

THE ROLE OF SIZE-SPECIFIC PREDATION IN THE EVOLUTION AND DIVERSIFICATION OF PREY LIFE HISTORIES

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Abstract.—Some of the best empirical examples of life-history evolution involve responses to predation. Nevertheless, most life-history theory dealing with responses to predation has not been formulated within an explicit dynamic food-web context. In particular, most previous theory does not explicitly consider the coupled population dynamics of the focal species and its predators and resources. Here we present a model of life-history evolution that explores the evolutionary consequences of size-specific predation on small individuals when there is a trade-off between growth and reproduction. The model explicitly describes the population dynamics of a predator, the prey of interest, and its resource. The selective forces that cause life-history evolution in the prey species emerge from the ecological interactions embodied by this model and can involve important elements of frequency dependence. Our results demonstrate that the strength of the coupling between predator and prey in the community determines many aspects of life-history evolution. If the coupling is weak (as is implicitly assumed in many previous models), differences in resource productivity have no effect on the nature of life-history evolution. A single life-history strategy is favored that minimizes the equilibrium resource density (if possible). If the coupling is strong, then higher resource productivities select for faster growth into the predation size refuge. Moreover, under strong coupling it is also possible for natural selection to favor an evolutionary diversification of life histories, possibly resulting in two coexisting species with divergent life-history strategies.

Key words.—Food web, life-history theory, predator, reproductive effort, resource gradient.

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Environmental sources of mortality represent one of the most important selective factors governing life-history evolution, and mortality is often size specific (Stearns 1992; Charlesworth 1994). Indeed, some of the best-documented empirical examples of life-history evolution represent responses to natural selection caused by size-specific predation. Preeminent among these is the study of life-history evolution in guppies (Reznick and Endler 1982; Reznick and Bryga 1987; Reznick et al. 1990, 1996). Differences in the mortality imposed on guppies by different fish predators have likely played a key role in the evolution of different patterns of reproductive effort. In particular, populations exposed to strong predation on large individuals have evolved an increased reproductive effort and attain maturity at a smaller size and earlier age compared with populations exposed to weaker predation on primarily small individuals (but for results suggesting that the situation is likely more complex, see Reznick et al. 1996; Reznick and Travis 1996). This type of size specificity characterizes many predator-prey systems, and it is often the case that prey can escape predation by growing sufficiently large (Werner and Gilliam 1984; Endler 1986; Cohen et al. 1990; Wellborn 1994; Chase 1999a,b; Johnson and Belk 1999, 2001; Persson et al. 1999).

Size-specific predation is also thought to be important in the evolution of life-history plasticity. Well-known examples include the developmental and life-history changes that occur among a variety of freshwater animals, including the zooplankton *Daphnia* (Spitze 1991), snails (Crowl and Covich 1990; Chase 1999b), and even fish (Brönmark and Miner 1992; Belk 1998). For example, Chase (1999b) conducted an experiment in which *Helisoma* snails were allowed to develop under different levels of perceived size-specific predation. His results demonstrated that snails appear to adjust their

life-history strategies adaptively, devoting more energy to growth and less to reproduction early in life, when exposed to high levels of predation on small individuals, to grow quickly into a size refuge. Interestingly, the extent to which this occurs also depends on the level of food resources available to the snails. High resource levels result in greater growth when individuals are exposed to size-specific predation, but have no effect when size-specific predation is absent.

Despite the apparent significance of size-specific predation for life-history evolution, most theory on life-history evolution has not been developed within a dynamic food-web context (Partridge and Harvey 1988; Stearns 1992; Roff 1992). In particular, most theoretical explorations of the importance of predation have not explicitly considered the way in which the population dynamics that result from ecological interactions between predator and prey (as well as those between the prey and its resource) produce the selective regimes that shape life-history evolution. Rather, much of this theory has treated predation as another source of density-independent mortality on the prey species, and thus has neglected possible indirect feedbacks between the population dynamics of predators and prey as well as the prey and its resources (Schaffer 1974a,b; Law 1979; Michod 1979).

The population dynamic consequences of predation are evolutionarily important, in large part because they usually generate frequency-dependent selection. In particular, the evolutionary success of any life-history strategy will likely depend strongly on the frequency of other life-history strategies in the population. The reason is that these other life-history strategies will affect resource and predator densities, which themselves will be important determinants of the evolutionary success of any life-history strategy. Previous the-

oretical results have demonstrated that the inclusion of frequency-dependent selection can, in general, substantially alter predictions about life-history evolution (Mirmirani and Oster 1978; Abrams 1983, 1989; Charlesworth 1993; Kawecki 1993; Day and Taylor 1996, 2000; Heino et al. 1997; Svensson and Sheldon 1998; Van Dooren and Metz 1998; Diekmann et al. 1999). Most interesting is the possibility of ecologically mediated disruptive selection. In such situations, natural selection can drive the evolution of a trait to a value at which the ecological interactions generate disruptive selection endogenously, favoring evolutionary diversification (Christiansen 1991; Abrams et al. 1993; Geritz et al. 1998; Doebeli and Dieckmann 2000). In the context of life-history evolution, this would mean that natural selection favors an evolutionary diversification of life histories, possibly ultimately resulting in the coexistence of two (or more) character-displaced life-history strategies. Such phenomena are excluded a priori by theory based on models that lack frequency dependence.

