evolution, and community interactions. Predation risk frequently induces decreased foraging and slow growth in prey. However, such strategies may not always be favored when prey can outgrow a predator's hunting ability. At the same time, a growing gape-limited predator broadens its hunting ability through time by expanding its gape and thereby creates a moving size refuge for susceptible prey. Here, I explore the ramifications of growing gape-limited predators for adaptive prey growth. A discrete demographic model for optimal foraging/growth strategies was derived under the realistic scenario of gape-limited and gape-unconstrained predation threats. Analytic and numerical results demonstrate a novel fitness minimum just above the growth rate of the gape-limited predator. This local fitness minimum separates a slow growth strategy that forages infrequently and accumulates low but constant predation risk from a fast growth strategy that forages frequently and experiences a high early predation risk in return for lower future predation risk and enhanced fecundity. Slow strategies generally were advantageous in communities dominated by gape-unconstrained predators whereas fast strategies were advantageous in gape-limited predator communities. Results were sensitive to the assumed relationships between prey size and fecundity and between prey growth and predation risk. Predator growth increased the parameter space favoring fast prey strategies. The model makes the testable predictions that prey should not grow at the same rate as their gape-limited predator and generally should grow faster than the fastest growing gape-limited predator. By focusing on predator constraints on prey capture, these results integrate the ecological and evolutionary implications of prey growth in diverse predator communities and offer an explanation for empirical growth patterns previously viewed to be anomalies.

*Key words:* demographic models; life history evolution; optimal growth; phenotypic plasticity; predator–prey interactions; prey size refuge.

*The same thing that makes you live can kill you in the end.*

—Neil Young

### INTRODUCTION

Growth plays a crucial role in shaping a population's demography and evolution because body size influences multiple fitness components (Werner and Gilliam 1984, Reznick et al. 1990, Skelly and Werner 1990, Abrams and Rowe 1996, de Roos et al. 2003). Growth can determine an individual's future fecundity, survival, access to mates and ability to perform ontogenetic habitat and trophic shifts (Werner and Gilliam 1984). However, growth also is associated with fitness costs structured either by intrinsic physiological trade-offs (Munch and Conover 2004) or environment-dependent mortality risks (Lima and Dill 1990). In this latter

category, foraging often decreases survival because it requires individuals to engage in behaviors or to use habitats that expose them to predators (Werner and Gilliam 1984, Lima and Dill 1990, Skelly and Werner 1990). Balancing these costs and benefits to growth creates a foraging–predation risk trade-off that applies to many organisms (Werner and Gilliam 1984, Lima and Dill 1990, Skelly and Werner 1990, Schmitz 1998, McPeck et al. 2001, Benard 2004).

Under a wide range of conditions, prey individuals are expected to decrease risky foraging behavior and growth in the presence of predators (Rowe and Ludwig 1991, Abrams and Rowe 1996). However, prey populations from high-predation-risk habitats sometimes forage more frequently or grow faster when exposed to predators (Fraser and Gilliam 1987, Leibold and Tessier 1991, Spitze 1991) or demonstrate plastic increases in foraging or growth rates in response to predator cues (Crowl and Covich 1990, Bronmark and Miner 1992, Black 1993, Chase 1999b, Schmidt and Van Buskirk 2004). Frequent observations of this counterintuitive response suggest a functional explanation.

Predator gape limitation on prey capture offers one potential adaptive explanation for rapid prey growth.

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The size of a predator's gape or capture apparatus frequently constrains its intake of larger prey (Wilson 1975, Hambright 1991, Ovadia and Schmitz 2002). When confronted with sustained risk from size-limited predators, a prey individual's rapid growth can diminish its predation threat by allowing it to reach a refuge body size (Paine 1976, Ludwig and Rowe 1990, Chase 1999a, Day et al. 2002). However, other predators may be unconstrained by a prey species' growth ontology because of the predator's large relative size (e.g., a zooplankter that cannot outgrow a planktivore's gape) or by adaptations that facilitate prey capture and handling independent of size (e.g., venom). In this way, potential constraints on prey capture determined by the identity and ontogeny of focal predator and prey populations offer a promising approach to categorizing natural selection on prey growth rates.

Prior theoretical studies indicate that a single, non-growing, and size-limited predator can increase the selective advantage for rapid prey growth (Case 1978, DeAngelis et al. 1985, Sibly et al. 1985, Day et al. 2002). Several of these models also assume that early rapid growth decreases or delays future reproduction (DeAngelis et al. 1985, Day et al. 2002). However, a different set of trade-offs may dominate for prey individuals that encounter multiple predators and for which future fecundity increases with prey size (McPeck and Peckarsky 1998). For these organisms, the dominant fitness cost to rapid growth is likely to be the elevated risk of mortality from predators (i.e., the growth-predation-risk trade-off [Werner and Gilliam 1984]). At the same time, the growth of gape-limited predators creates a moving target for prey growing toward a potential size refuge. Here, I develop a demographic optimality model of prey growth that incorporates a potential size refuge from a growing gape-limited predator and additional costs to growth attributed to gape-unconstrained predators. Results are generally applicable to the many species with discrete and complex life histories (Werner 1988). The predator's gape limitation and growth rate relative to prey size is used to derive an explicit mechanistic relationship between prey growth rate and time until prey size refuge. Analytical solutions and numerical approximations under a range of parameter values address the following questions: (1) How does an explicit size refuge from a gape-limited predator modify predictions of optimal prey growth rate in the context of standard foraging-predation risk trade-offs? (2) How does the growth rate of the gape-limited predator affect these predictions? (3) What effect do multiple gape-limited predators with different growth rates have on adaptive prey growth?

#### MODELING FRAMEWORK AND ASSUMPTIONS

##### *General approach*

I modify a general demographic model of organisms with basic but complex life cycles (McPeck and

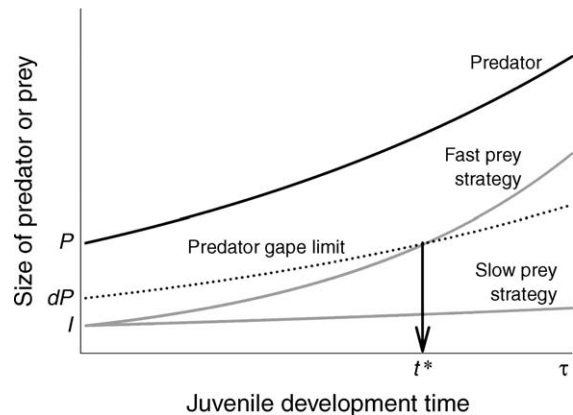


FIG. 1. The underlying model assumed to characterize gape-limited predation risk for two prey strategies. The predator (black line) and prey (gray lines) grow exponentially from initial sizes  $P$  and  $I$ , respectively. The predator only can capture prey individuals less than some proportion ( $d$ ) of its size (dotted line). After time  $t^*$ , the prey demonstrating the fast growth strategy are larger than the predator's gape and have entered a size refuge. Prey individuals adopting a slow strategy encounter predation risk for the full developmental period ( $\tau$ ).