More recent theory has incorporated some element of indirect ecological feedbacks on life-history evolution. Abrams and Rowe (1996) present a general analysis of the effects of predation on age and size of maturity of their prey. Their analysis includes the response of the prey's resources to the lower prey population densities produced by predators. However, it does not analyze the feedback between prey life history and predator density. Heino et al. (1997) explored a model for the evolution of semelparity versus iteroparity that allowed for some forms of ecological interactions. However, they did not address the issue of size-specific predation per se. Lastly, Chase (1999b) analyzed a model that was explicitly based on a food web involving dynamics of the predator, a prey species with the potential for predator-induced life-history plasticity, and the prey's resources. This model examined the ecological outcomes of a species with adaptive life-history plasticity, but if the same trade-off governs adaptive plasticity as does the evolution of life-history strategies, then his results might also be viewed as evolutionary responses rather than plastic ones. Nevertheless, the method of analysis a priori excluded some interesting outcomes, such as the potential for mixed life-history strategies (where individuals devote some energy to both growth and reproduction) as well as the potential for ecologically mediated disruptive selection, which can result in evolutionary diversification and the coexistence of two character-displaced life-history strategies.

We explore how the selective regime arising from competition for resources and size-specific predation shape life-history evolution. We assume the prey species experiences a trade-off between growth to large size versus reproduction at a small size. We also suppose that both large and small prey compete with one another for resources and that small individuals suffer additional mortality due to predation by a top predator. We use an explicit, dynamic food-web model of these interactions and the selective pressures shaping life-history evolution of the prey emerge from these ecological dynamics. We concentrate on two extreme assumptions about predator population dynamics: (1) a dynamic predator, meaning that the predator's per capita growth rate is affected only by its intake rate of the prey (and density-independent mor-

tality); and (2) a static predator, meaning that predator density is constant regardless of the population densities of other elements of the food web.

The model is used to address two main questions. First, when there is an evolutionarily stable life history in this model, we are interested in determining how the parameters governing the various ecological interactions affect the nature of this ESS. For example, under what conditions do we expect evolution of a life-history strategy that entails rapid growth to a large size at the expense of reproduction while small and vice versa? Second, under what conditions do we expect ecologically mediated disruptive selection to favor the evolutionary diversification of life-history strategies?

THE MODEL

The ecological model employed is similar to a diamond-shaped food web in which there is one resource, one predator, and two consumer (prey) species that share both predator and resource (Armstrong 1979; Holt et al. 1994). Here, there is only a single prey species that occupies the middle trophic level, but it is divided into two stages indexed by s and b for small and big (see also Chase 1999b). Throughout this paper we assume that the big individuals are immune to predation, whereas the small individuals suffer predation at a per capita rate s_p . Thus, there is an advantage to growing quickly through the small size class to reach the predation size refuge. The life-history parameter, g , represents the growth strategy of the organism in question and is the trait that is assumed to be evolutionarily labile. We assume that it lies between zero and one and that small individuals become large individuals at a per capita rate gg_{\max} , where g_{\max} is the maximum rate.

Both stages consume the same resource with attack rates a_s and a_b , and both can produce small individuals through reproduction. The parameters b_s and b_b represent the conversion coefficients of resource into offspring by small and big individuals, respectively, and we assume that the cost of growing quickly into the size refuge is a reduced rate of offspring production as a small individual. In other words, there is a trade-off between g and b_s such that b_s is a decreasing function of g . This function is assumed to reach a maximum value of ϕ at $g = 0$ and a minimum of zero at $g = 1$. Strictly speaking, this function represents a constraint rather than a trade-off because there might be genotypes with a low growth rate to large size as well as a low rate of reproduction when small. This would result in a negative genetic correlation between g and b_s in the population that is less than perfect (as is typically observed). For a given level of g , however, those genotypes with the largest value of b_s will be selectively favored. Therefore the trade-off curve described above can be thought of as a boundary in $g - b_s$ space beyond which there is no genetic variation.

Both small and big individuals suffer density-independent mortality at per capita rates d_s and d_b . Resources for the prey species in question are assumed to be replenished according to a logistic equation, where K is their carrying capacity in the absence of the prey species and ρ is the per capita growth rate of the resource when it is at low density. Finally, a parameter β gives the conversion rate of consumed small

individuals into new predators, and μ is the per capita mortality rate of the predator. This results in the system of differential equations,

$$\frac{dR}{dt} = \rho R \left(1 - \frac{R}{K} \right) - a_s N_s R - a_b N_b R \tag{1}$$

$$\begin{aligned} \frac{dN_s}{dt} = & a_s N_s R b_s(g) - g g_{\max} a_s N_s R - d_s N_s + b_b a_b N_b R \\ & - s_s P N_s, \end{aligned} \tag{2}$$

$$\frac{dN_b}{dt} = g g_{\max} a_s N_s R - d_b N_b, \text{ and} \tag{3}$$

$$\frac{dP}{dt} = \beta s_s P N_s - \mu P. \tag{4}$$

The above system assumes that the predator density changes dynamically in response to the consumer density and the consumer's size structure (the dynamic predator case). The other situation to be examined is one in which predator density is constant regardless of the consumer and resource dynamics (the static predator case). This assumption might apply if predator density is largely determined by a higher level predator, a nonfood resource not represented in the model (e.g., nesting sites), or perhaps even the density of some other prey species. It is worth noting, however, that because a constant predator density simply acts as an additional source of density-independent mortality on the consumer, the static predator case is also formally equivalent to a no-predator model. To model the static predator scenario we use the above dynamical system but we suppose that P is constant (and thus we do not need eq. 4).

As already mentioned, our goal is to explore the way in which the ecological interactions embodied by the above model affect the evolution of the life-history parameter, g . For example, which parameter combinations result in natural selection favoring rapid growth into the size refuge at the expense of reduced reproductive output as a small individual, and which combinations favor the reverse? Moreover, is it possible that frequency-dependent selection will result in the evolutionary diversification of life-history strategies?