Peckarsky 1998) that belongs to a larger set of discrete demographic models frequently used to predict patterns of life history variation (Werner and Gilliam 1984, Ludwig and Rowe 1990, Abrams and Rowe 1996, Abrams et al. 1996). A juvenile grows for a fixed time interval to metamorphosis as might be the case for an amphibian larva or insect (Fig. 1). During this time period, the juvenile can enter a prey-size refuge if it outgrows a growing predator's ability to capture it. Otherwise, the individual experiences chronic predation risk for the entire developmental period. Prey body size at metamorphosis determines future fecundity (Abrams and Rowe 1996). Variation in growth trajectories is introduced through a model of phenotypic evolution. Table 1 provides a list of variables, their description, and parameters explored in numerical analyses. The Appendix details variations on the general model that assume an iteroparous species, that predator growth rate is linked to prey mortality, plastic growth trajectories, and prey size-dependent predation risks.

##### *Prey growth and survival*

Predators and prey juveniles are assumed to grow exponentially at size-specific rates  $a$  and  $g$  from an initial size ( $P$  and  $I$ ) for time period  $t$  such that predator and prey growth are  $P \times e^{at}$  and  $I \times e^{gt}$  (Fig. 1). Exponential growth generally applies to juvenile growth in many organisms such as insects and amphibians (Alford and Jackson 1993, Abrams and Rowe 1996, McPeck and Peckarsky 1998). I assumed that prey individuals must reach a minimum critical size before the end of the season such as is necessary for metamorphosis in many species (e.g., Wilbur and Collins 1973). This fixed developmental time results in a minimum prey growth rate ( $g_{\min}$ ), below which fitness is assumed to be zero. A

TABLE 1. Variables, parameters, and parameter values used in numerical solutions.

Symbol	Description	Parameter values used in numerical solutions
Variables		
$\lambda$	geometric rate of increase of the prey population at a given growth rate	
$t^*$	time until prey size refuge from gape-limited predator	
Parameters		
$\alpha$	number of prey offspring born to a female with a given metamorphic size	1
$\beta$	exponent that determines the shape of the fecundity–metamorphic size relationship	0–2
$\tau$	juvenile development time for prey	300
$\omega$	exponent that determines the shape of the gape-limited mortality–growth relationship	0–2
$a$	gape-limited predators’ size-specific growth rate	0.01
$b$	gape-unconstrained predator mortality risk per unit prey growth and time	1
$d$	ratio of the predator gape: prey size above which predation no longer occurs	0.5
$g$	prey size-specific growth rate	0.005–0.05
$I$	initial prey size at time zero	2
$m$	gape-limited predator mortality risk per unit prey growth and scaled to time	1, 10
$P$	initial predator size at time zero	8
$r$	difference between initial predator gape limitation and prey size that must be overcome for prey individuals to reach a size refuge, ignoring prey and predator growth rates; equals $\ln(dP/I)$	$\ln(2) = 0.69$

size refuge occurs when a relevant dimension of prey size (e.g., head width, body depth) exceeds some proportion of a predator’s gape ( $d$ ) (Fig. 1). Thus,  $d$  times predator size equals prey size at the time at prey size refuge ( $t^*$ ). Taking the log of both sides and rearranging gives the time at size refuge:

$$t^* = \frac{r}{(g - a)} \tag{1}$$

where  $r = \ln(dP/I)$  and provides a measure of the initial difference in size between predator and prey that must be overcome for a size refuge to be attained prior to metamorphosis at fixed time ( $\tau$ ). Therefore  $t^*$  must be less than  $\tau$ , a relation that yields the inequality

$$g > a + \frac{r}{\tau} \tag{2}$$

Hereafter, I refer to Eq. 2 as the size refuge threshold. To enter a size refuge, prey individuals must grow faster than the predator ( $a$ ) and overcome the initial size difference between predator and prey within the developmental period ( $r/\tau$ ). The size refuge threshold separates model outcomes into those for which gape-limited predation risk lasts the entire developmental period and those for which juveniles experience risk for a more limited period before entry into a size refuge.

The proportional survival to metamorphosis under gape-limited predation risk is

$$S = e^{-(m \times r \times g^\omega)/(g-a)} \tag{3}$$

where  $m$  is the prey mortality per increment in growth scaled to its exponent and  $\omega$  is the exponent that determines the shape of the growth-mortality relationship (Case 1978, Abrams et al. 1996). Predation risk decelerates with growth if  $\omega < 1$ , is proportional if  $\omega = 1$ , and accelerates if  $\omega > 1$ . Eq. 3 holds only if Eq. 2 is true. Otherwise, prey experience predation risk during the entire larval period ( $\tau$ ):

$$S = e^{-m \times \tau \times g^\omega} \tag{4}$$

Set in theoretical context, Eqs. 3 and 4 modify the growth- and time-dependent predation function in Case (1978) to include a body size refuge from a growing predator.

*Demographic model for a prey size refuge*

A demographic model is next derived such that prey future fecundity and juvenile survival depend on prey growth rate and predator gape limitation and growth rate. Let  $\alpha$  and  $\beta$  be the scaling parameter and exponent that relate size at metamorphosis to future fecundity ( $\alpha(I \times e^{g\tau})^\beta$ ).  $\beta$  allows for decelerating ( $\beta < 1$ ), linear, or accelerating ( $\beta > 1$ ) fecundity with size (McPeck and Peckarsky 1998). Prey survival is broken into two parts. The first part describes the survival of prey in the presence of gape-unconstrained predators as  $\exp(-b \times g \times \tau)$ , where the coefficient  $b$  linearly scales prey growth rate to gape-unconstrained mortality risk. Alternatively, this mortality might result from an intrinsic physiological cost to growth (Munch and Conover 2004). In the second survival term,  $m$  scales growth rate to the prey individual’s gape-limited predation mortality risk for the time period until prey refuge (Eq. 3) or for total development time (Eq. 4) depending on the size refuge threshold (Eq. 2). Adult fecundity and juvenile survival are multiplied to produce a fitness measure, the geometric rate of population increase ( $\lambda$ ), for prey with a potential size refuge:

$$\lambda = \begin{cases} \alpha I^\beta e^{g \times \tau(\beta-b) - m \times \tau \times g^\omega} & \text{if } g_{\min} \leq g \leq a + \frac{r}{\tau} \\ \alpha I^\beta e^{g \times \tau(\beta-b) - (m \times r \times g^\omega)/(g-a)} & \text{if } g > a + \frac{r}{\tau} \end{cases} \tag{5}$$

TABLE 2. Fitness derivatives and conditions favoring rapid growth under various predator community contexts assuming  $g_{\min} = 0$  and  $\omega = 1$ .

Predator context	$\delta \ln(\lambda) / \delta g$ , no size refuge	$\delta \ln(\lambda) / \delta g$ , size refuge	Conditions favoring rapid growth	
			Fecundity criterion	Maximum growth criterion
Gape-unconstrained predator only	$(\beta - b)\tau$		$\beta > b$	$g_{\max} > 0$
Gape-limited predator only	$(\beta - m)\tau$	$\beta\tau + \frac{mra}{(g - a)^2}$	$\beta > 0$	$g_{\max} > a + \frac{mr}{\beta\tau}$
Gape-unconstrained and gape-limited predators	$(\beta - b - m)\tau$	$(\beta - b)\tau + \frac{mra}{(g - a)^2}$	$\beta > b$	$g_{\max} > a + \frac{mr}{(\beta - b)\tau}$

Note: A maximum growth rate ( $g_{\max}$ ) also is assumed that could preclude the evolution of a rapid growth strategy that is globally optimal, but occurs at a growth rate above that allowed by physiology and resource supply.

If  $g < g_{\min}$ , prey individuals do not reach a sufficient size to reach metamorphosis and  $\lambda = 0$ . I also assume that ecological and evolutionary constraints set a maximum growth rate ( $g_{\max}$ ). Although an annual species is assumed, the model predicts similar results for an iteroparous species faced with variable gape-limited predation risks through time (Appendix).

To determine the predicted evolutionary outcome, the prey growth rate that maximizes fitness is calculated. Analytic solutions to the model are possible when the growth-predation risk shape parameter ( $\omega$ ) equals one. Therefore analytic predictions are first derived for the case where  $\omega = 1$  and  $g_{\min}$  becomes vanishingly small to build comprehension about more sophisticated, but analytically intractable, models. Numerical results then are obtained for a model assuming a non-zero  $g_{\min}$  across a realistic range of  $\omega$  (0–2) and  $\beta$  (0–2) to explore sensitivity of model outcomes to these key parameters.

RESULTS

Analytical results under varying predator community contexts

The evolution of rapid growth into a size refuge requires that both a fecundity criterion and a maximum

growth criterion are met (Table 2). When the fecundity and maximum growth conditions in Table 2 are not met,  $g_{\min}$  is optimal. Regardless of the type of predation risk, rapid prey growth is favored whenever the fecundity exponent ( $\beta$ ) exceeds the gape-unconstrained predation risk coefficient ( $b$ ) and the appropriate maximum growth criterion is met. Rapid growth is favored under these circumstances because the fitness benefits of increased fecundity through large size outweigh the fitness costs of increased predation risk. Under gape-limited predation risk, a broader range of fecundity parameters support rapid growth: rapid prey growth is always optimal as long as body size has a positive effect on future fecundity ( $\beta > 0$ ) and prey individuals can grow faster than  $a + (m \times r) / (\beta \times \tau)$ .

A novel fitness minimum with gape-limited and unconstrained predation risk

Next, I explore the general case of gape-limited and gape-unconstrained predation risk under different  $\omega$  values. Sufficient conditions for  $g$  to maximize fitness are shown in Eqs. 6 and 7. Without a size refuge, the local optimal growth rate is  $g_{\min}$  when the fecundity coefficient ( $\beta$ ) is less than the background predation risk coefficient ( $b$ ). When  $\beta > b$ , local optimal growth is

$$\frac{\partial \ln(\lambda)}{\partial g} = \begin{cases} (\beta - b)\tau - (\omega \times m \times \tau \times g^{\omega-1}) & \text{if } g_{\min} \leq g \leq a + \frac{r}{\tau} \\ (\beta - b)\tau + (m \times r \times g^{\omega-1}) \frac{(1 - \omega)g + a \times \omega}{(g - a)^2} & \text{if } g > a + \frac{r}{\tau} \end{cases}$$

$$= 0 \tag{6}$$

$$\frac{\partial^2 \ln(\lambda)}{\partial g^2} = \begin{cases} -\omega(\omega - 1)m \times \tau \times g^{\omega-2} & \text{if } g_{\min} \leq g \leq a + \frac{r}{\tau} \\ -\frac{(m \times r \times g^{\omega-2})}{(g - a)^4} \{ \omega(\omega - 1) + [(1 - \omega)g + a \times \omega]g(2g - a) \} & \text{if } g > a + \frac{r}{\tau} \end{cases}$$