To address these evolutionary issues, we need to allow for variation in the life-history strategy g within the population. The approach we use is basically a game-theoretic one (Maynard Smith 1982). We allow at most two different life-history strategies to be present at any given time. We suppose that a particular strategy makes up most of the population, and we consider the invasion of this population by alternative life-history types. Evolutionary change is thus viewed as a series of successive invasion attempts and the occasional replacement of alleles coding for different values of the life-history parameter. This approach can be used to determine evolutionarily stable life-history strategies, and it can also be used to determine when we expect natural selection to favor an evolutionary diversification of life-history strategies (Christiansen 1991; Geritz et al. 1998). We also point out that the evolution of traits under this general approach are very similar to those produced by quantitative genetic models (Iwasa et al. 1991; Abrams et al. 1993; Taylor 1996; Taylor and Day 1997; Abrams 2001). Additionally, as with much

previous life-history theory based on optimality models, our approach assumes that genetic constraints do not prevent natural selection from driving the population to the evolutionarily stable life history. As such, the results presented here are best thought of as being indicative of the nature of selection arising from the ecological interactions under consideration. Of course, the ultimate outcome of evolution will be the result of such selective factors interacting with potential genetic constraints, as well as other evolutionary processes such as genetic drift.

To carry out our analysis, we augment the above model (eqs. 1–4) to allow for another life-history type that has a different pattern of growth versus reproduction (i.e., a different value of g , which we denote by \hat{g}). An evolutionarily stable life-history strategy (i.e., an ESS) has the property that, if this strategy dominates the population, then no other life-history strategy can increase when rare (Maynard Smith 1982). If we use $\lambda(\hat{g}, g)$ to denote the growth rate of life-history strategy \hat{g} (when rare) in a population dominated by life-history strategy g , then an ESS life-history strategy, g^* , satisfies the condition $\lambda(\hat{g}, g^*) \leq \lambda(g^*, g^*)$ for all $\hat{g} \neq g^*$. The growth rate of a mutant life-history strategy depends on the resident life-history strategy because the resident life-history strategy will determine the equilibrium density of the resource and the predator (in the case of a dynamic predator), and these food-web components will obviously play an important role in determining whether the mutant can invade. For example, a mutant life-history strategy might be able to increase when rare for some resident life-history strategies and not for others. This illustrates the inherent frequency-dependent nature of selection that arises from the ecological interactions (Abrams 1989; Abrams et al. 1993).

The above ESS condition is typically difficult to work with, and consequently we will focus on local conditions. In particular, because λ must be maximized in \hat{g} when $\hat{g} = g^*$, the following first derivative condition must hold for $0 < g^* < 1$:

$$\left. \frac{\partial \lambda(\hat{g}, g)}{\partial \hat{g}} \right|_{\hat{g}=g^*} = 0. \tag{5}$$

Values of g^* satisfying condition (5) will be referred to as ‘‘evolutionary equilibria’’ because directional selection ceases to act when (5) holds. In particular, $\partial \lambda / \partial \hat{g}|_{\hat{g}=g}$ is a measure of the strength of directional selection. For evolutionary equilibria identified by condition (5) to be of biological relevance, directional selection must favor life-history strategies closer to g^* if the resident strategy, g , is slightly displaced from this equilibrium. In other words, directional selection should be positive, favoring larger strategies if $g < g^*$, and it should be negative, favoring smaller strategies if $g > g^*$. Together, this implies that the following (local) convergence condition must hold:

$$\left. \frac{d}{dg} \left[\frac{\partial \lambda(\hat{g}, g)}{\partial \hat{g}} \right] \right|_{g=g^*} < 0 \tag{6}$$

(Eshel 1983; Taylor 1989; Christiansen 1991; Abrams et al. 1993; Gertiz et al. 1998).

Whether selection is disruptive or stabilizing will be de-

terminated by the sign of the second derivative of λ with respect to \hat{g} . If

$$\frac{\partial^2 \lambda(\hat{g}, g)}{\partial \hat{g}^2} \Big|_{g=g^*} < 0, \tag{7}$$

then selection will be stabilizing, whereas if condition (7) is reversed, then selection will be disruptive. Lastly we note that the above three conditions assume we are dealing with an intermediate value of g^* (rather than $g^* = 0$ or $g^* = 1$). Values of g^* on the boundaries must be treated separately. We will concentrate primarily on intermediate values in the results below.

RESULTS

We only explore parameter ranges for which all components of the food web remain extant and for which a stable demographic equilibrium is attained. In both the dynamic and the static predator scenarios, the equilibrium condition (5) for g^* is given by

$$g_{\max} \frac{a_b b_b R^*|_{g=g^*}}{d_b} + \left(\frac{db_s}{dg} \Big|_{g=g^*} - g_{\max} \right) = 0 \tag{8}$$

(Appendix), where $R^*|_{g=g^*}$ is the equilibrium resource density attained when the consumer population is using the ESS life-history strategy, g^* .

Condition (8) can be understood by considering the expected lifetime reproductive output of an individual with a mutant life-history strategy, g . The expected amount of time spent as a small individual is $1/(a_s g_{\max} gR + d_s + s_s P)$, during which the rate of reproduction is $a_s b_s R$. The probability that a small individual becomes big (rather than dying) is $a_s g_{\max} gR / (a_s g_{\max} gR + d_s + s_s P)$, and the expected reproductive output of a big individual is $a_b b_b R / d_b$. Therefore, the total expected reproductive output of a mutant is

$$\frac{a_s b_s \hat{R}}{a_s g_{\max} g \hat{R} + d_s + s_s \hat{P}} + \frac{a_s g_{\max} g \hat{R}}{a_s g_{\max} g \hat{R} + d_s + s_s \hat{P}} \frac{a_b b_b \hat{R}}{d_b}, \tag{9}$$

where the resource, \hat{R} , and predator, \hat{P} , densities are determined by the resident life-history strategy. The ESS life-history strategy is one that maximizes the total expected lifetime reproductive output (eq. 9) with respect to g . Differentiating this expression with respect to g (to obtain a first-order condition characterizing the ESS) produces the left side of (8). This expression simply represents the effect of increasing g slightly from g^* , so that reproduction as a small individual is decreased slightly but growth into the big size class is slightly faster. The terms $db_s/dg|_{g=g^*} - g_{\max}$ give the decrease in reproductive output when small that occurs from a small increase in g , whereas $g_{\max} a_b b_b R^* / d_b$ gives the increase in growth-mediated reproductive output that occurs from a small increase in g , both effects being measured in terms of new offspring. At evolutionary equilibrium, these costs and benefits must exactly balance. Also notice that the difference between the dynamic and static predator scenarios lies solely in how the equilibrium resource density, R^* , depends on the life-history strategy, g .