$$< 0. \tag{7}$$

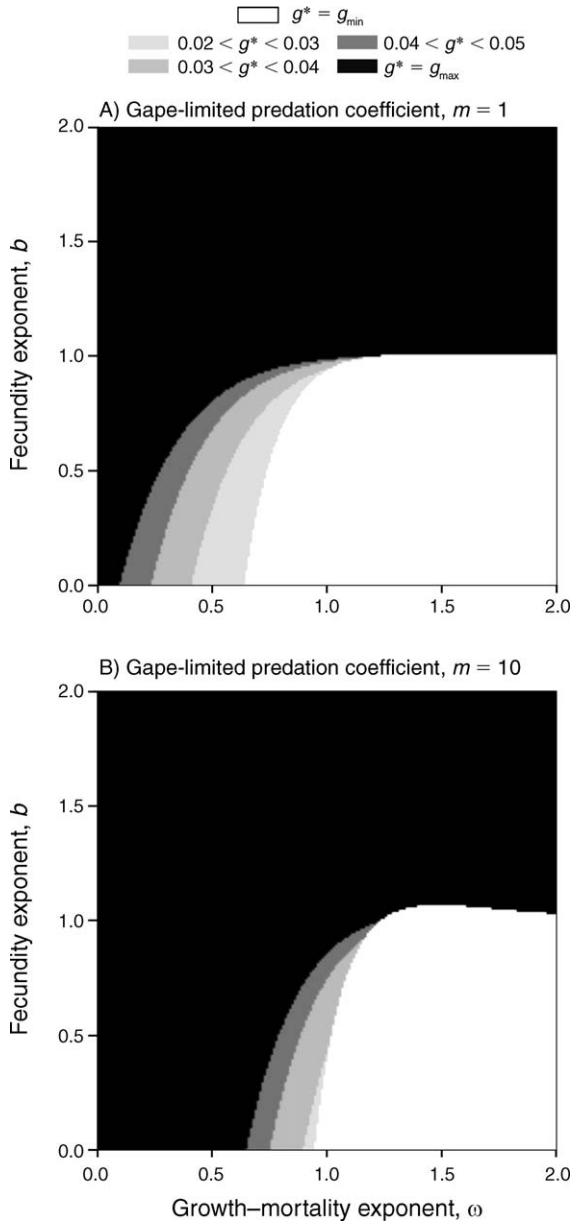


FIG. 2. Optimal growth rates as a function of the fecundity-growth exponent ( $\beta$ ) and the gape-limited-predation-risk-growth exponent ( $\omega$ ) for (A) low ( $m = 1$ ) and (B) high ( $m = 10$ ) gape-limited predation risk. Optimal growth rates were determined through a numerical search ( $\Delta g = 0.0001$ ) for maximum fitness from  $g_{\min} = 0.005$  to  $g_{\max} = 0.05$ . The following generic parameters were applied:  $b = 1$ ,  $\tau = 300$ ,  $a = 0.01$ , and  $r = \ln(2)$ .

$$g^* = \left[ \frac{(\beta - b)}{\omega \times m} \right]^{1/(\omega - 1)} \quad (8)$$

if  $\omega > 1$ . Otherwise, this growth rate is a minimum and selection is disruptive.

When growth allows entry into a size refuge, fitness increases with growth rate when the fecundity-growth

exponent ( $\beta$ ) exceeds gape-unconstrained mortality ( $b$ ) and  $(1 - \omega)g + a\omega$  is greater than zero, or when either of these terms exceeds the negative quantity in the other term. The first fecundity criterion might characterize a community where gape-unconstrained predation risks are low or gains in future fecundity accelerate with metamorphic size as has been observed for some invertebrates (McPeck and Peckarsky 1998). The second size refuge criterion is always met when  $\omega \leq 1$ , but becomes increasingly restricted when  $\omega > 1$  by the requirement that an intermediate  $g^*$  exists below  $a\omega/(\omega - 1)$ . When  $\omega > 1$  and  $\beta > b$ , an equilibrium growth rate can exist. In this case, a global solution for  $g^*$  is not available without specifying  $\omega$ .

To determine the global growth optimum, numerical solutions are calculated from Eq. 5 for a broad parameter space that includes variation in the fecundity exponent ( $\beta$ ) relative to the gape-unconstrained predation risk coefficient ( $b$ ) and different growth-mortality relationships ( $\omega$ ). Under both low ( $m = 1$ ) and high ( $m = 10$ ) gape-limited predation risks, maximum growth rate usually maximizes global fitness when  $\beta > b$  (in Fig. 2A, B where  $\beta > 1$ ). Under these conditions, even a small fecundity advantage can translate into a large fitness gain after multiplication by maximum growth rate and development time [ $g_{\max}(\beta - b)\tau$ ]. Minimum growth generally maximizes fitness when  $\beta < b$ , and  $\omega > 1$  (lower right quadrant in Fig. 2) because slow growth in the absence of a size refuge minimizes predation mortality. Intermediate growth rates are optimal for a small region where  $\omega < 1$  and  $\beta < b$ . Interestingly, none of the intermediate growth rates take values between  $g_{\min} = 0.005$  and  $g = 0.02$  (Fig. 2). This is because, under a wide range of conditions, a fitness minimum occurs for prey individuals that grow near the size refuge threshold

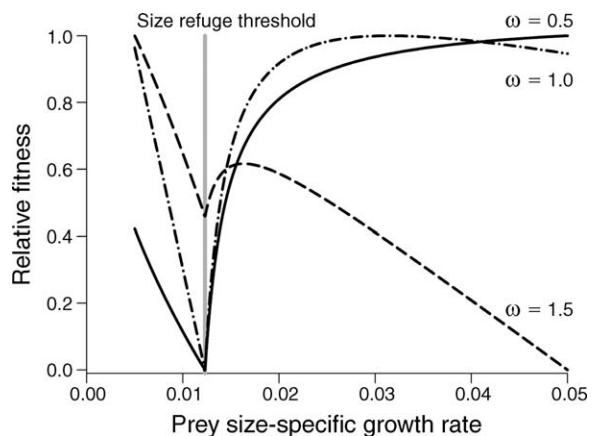


FIG. 3. Relative prey fitness as a function of size-specific prey growth rate under gape-limited predation risk. Decelerating ( $\omega = 0.5$ ), linear ( $\omega = 1$ ), and accelerating ( $\omega = 2$ ) relationships between growth and predation risk are presented. The gray vertical line indicates the size refuge threshold. I set the fecundity exponent to 0.5; other parameters are the same as in Fig. 2.

( $a + r/\tau = 0.012$ ; Fig. 3). As a rule of thumb, prey individuals should not grow near the same rate as their gape-limited predator because this strategy incurs all of the fitness decrements of increased predation risk from foraging activity and none of the fitness benefits of a size refuge.

*Does predator growth matter?*

In general, allowing for the growth of gape-limited predators alters the conditions determining whether prey should adopt fast or slow growth strategies. Gape-limited predator growth increases the size refuge threshold separating fast and slow prey lifestyles (see Eq. 2), raises the optimal growth rate into a size refuge when such a solution exists less than  $g_{max}$ , and generally broadens the parameter space in which maximum growth is optimal. This last point can be demonstrated analytically with Eq. 6. The change in fitness with a change in growth can be positive when  $(1 - \omega)g + a\omega > 0$ . Higher predator growth rates increase the last term ( $a\omega$ ) and thereby increase the likelihood that the entire fitness equation will be positive and support maximum growth. However, because higher predator growth rates also require a higher maximum prey growth rate (Table 2), this effect may be moderated in natural prey populations where growth is constrained by genetic variation or limited food resources.

*How does variable growth among gape-limited predator species affect predictions?*

To answer this question, two gape-limited predators are assumed that grow at different rates  $a_1$  and  $a_2$ , where  $a_2 > a_1$ . These predators are assumed only to differ in growth and not in their initial gape sizes ( $dP$ ) or hunting abilities ( $m$ ). The new fitness equation is shown in Eq. 9. This equation generates two local fitness minima and four potential growth solutions:  $g_{min}$ ,  $g_1^*$ ,  $g_2^*$ , and  $g_{max}$ . In the analytically tractable case with  $\omega = 1$ , and  $g_{min} \rightarrow 0$  and  $g_{max} \rightarrow \infty$ , the solution is either for  $g_{max}$  or  $g_{min}$ , just as in the single gape-limited predator case. This is because when  $\beta \leq b$ ,  $g_{min} = 0$  is globally optimal because fitness becomes  $\beta \ln(\alpha I)$  while prey adopting more rapid growth solutions accrue higher costs from mortality. When  $\beta > b$ ,  $g_{max}$  becomes the globally optimal solution because the fastest growing prey strategy (Eq. 9) can accrue positive fitness through the fecundity term while

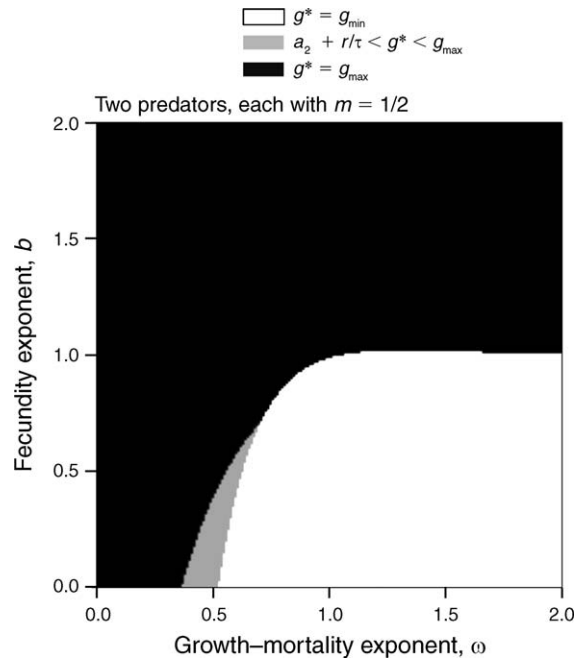


FIG. 4. Optimal growth rates with parameters used in Fig. 2, except that here prey encounter two gape-limited predators with different growth rates ( $a_1 = 0.01$ ,  $a_2 = 0.03$ ) but under the same total gape-limited mortality risk ( $m = 1/2$ ). Only  $g_{max}$ ,  $g_{min}$ , and an intermediate  $g^* > a_2 + r/\tau$  are supported in this parameter space.

at the same time minimizing gape-limited predation risks as  $-(m \times r \times g)/(g - a_x) \rightarrow -(m \times r)$  in the limit as  $g \rightarrow \infty$ . The other potential solution is the intermediate value for the central  $g_1^*$ . But this solution is suboptimal because only one size refuge can be attained and intermediate growth rates do not accrue the same fitness benefits from fecundity as those attained by the fastest growth strategy. In practice, this intermediate growth solution can be globally optimal when  $g_{min}$  and  $g_{max}$  take values close to either of the intermediate fitness minima. However, numerical results obtained across a range of key parameter values support the finding that, if prey individuals grow rapidly, they are expected to grow faster than the fastest growing gape-limited predator (Fig. 4).

$$\ln(\lambda) = \begin{cases} \beta \ln(\alpha I) + g(\beta - b)\tau - 2(m \times \tau \times g^{\omega}) & \text{if } g_{min} \leq g \leq a_1 + \frac{r}{\tau} \\ \beta \ln(\alpha I) + g(\beta - b)\tau - (m \times \tau \times g^{\omega}) - \frac{(m \times r \times g^{\omega})}{(g - a_1)} & \text{if } a_1 + \frac{r}{\tau} < g \leq a_2 + \frac{r}{\tau} \\ \beta \ln(\alpha I) + g(\beta - b)\tau - (m \times r \times g^{\omega}) \left[ \frac{1}{(g - a_1)} + \frac{1}{(g - a_2)} \right] & \text{if } g > a_2 + \frac{r}{\tau} \end{cases} \quad (9)$$

## DISCUSSION

Foraging–predation risk trade-offs are widespread and of great importance in shaping population and community dynamics and life history evolution (Werner and Gilliam 1984, Lima and Dill 1990, Skelly and Werner 1990, Werner and Anholt 1993, Abrams and Rowe 1996, McPeck and Peckarsky 1998, Schmitz 1998, McPeck et al. 2001, Benard 2004). Prey subject to growth-correlated predation risk generally are expected to maintain or to decrease their foraging and to lower their growth rate assuming density-independent growth and a fixed age of maturity (Abrams and Rowe 1996). However, experimental data suggests that prey individuals sometimes grow faster when exposed to elevated predation threats (Crowl and Covich 1990, Spitze 1991, Chase 1999b). One reason may be that growth quickens entry into a refuge body size (Paine 1976, Crowl and Covich 1990, Chase 1999b, Schmidt and Van Buskirk 2004). When threatened by gape-limited predators, the basic evolutionary trade-off faced by an organism is whether to grow fast into a size refuge despite the initial mortality risks of elevated foraging or to grow slowly and diminish its future fecundity.