Condition (8) reveals when directional selection ceases, but, as mentioned earlier, this is only of interest for equilibria

for which condition (6) is satisfied because it is only such equilibria that the population will attain. The Appendix shows that, for both the static and the dynamic predator cases, this condition evaluates to

$$g_{\max} \frac{a_b b_b}{d_b} \frac{dR^*}{dg} \Big|_{g=g^*} + \frac{d^2 b_s}{dg^2} \Big|_{g=g^*} < 0. \tag{10}$$

Finally, as mentioned above, condition (7) determines whether selection at equilibrium is stabilizing or disruptive. For both the static and the dynamic predator cases this condition evaluates to

$$\frac{d^2 b_s}{dg^2} \Big|_{g=g^*} < 0 \tag{11}$$

(Appendix).

Some interesting conclusions can be drawn immediately from the above general results. First, notice that the same three equilibrium and stability conditions arise for both the static and the dynamic predator cases. The sole difference between these cases lies in the way that the equilibrium resource density is determined by the resident life-history strategy, g^* . Second, recall that for the population mean life-history strategy to evolve to a point at which natural selection favors an evolutionary diversification, condition (10) must hold when condition (11) fails (implying disruptive selection at the evolutionary equilibrium). It can be seen from condition (10) that this requires $dR^*/dg < 0$. Therefore, we expect natural selection to drive the population to a point where evolutionary diversification occurs, only when the equilibrium resource density decreases with an increase in the life-history strategy (i.e., increase in the growth rate of small individuals to large). As will be seen next, the static and dynamic predator cases yield different predictions as a result of this effect.

Dynamic Predator

For the case in which the predator density is dynamically coupled to the consumer species of interest, the equilibrium resource density is given by

$$R^*(g) = \frac{d_b K (s_s \beta \rho - a_s \mu)}{a_b a_s g g_{\max} K \mu + d_b s_s \beta \rho}. \tag{12}$$

Conditions (10) and (11) then show that, provided the relationship between b_s and g is concave-down, equilibria given by condition (8) are evolutionarily stable. In other words, natural selection will drive the mean life-history strategy to the value given by condition (8), and the population will remain there indefinitely (Fig. 1).

Now we can use expression (12) in condition (8) to determine how various ecological factors affect the evolutionarily stable life history. In particular, if

$$\frac{a_b b_b}{d_b} R^* - 1 \tag{13}$$

(which must be positive for condition 8 to hold) increases with some parameter (e.g., the carrying capacity of the resource, K), then, for the equality in (8) to always hold, $db_s/dg|_{g=g^*}$ (which is negative) must become more negative. Giv-

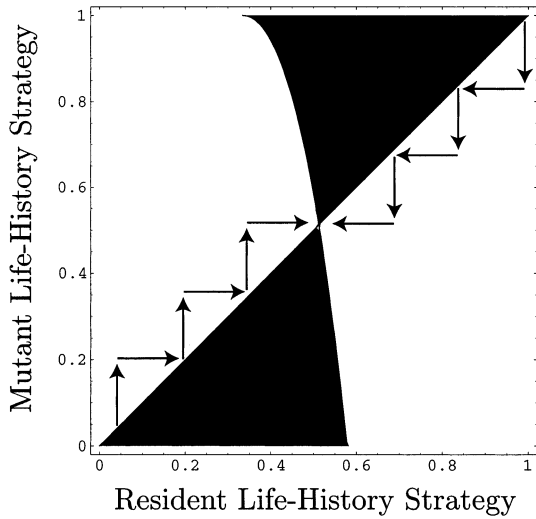


FIG. 1. A pairwise invasibility plot (Geritz et al. 1998) for a set of assumptions and parameters values under which there is an intermediate, monomorphic evolutionarily stable life-history strategy. The trade-off function is $b_s(g) = \phi(1 - x)^{0.5}$, and parameter values are as follows: $g_{\max} = 1$, $\rho = 1$, $K = 100$, $a_s = 0.06$, $a_b = 0.01$, $d_s = 0.01$, $d_b = 0.001$, $b_b = 0.5$, $\beta = 0.3$, $s_s = 0.005$, $\mu = 0.005$, $\phi = 4$. The x-axis is the different possible life-history strategies for the resident and the y-axis is the different possible life-history strategies for the mutant that is attempting to invade. Black regions are combinations of mutant-resident life-history strategies for which the mutant is not able to invade, whereas white regions are combinations for which the mutant is able to invade. The series of arrows shows a potential evolutionary pathway of mutant invasions and replacements (assuming small mutational steps) from either small or high values of the life-history strategy for the resident. Below the evolutionary equilibrium (which occurs at $g = 0.512$ in this example) mutants with a larger life-history strategy can invade, whereas the reverse is true above the evolutionary equilibrium. This reveals that the evolutionary equilibrium is convergence stable (i.e., satisfies condition 6). At the evolutionary equilibrium no mutants above or below can invade, revealing that it is an evolutionarily stable life-history strategy (i.e., satisfies condition 7).

en that the relationship between b_s and g is concave-down, this implies that g^* must increase. Thus, g^* changes in the same direction as expression (13) when any parameter is increased.