The demographic model presented here suggests that a prey size refuge can provide an adaptive explanation for elevated growth rates in response to gape-limited predation risk while retaining predictions for reduced growth under certain conditions. The model predicts the novel outcome that prey should not grow near the same rate as gape-limited predators. A potential size refuge introduces an intermediate fitness minimum just above the gape-limited predator's growth rate (Fig. 3) because growing at a rate similar to the gape-limited predator imparts none of the benefits of the size refuge and all of the growth-associated mortality costs. A fast prey lifestyle, characterized by increased foraging and rapid growth, originally was used to describe prey populations that escape predation risk by living in habitats that are too ephemeral or too stressful for most predators (Sih 1987). Model outcomes indicate that a fast prey lifestyle can evolve even in a permanent or non-stressful habitat that is populated by gape-limited predators. Fast growth strategies offer a fitness-optimizing solution to gape-limited predation risks when size-based fecundity is high relative to gape-unconstrained predation risk and when gape-limited predation risk decelerates at higher prey growth rates (Fig. 2). But rapid growth also can elevate predation risk when foraging requires risky behavior. When this additional predation risk outstrips the advantages of a size refuge and future fecundity, a slow growth strategy is optimal. Hence, gape-limited predation introduces an important modification of the classic growth-predation risk trade-off by introducing an additional advantage to growth.

The model is robust to variation in multi-predator growth rates (Fig. 4) and to assuming iteroparous breeders, a link between predator growth and prey mortality, size-proportional predation risk prior to size

refuge, and prey growth plasticity (Appendix). Growth plasticity increases the parameter space over which rapid growth maximizes fitness because the additional costs of growth due to gape-unconstrained predators can be minimized upon entry into a size refuge by reducing the prey growth rate to that of the predator. Assuming a dynamic specialist predator created a more stringent constraint on the evolution of fast strategies. Fast strategies would be slightly less likely to evolve under selection by a specialist gape-limited predator.

These outcomes extend and generalize predictions made by prior models of size-dependent mortality. Case (1978) derived a growth- and time-dependent survival function without a growing predator. His model and one modified in its application to birds (Ricklefs 1984) predicted rapid early growth rates when growth facilitated entry into safer sub-adult stages. A model without fecundity benefits suggested that growth rates should increase when extrinsic mortality declined with size and decelerated with growth rate, but not otherwise (Sibly et al. 1985). In a model of prey energy allocation to defenses, growth and reproduction, DeAngelis and colleagues (1985) found evidence for strategies that maximized growth at the cost of future reproduction and predator defense. Werner and Anholt (1993) were interested in optimal foraging behavior and used a dynamic programming approach to determine optimal foraging movement speeds given the need to obtain resources despite predation risk. Assuming a negative relationship between mortality risk and prey size led to predictions of increased foraging speeds unless prey were much smaller than predators. In more recent food chain models, Chase (1999a) derived expectations for appropriate plastic prey growth responses in a food chain model with prey size refugia assuming continuous population dynamics. Although lacking explicit evolutionary dynamics, prey strategies with or without a prey size refuge were possible depending on initial conditions (Chase 1999a). Extending this approach, Day et al. (2002) explored the joint adaptive and ecological dynamics of linked predator, prey, and resource continuous equations using an adaptive dynamics approach. They assumed that a decline in future fecundity accompanied rapid growth into a size refuge and that membership in either a vulnerable or invulnerable size class determined fixed mortality and fecundity rates. Higher predation risk generally selected for increased evolutionary stable growth rates (Day et al. 2002). However, selection was disruptive when predators dynamically responded to prey populations and growth and fecundity in vulnerable individuals were related by a concave-up function.

The model presented here contrasts from previous work in three main ways. First, the model includes the assumption that multi-predator mortality risks generate costs to rapid growth rather than assuming that fecundity declines with growth (Day et al. 2002). For many organisms, fecundity correlates positively with

adult size (Kaplan and Salthe 1979) and most prey are faced with a diverse set of predators that also differ in their gape constraints on focal prey (Wissinger 1992, Wilbur 1997). Second, predictions for optimal growth are derived as an explicit function of time until refuge from a growing predator. Previous work instead usually assumed a static transition between vulnerable and invulnerable size classes and omitted predator growth. The mechanistic characterization of size-dependent predation risk in the model was critical for demonstrating a novel fitness minimum determined by predator growth rate and initial size differences. Third, in this model, juveniles enter a predator-invulnerable stage prior to reproduction and thereby accrue additional growth after achieving a size refuge. This assumption provides a realistic description of growth in a seasonal environment and allows the possibility of within-season growth plasticity.

The predicted strategies were obtained after assuming a fitness–optimality criterion that is applicable to phenotypic evolution in asexual haploid organisms. Optimality models sacrifice the more sophisticated genetic details incorporated in other approaches to obtain analytical results under complex ecological scenarios (Stearns 1992). In this case, dynamic simulations incorporating sexual recombination and multi-locus genetics suggest that these results are robust to more complex sexual and multi-allelic genetic architectures (Urban 2006). The model also omits predator selectivity for intermediate prey sizes (Wilson 1975). However, such foraging patterns should strengthen the disruptive selection on body growth elicited by a size refuge. Sufficient resources are assumed to be available for prey individuals to sustain peak growth rates. Including resource dynamics likely would change predictions by supplying an additional constraint on fast prey strategies (Arendt and Wilson 1997, Chase 1999a, Day et al. 2002, Abrams 2003) and presents an interesting direction for future work.

In my model, I assumed a fixed developmental period that might characterize organisms that only perform habitat shifts when (non-predatory) environmental conditions deteriorate (e.g., pond drying) and for which suboptimal survival/growth conditions predominate in the secondary habitat (e.g., Werner and Gilliam 1984). However, the early departure of young individuals from habitats characterized by high predation risk offers an additional solution by which prey might increase lifetime fitness with or without changes in growth rate (Werner and Gilliam 1984, Rowe and Ludwig 1991, Abrams and Rowe 1996). In a model assuming flexible growth effort and developmental period, growth rate is predicted to decrease with increasing predation risk while the development time can either increase or decrease depending on the relative fitness costs and benefits to growth (Abrams and Rowe 1996). Experimental results suggest that organisms with complex life histories display a wide range of plastic adjustments in their

development time and size at metamorphosis when subjected to predatory cues (Benard 2004). Hence, future research is needed to determine the optimal combinations of developmental and growth rates for prey exposed to different gape-limited and gape-unconstrained predation threats.

Model outcomes provide a set of intriguing predictions that could explain unanticipated empirical results in future and existing studies. Because the theory is based on a general demographic model, many of the parameters can be estimated from standard field observations or experiments (McPeck and Peckarsky 1998). For instance, model predictions can be tested by examining common garden growth differences in prey originating from populations with varying exposure to gape-limited and unconstrained predators. However, more work is needed to define the shapes of the fecundity–size and predation-risk–growth relationships ( $\omega$  and  $\beta$ ) in order to produce quantitative predictions from the parameterized model. One promising way to obtain these critical parameters is to measure size-dependent variation in fecundity and predation risk among individuals with manipulated phenotypes or known genetic differences in growth rate (Gotthard 2000, Munch and Conover 2004, Sundstrom et al. 2005).

Predator gape limitation provides an important modification to standard predictions generated by theories on growth/predation risk trade-offs. A number of studies report induced increases in growth or foraging rates in response to gape-limited predators (Crowl and Covich 1990, Bronmark and Miner 1992, Chase 1999b). In one instance, larval spotted salamander (*Ambystoma maculatum*) larvae raised in a common garden grew faster when exposed to chemical cues from gape-limited newt predators (Urban 2006). In another example, crested newts of one phylogenetic clade increased their activity when exposed to dragonfly predators. However, newt species belonging to a closely related clade reduced their activity under the same conditions (Schmidt and Van Buskirk 2004). Critically, the benefits of a size refuge were greater for the newt species with a risk-prone foraging strategy as compared to a representative newt species from the risk-averse clade (Schmidt and Van Buskirk 2004). One potential explanation is that phylogenetically related newt species employ divergent growth strategies predicated on the differential costs and benefits of growing into a prey size refuge.

Research on trout in whole-lake experiments indicates a comparable pattern of rapid growth into a size refuge despite the early fitness costs associated with high predator-induced mortality. Rainbow trout (*Oncorhynchus mykiss*) allocated most of their energy to growth at early stages to decrease time spent in a vulnerable stage (Biro et al. 2005). This rapid growth strategy required increased foraging in risky habitats which, in turn, was associated with higher mortality (Biro et al. 2006). However, once trout grew into a size refuge from cannibalism, they increasingly diverted energy from

growth into lipid storage to fuel winter survival (Biro et al. 2005). This example suggests that rapid growth under size-selective predation risk can be found in natural communities, not just in highly simplified laboratory or mesocosm experiments.

Examples that accord with predicted increases in foraging and growth also can be found in common garden experiments designed to uncover phenotypic differences among populations exposed to heterogeneous predator regimes. *A. maculatum* larvae from sites with high gape-limited predation risk foraged more actively than those populations from sites with low gape-limited predation risk (Urban 2006). In this example, the variation in growth rates among populations corresponded well with quantitative model predictions generated using parameter values measured in the system. In another study, Fraser and Gilliam (1987) found that populations of two fish species from high-predation risk sites tended to forage more frequently under higher predation risk. At least one of the predators at the high-predation risk sites is known to be gape-limited (Reznick et al. 1996). Populations of pumpkinseed sunfish (*Lepomis gibbosus*) from lakes sympatric with a competitor, the bluegill sunfish (*Lepomis macrochirus*), grew quicker than those from lakes without this competitor (Arendt and Wilson 1997). One potential explanation for this rapid growth is that competitive interactions forced the pumpkinseed sunfish to forage in risky habitats which, in turn, led to selection for rapid growth into a size refuge (Arendt and Wilson 1997).

Results are mixed for approaches involving experimental evolution. *Daphnia pulex* exposed to size-limited *Chaoborus* predators evolved faster growth in laboratory populations (Spitze 1991). However, guppies (*Poecilia reticulata*) did not evolve increased growth rates after introduction to habitats with high gape-limited predation risk, and, at least in one case, guppies evolved slower growth rates (Arendt and Reznick 2005). For guppies, differences in resource levels between different predator habitats likely drives cogradient selection for rapid growth in high-resource environments (Arendt and Reznick 2005). This latter example suggests caution in predicting optimal growth strategies in natural systems without first evaluating the possible covariation of resource and predation risk gradients.

Empirical data also suggests that some species increase body width to avoid capture by gape-limited predators without necessarily increasing foraging rate and overall body size. Size-selective pike predators induce crucian carp (*Carassius carassius*) to develop deeper bodies (Bronmark and Miner 1992) and gape-limited salamander larvae induce a bulgy morphology in *Rana pirica* tadpoles (Kishida and Nishimura 2004). The ciliate *Euplotes octocarinatus* develops lateral wings in response to the gape-limited predatory ciliate *Lembadion bullinum* (Kopp and Tollrian 2003). In the context of my model, this adaptation would be akin to decreasing the

time until size refuge without increasing predation risk by requiring more risky foraging strategies. If possible within the realm of allometric constraints, this strategy would be preferable over a simple increase in body size. Yet, these morphological changes often require additional resources and may be associated with fitness costs of their own (Kishida and Nishimura 2004). It is worth noting that in the ciliate example, the predator can respond to the induced wings of prey by increasing its gape size (Kopp and Tollrian 2003). Other predators increase their gape size in habitats characterized by large-bodied prey (Magnhagen and Heibo 2001). Hence, future theoretical and empirical work should consider the possible coevolutionary arms race that might emerge between predator gape limitation and their rapidly growing prey.

Rapid prey growth in response to gape-limited predation risk is expected across a wide range of parameter space. Why then does reduced growth (e.g., Benard 2004) appear to be the more common response in empirical studies? One answer is that results hold only for gape-limited predators and therefore specifically exclude large predators for which focal prey cannot grow out of risk. Even when faced with a gape-limited predator, high gape-unconstrained predation risk may swamp out the fitness benefits of rapid growth and instead select for slow growth strategies. Perhaps the most common reason may be that the rapid growth strategy often requires a growth rate too high to be found under existing genetic constraints and resource limitations. Finally, it is entirely possible that many more examples of fast prey strategies exist that have not yet been established empirically. For instance, most experiments on amphibian growth plasticity reviewed by Benard (2004) used predator cues originating from large insect predators rather than potentially more gape-limited fish or salamander species. Theory offered here provides a roadmap of the general conditions under which prey populations are most likely to demonstrate rapid growth under predation threat.

Overall, model results expand predictions of growth responses to a shifting mosaic of functionally divergent predators. Regional variation in patch-specific predation risks may select for either fast- and slow-growth prey strategies depending on the relative occurrence of functionally divergent predators in space and time. Selection heterogeneity, in turn, may generate variable trait patterns in space whereas gene flow and migration will tend to homogenize trait and population dynamics (Thompson 2005, Urban and Skelly 2006). Therefore, predictions of adaptive growth variation in nature often will require knowledge about the constituent community ecologies and population genetics of interacting species.