Table 1 reveals the predicted change in the ESS life-history strategy, g^* , that occurs with an increase in various parameters. Notice that the ESS life history is independent of the mortality rate of the small stage, d_s . At first one might expect increased density-independent mortality, d_s , to favor a larger g^* because the mortality cost of being a small individual is then larger. This is not the case, however, because increased d_s eventually results in a decreased equilibrium density of the predator. This reduces the mortality cost of being small due to predation, cancelling the increased mortality cost arising from the larger density-independent mortality rate, d_s . This can be inferred by setting equation (4) equal to zero, which shows that the equilibrium density of small individuals is independent of d_s . We note, however, that this result no longer holds if predators also eat big individuals to some extent (unpubl. results). In that case, increasing d_s does result in an increase in g^* , but the effect is small if big individuals are only rarely eaten (unpubl. results).

TABLE 1. The effect of increasing various parameters of the model on the evolutionarily stable life-history strategy when the $b_s - g$ trade-off is concave-down. Results are for a dynamic predator.

Parameter	Effect on g^*
b_b	increase
a_b	increase
d_b	decrease
β	increase
a_s	decrease
μ	decrease
s	increase
d_s	none
K	increase

Another nonintuitive result is that a larger resource carrying capacity, K , results in faster growth to a large size (i.e., a higher g^*). Because the predator density changes dynamically in response to the density of small individuals, the equilibrium density of small individuals is independent of K . Therefore, it is only by increasing g^* when resources become more plentiful that the consumer can actually translate these extra resources into consumers. Otherwise the extra resources are simply converted into an increased predator population. Importantly, this qualitative result continues to hold if big individuals are also eaten by the predator but at some low rate (unpubl. results).

Table 1 also reveals some more intuitive conclusions. A larger reproductive rate for big individuals, b_b , a larger resource attack rate for big individuals, a_b , and smaller density-independent death rate for big individuals, d_b , all result in a higher g^* because they all result in greater relative benefits to being big (Fig. 2). However, a larger resource attack rate when small, a_s , a smaller susceptibility to predation when small, s , a lower predator efficiency, β , or a higher predator death rate, μ , all result in a lower g^* because they all result in greater relative benefits to being small (Fig. 3).

The other question of interest is whether we might expect some form of evolutionary diversification in life-history strategies. For this to occur we require that condition (10) hold while condition (11) fails. As already mentioned, this requirement necessitates that the relationship between b_s and g be concave-up (i.e., $d^2b_s/dg^2|_{g=g^*} > 0$), and that the equilibrium resource density declines with an increase in the resident value of g (i.e., $dR^*/dg|_{g=g^*} < 0$). From expression (12) we can see that the latter condition holds. Because the equilibrium density of small individuals is independent of g (the predator density responds dynamically to keep the density of small individuals constant when g changes) and because increasing g will increase the density of big individuals, the overall density of consumers will increase, thereby decreasing the density of the resource. Therefore, provided that the trade-off function is concave-up, it is possible for evolutionary diversification to occur (Fig. 4). When this happens, numerical results and simulations suggest that the a pair of character-displaced life histories then forms an evolutionarily stable coalition, with one type having very rapid growth to a large size and not reproducing at all as a small individual (i.e., $g^* = 1$) and the other type devoting all of its energy as a small individual to reproduction (i.e., $g^* = 0$). There are other possible outcomes, however, including the possi-

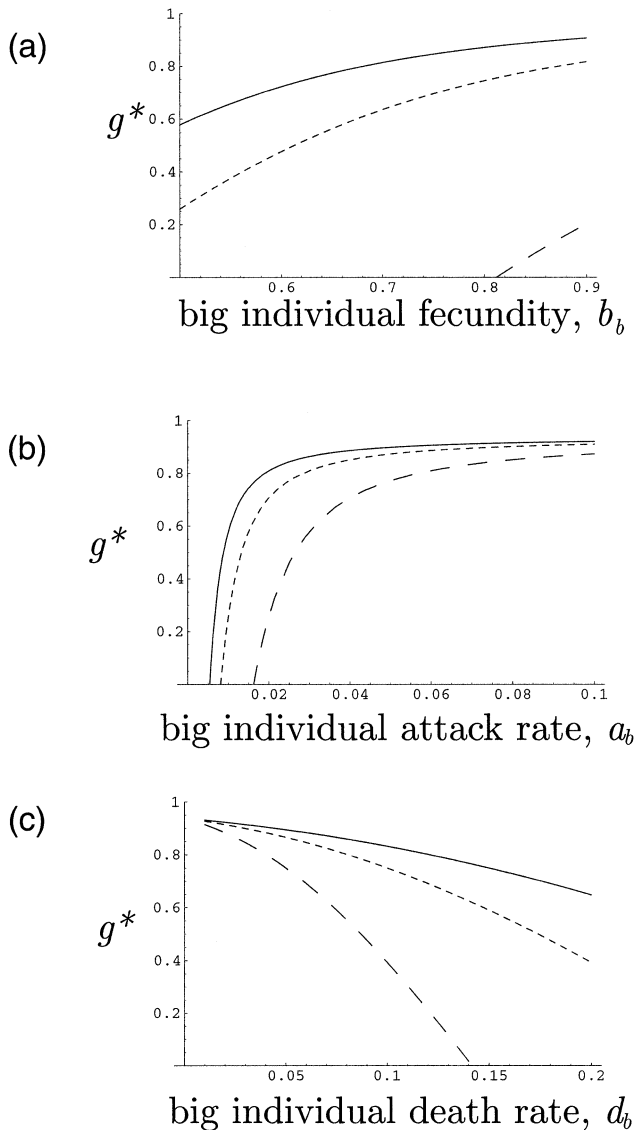


FIG. 2. The relationship between the evolutionarily stable life history, g^* , and various parameters related to large individuals: (a) big individual fecundity, b_b ; (b) big individual resource attack rate, a_b ; (c) big individual death rate, d_b . For each panel the three lines correspond to different resource carrying capacities. Solid line is $K = 150$, dotted line is $K = 100$, and dashed line is $K = 50$. Remaining parameter values for all plots are as follows (when required): $g_{\max} = 1$, $\rho = 1$, $a_s = 0.06$, $a_b = 0.01$, $d_s = 0.01$, $d_b = 0.23$, $b_b = 0.5$, $\beta = 0.2$, $s_s = 0.01$, $\mu = 0.005$ and $b_s(g) = (1 - x)^{0.5}$.

bility of a single, monomorphic life-history strategy being locally evolutionarily stable. Figure 5 presents an example in which, if the population mean life history starts out with a large enough value ($g > 0.94$), then, assuming small mutations, evolution drives the population toward the boundary value of $g^* = 1$. The population will then remain in this monomorphic state (in which small individuals devote all available energy to growth) provided that mutations are small enough. If large mutations occur, however, then the ultimate evolutionary outcome is again a pair of character-displaced life-history strategies.

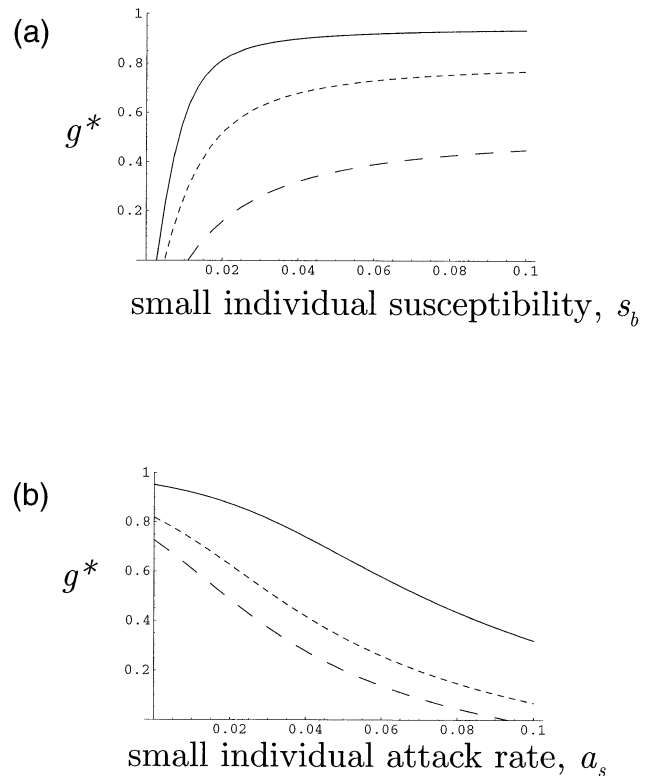


FIG. 3. The relationship between the evolutionarily stable life history, g^* , and various parameters related to small individuals: (a) small individual susceptibility to predation, s_b ; (b) small individual resource attack rate, a_s . For each panel the three lines correspond to different resource carrying capacities. For panel (a) solid line is $K = 150$, dotted line is $K = 100$, and dashed line is $K = 60$. For panel (b) solid line is $K = 150$, dotted line is $K = 100$, and dashed line is $K = 90$. Remaining parameter values for all plots are as follows (when required): $g_{\max} = 1$, $\rho = 1$, $a_s = 0.06$, $a_b = 0.01$, $d_s = 0.01$, $d_b = 0.23$, $b_b = 0.5$, $\beta = 0.2$, $s_s = 0.01$, $\mu = 0.005$, and $b_s(g) = (1 - x)^{0.5}$.

In addition to concave-down and concave-up trade-offs between b_s and g , it is also of interest to consider the linear trade-off case. In this situation we have $d^2b_s/dg^2|_{g=g^*} = 0$ and therefore, for a dynamic predator, condition (10) is always satisfied. Therefore, natural selection drives the population toward the life-history strategy defined by condition (8), but now, once the population is at the ESS, all life-history strategies are neutral with respect to selection. We also note that the ESS life-history strategy, g^* , in this case can still be shown to satisfy all of the predictions in Table 1.

Static Predator

For the case in which the predator is not dynamically coupled to the consumer population, it can be shown that the equilibrium resource density is given by

$$R^*(g) = \{a_s d_b g g_{\max} - a_s d_b b_s(g) + [(a_s d_b g g_{\max} - a_s d_b b_s(g))^2 + 4a_b a_s b_b d_b (d_s + s\hat{P}) g g_{\max}]^{1/2}\} \div (2a_b a_s b_b g g_{\max}). \tag{14}$$