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## LITERATURE CITED

- Abrams, P. A. 2003. Can adaptive evolution or behaviour lead to diversification of traits determining a trade-off between foraging gain and predation risk. *Evolutionary Ecology Research* 5:653–670.
- Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and developmental times in a seasonal environment. *American Naturalist* 147:381–385.
- Abrams, P. A., and L. Rowe. 1996. The effects of predation on the age and size of maturity of prey. *Evolution* 50:1052–1061.
- Alford, R. A., and G. D. Jackson. 1993. Do cephalopods and larvae of other taxa grow asymptotically? *American Naturalist* 141:717–728.
- Arendt, J. D., and D. N. Reznick. 2005. Evolution of juvenile growth rates in female guppies (*Poecilia reticulata*): predator regime or resource level? Proceedings of the Royal Society of London B. *Biological Sciences*. 272:333–337.
- Arendt, J. D., and D. S. Wilson. 1997. Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). *Evolution* 51:1946–1954.
- Benard, M. F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Annual Review of Ecology and Systematics* 35:651–673.
- Biro, P. A., M. V. Abrahams, J. R. Post, and E. A. Parkinson. 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology* 75:1165–1171.
- Biro, P. A., J. R. Post, and M. V. Abrahams. 2005. Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts. Proceedings of the Royal Society of London B *Biological Sciences*. 272:1443–1448.
- Black, A. R. 1993. Predator-induced phenotypic plasticity in *Daphnia pulex*: life history and morphological responses to *Notonecta* and *Chaoborus*. *Limnology and Oceanography* 38: 986–996.
- Bronmark, C., and J. G. Miner. 1992. Predator-induced phenotypical change in body morphology in Crucian Carp. *Science* 258:1348–1350.
- Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *The Quarterly Review of Biology* 53:243–282.
- Chase, J. M. 1999a. Food web effects of prey size refugia: variable interactions and alternative stable equilibria. *American Naturalist* 154:559–570.
- Chase, J. M. 1999b. To grow or to reproduce? The role of life-history plasticity in food web dynamics. *American Naturalist* 154:571–586.
- Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247:949–951.
- Day, T., P. A. Abrams, and J. M. Chase. 2002. The role of size-specific predation in the evolution and diversification of prey life histories. *Evolution* 56:877–887.
- DeAngelis, D. L., J. A. Kitchell, and W. M. Post. 1985. The influence of Naticid predation on evolutionary strategies of bivalve prey: conclusions from a model. *American Naturalist* 126:817–842.
- de Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* 6:473–487.
- Fraser, D. J., and J. F. Gilliam. 1987. Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behavioral Ecology and Sociobiology* 21:203–209.
- Gotthard, K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. *Journal of Animal Ecology* 69:896–902.
- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500–508.
- Kaplan, R. H., and S. N. Salthe. 1979. The allometry of reproduction: an empirical view in salamanders. *American Naturalist* 113:671–689.
- Kishida, O., and K. Nishimura. 2004. Bulgy tadpoles: inducible defense morph. *Oecologia* 140:414–421.
- Kopp, M., and R. Tollrian. 2003. Reciprocal phenotypic plasticity in a predator-prey system: inducible offences against inducible defenses? *Ecology Letters* 6:742–748.
- Leibold, M., and A. J. Tessier. 1991. Contrasting patterns of body size for *Daphnia* species that segregate by habitat. *Oecologia* 86:342–348.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Ludwig, D., and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* 135:686–707.
- Magnhagen, C., and E. Heibo. 2001. Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. *Functional Ecology* 15:754–762.
- McPeck, M. A., M. Grace, and J. M. L. Richardson. 2001. Physiological and behavioral responses to predator shape: the growth/predation risk trade-off in damselflies. *Ecology* 82:1535–1545.
- McPeck, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. *Ecology* 79:867–879.
- Munch, S. B., and D. O. Conover. 2004. Nonlinear growth cost in *Menidia menidia*: theory and empirical evidence. *Evolution* 58:661–664.
- Ovadia, O., and O. J. Schmitz. 2002. Linking individuals with ecosystems: experimentally identifying the relevant organizational scale for predicting trophic abundances. Proceedings of the National Academy of Sciences (USA) 99:12927–12931.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57:858–873.
- Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- Reznick, D., M. J. Butler, F. H. Rodd, and P. Ross. 1996. Life history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* 50:1651–1660.
- Ricklefs, R. E. 1984. The optimization of growth rate in altricial birds. *Ecology* 65:1602–1616.
- Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* 72:413–427.
- Schmidt, B. R., and J. Van Buskirk. 2004. A comparative analysis of predator-induced plasticity in larval *Triturus* newts. *Journal of Evolutionary Biology* 18:415–425.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* 151:327–342.
- Sibly, R., P. Calow, and N. Nichols. 1985. Are patterns of growth adaptive? *Journal of Theoretical Biology* 112:553–574.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203–224 in W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. New England University Press, Hanover, New Hampshire, USA.

- Skelly, D. K., and E. E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an Odonate predator. *Ecology* 71:2313–2322.
- Spitze, K. 1991. *Chaoborus* predation and life-history evolution in *Daphnia pulex*: temporal patterns of population diversity, fitness, and mean life history. *Evolution* 45:82–92.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.
- Sundstrom, L. F., M. Lohmus, and R. H. Devlin. 2005. Selection on increased intrinsic growth rates in Coho Salmon, *Oncorhynchus kisutch*. *Evolution* 59:1560–1569.
- Thompson, J. N. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago, Illinois, USA.
- Urban, M. C. 2006. Evolution and ecology of species interactions across multiple spatial scales. Dissertation. Yale University, New Haven, Connecticut, USA.
- Urban, M. C., and D. K. Skelly. 2006. Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* 87:1616–1626.
- Werner, E. E. 1988. Size, scaling and the evolution of life. Pages 60–81 in B. Ebenman and L. Persson, editors. *Size-structured populations: ecology and evolution*. Springer-Verlag, Heidelberg, Germany, USA.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242–272.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Wilbur, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* 78:2279–2302.
- Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182:1305–1314.
- Wilson, D. S. 1975. The adequacy of body size as a niche difference. *American Naturalist* 109:769–784.
- Wissinger, S. A. 1992. Niche overlap and the potential for competition and intraguild predation between size-structured populations. *Ecology* 73:1431–1444.

#### APPENDIX

The outcome of model extensions to iteroparity, predators with growth linked to prey capture, prey-size-dependent predator growth, and prey growth plasticity (*Ecological Archives* E088-156-A1).