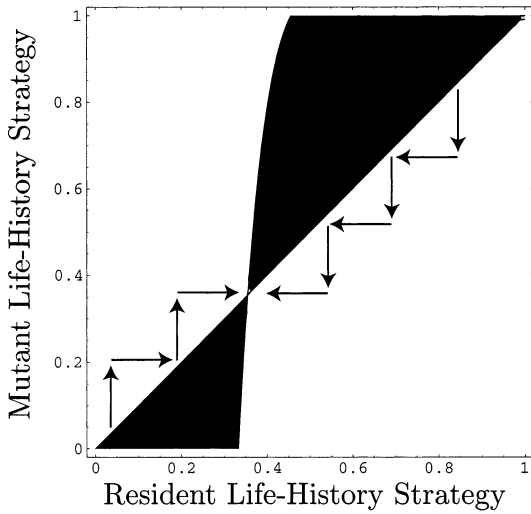


FIG. 4. A pairwise invasibility plot (Geritz et al. 1998) for a set of assumptions and parameters values under which there is not an intermediate, monomorphic evolutionarily stable life-history strategy. The trade-off function is $b_s(g) = \phi(1 - x)^{1.3}$, and parameter values are as follows: $g^{\max} = 1$, $\rho = 1$, $K = 100$, $a_s = 0.06$, $a_b = 0.01$, $d_s = 0.01$, $d_b = 0.001$, $b_b = 0.5$, $\beta = 0.3$, $s_s = 0.005$, $\mu = 0.005$, $\phi = 4$. The x-axis is the different possible life-history strategies for the resident and the y-axis is the different possible life-history strategies for the mutant that is attempting to invade. Black regions are combinations of mutant-resident life-history strategies for which the mutant is not able to invade, whereas white regions are combinations for which the mutant is able to invade. The series of arrows shows a potential evolutionary pathway of mutant invasions and replacements (assuming small mutational steps) from either small or high values of the life-history strategy for the resident. Below the evolutionary equilibrium (which occurs at $g = 0.3547$ in this example) mutants with a larger life-history strategy can invade, whereas the reverse is true above the evolutionary equilibrium. This reveals that the evolutionary equilibrium is convergence stable (i.e., satisfies condition 6). At the evolutionary equilibrium all mutants above and below can invade, revealing that the evolutionary equilibrium is under disruptive selection, which favors life-history diversification (i.e., does not satisfy condition 7).

Again, provided the relationship between b_s and g is concave-down, equilibria given by condition (8) are evolutionarily stable. Following an analysis similar to that used for the dynamic predator case, we can again see that, for an increase in any of the parameters of the model, the change in g^* is in the same direction as the change in expression (13), where R^* is now given by (14).

Table 2 presents the results of this analysis. Unlike the case with a dynamic predator, increasing the density-independent mortality rate of small individuals, d_s (or equivalently their susceptibility to predation in this case, s_s) results in a larger value of g^* . The reason is that increases in this mortality rate are no longer compensated for by a decreased predator density. Thus, the overall mortality cost of being small now increases, favoring faster growth to a large size rather than reproduction while small. Also, unlike the dynamic predator case, increasing the resource carrying capacity, K , has no effect on g^* in the static predator case. Again, with a static predator density the relative value of resources to both small and big consumers is the same.

The more intuitive conclusions for the dynamic predator case remain true in the static predator case as well. A larger

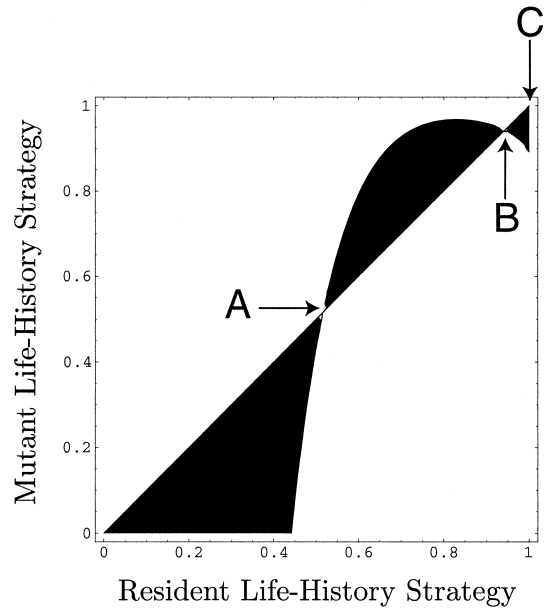


FIG. 5. A pairwise invasibility plot (Geritz et al. 1998) for a set of assumptions and parameters values under which there is not an intermediate, monomorphic evolutionarily stable life-history strategy, but for which an extreme strategy ($g^* = 1$) is a local, monomorphic evolutionarily stable strategy. The trade-off function is $b_s(g) = \phi(1 - x)^{1.3}$, and parameter values are as follows: $g^{\max} = 1$, $\rho = 1$, $K = 100$, $a_s = 0.06$, $a_b = 0.01$, $d_s = 0.01$, $d_b = 0.01$, $b_b = 0.5$, $\beta = 0.3$, $s_s = 0.005$, $\mu = 0.005$, $\phi = 4$. The x-axis is the different possible life-history strategies for the resident and the y-axis is the different possible life-history strategies for the mutant that is attempting to invade. Black regions are combinations of mutant-resident life-history strategies for which the mutant is not able to invade, whereas white regions are combinations for which the mutant is able to invade. The point labeled A is an attracting evolutionary equilibrium that experiences disruptive selection (as in Fig. 4), whereas the point labeled B is a repelling evolutionary equilibrium (i.e., one that the population will never experience because condition 6 is not satisfied). The point labelled C is a local monomorphic evolutionarily stable strategy that the population will evolve toward provided that the initial resident life-history strategy lies above the repelling point labeled B.

reproductive rate for big individuals, b_b , a larger resource attack rate for big individuals, a_b , and smaller density-independent death rate for big individuals, d_b , all result in a higher g^* because they all result in greater relative benefits to being big. Similarly, a larger resource attack rate when

TABLE 2. The effect of increasing various parameters of the model on the evolutionarily stable life-history strategy when $b_s - g$ trade-off is concave-down. Results are for a static predator.

Parameter	Effect on g^*
b_b	increase
a_b	increase
d_b	decrease
β	not applicable
a_s	decrease
μ	not applicable
s	increase
d_s	increase
K	none

small, a_s , results in a lower g^* because it results in a greater relative benefit to being small.

There are also important differences between the static and dynamic predator cases in terms of the evolutionary diversification of life-history strategies. Recall that for diversification we require that condition (10) hold while condition (11) fails. As already mentioned, this requirement necessitates that the $b_s - g$ relationship be concave-up (i.e., $d^2b_s/dg^2|_{g=g^*} > 0$) and that the equilibrium resource density declines with an increase in the resident value of g (i.e., $dR^*/dg|_{g=g^*} < 0$). For a static predator, however, it can be shown that $dR^*/dg|_{g=g^*} = 0$ at the ESS life-history strategy. The reason is that, because there is a single resource and because the predator is now acting simply as another (constant) source of density-independent mortality, the ESS is one that minimizes the resource density at equilibrium, R^* (and this implies $dR^*/dg|_{g=g^*} = 0$). Thus, we can see that conditions (10) and (11) are now identical. Therefore, it is not possible for evolutionary diversification to occur. Also, as with the dynamic predator case, there cannot be an intermediate ESS life-history strategy for concave-up trade-offs between b_s and g . Unlike the dynamic predator case, however, in the static predator case such intermediate ESSs are not possible with linear $b_s - g$ trade-offs either (see also Heino et al. 1997).

DISCUSSION

The results presented here demonstrate that the incorporation of explicit food-web dynamics into life-history theory can have important and perhaps somewhat unanticipated effects. In particular, one of our main qualitative conclusions is that the extent to which the population densities of the species in an ecological community are tightly coupled has an important impact on the evolution of life-history strategies.

In the dynamic predator case, the predator's per capita population growth is determined by its intake of the prey in question. As a result, the predator population density is strongly affected by that of the prey, and there can be non-obvious, indirect effects that result from this interaction. For example, when there is an intermediate, ESS life-history strategy, the nature of this strategy is unaffected by the density-independent mortality rate of small individuals. Although one might expect higher mortality of small individuals to favor the evolution of faster growth to a large size, this does not occur because this higher mortality is exactly compensated for by a decreased predator density and thereby a decreased predator-mediated mortality rate. Another important prediction with a dynamic predator is that an increase in the resource carrying capacity leads to the evolution of an increase in the life-history strategy (meaning greater growth into the size refuge).

In the static predator case, the predator is assumed to be only weakly tied to the prey population. As a result, its density remains largely constant and independent of that of the prey. This might occur if predator density is largely determined by a higher-level predator, a nonfood resource not represented in the model (e.g., nesting sites), or perhaps even the density of some other prey species. It might also occur if there is a suite of predators that have largely the same

effect on the prey species. In the latter case, the overall predation intensity might remain relatively constant even if individual predator species fluctuate in density. As already noted, however, the static predator case is also formally equivalent to a no-predator case because mortality due to predation is simply an additional source of density-independent mortality for the prey in this case. Under these conditions there is no longer any compensation by the predator population when the mortality rate of small individuals increases and therefore this now selects for the evolution of greater growth into the size refuge. Also, with a static predator an increase in the resource carrying capacity no longer has any effect on the evolution of the life-history strategy.

The strength of coupling in these ecological interactions also has important effects on the evolutionary diversification of life-history strategies. In the static predator case it is never possible for ecologically mediated disruptive selection to occur. Rather, there is always only a single ESS life-history strategy that the population converges to. In the dynamic predator case, however, provided that the reproduction-growth trade-off is concave-up, natural selection can sometimes drive life-history evolution to a point at which ecologically mediated disruptive selection occurs, favoring a diversification of life histories. Preliminary numerical results in this case indicate that, if sympatric speciation occurs or if a second closely related (but reproductively isolated) species is introduced into the community, then the system will evolve to point at which there are two coexisting species with character-displaced life histories. One species gains the benefit of reproducing at a small size at the expense of remaining vulnerable to predator, whereas the other species gains the benefit of growing quickly into a size refuge from predation at the expense of forgoing reproduction when small.

Although we were primarily interested in the difference between the static and dynamic predator cases, it is interesting to note that the same general analytical results (i.e., conditions 8, 10, and 11) are valid for the case of a dynamic predator and a static resource density. In this case, however, the equilibrium resource level, R^* , is simply a parameter rather than a dynamic variable in these conditions. As a result, we can use an analysis similar to that earlier to see that a single, intermediate, monomorphic life-history strategy will be evolutionarily stable only when the $b_j - g$ trade-off is concave-down (as with a static predator). Moreover, an evolutionary diversification of life-history strategies is not possible with static resources either. In fact the ESS life history is now one that *maximizes* the predator density, and this ESS growth strategy will be larger if the resource density is larger.

It is also interesting to compare the findings presented here with closely related theories. Heino et al. (1997) presented a model that is similar to the case explored here with a linear trade-off between growth of reproduction. They did not explore the effects of size-specific predation per se, but they did find that an intermediate ESS life history was possible only when the ecological feedback had two dimensions (e.g., via both predators and resources). Our dynamic predator case is an example of this—the resource dynamics and the predator dynamics are part of the ecological feedback. Abrams and Rowe (1996) considered a range of models of life-history evolution in response to changes in predator pressure. These

models all involved predator populations that were decoupled from their prey, but that could produce an indirect response in their prey's resource. They found that the direction of change in age and/or size of maturity among prey in response to a given change in predation intensity could be reversed when resources were dynamic rather than static. Similar kinds of results are found here if we compare the dynamic predator/dynamic resource results with the dynamic predator/static resource results (mentioned briefly above). Increasing the predation intensity can be accomplished by increasing the prey's susceptibility, s , and Table 1 shows that this leads to an increase in the evolutionarily stable growth rate when both predator and resources are dynamic. When the resources are static, however, condition (8) shows that the evolutionarily stable growth rate is unaffected by s (because R^* is then a constant parameter). Thus, although not a reversal of the prediction, the difference in resource dynamics yields qualitatively different predictions.

The two scenarios considered here, namely the static and dynamic predator cases, are really two extremes along a continuum of ecological coupling between predator and prey. It would be useful to know the way in which results are altered by allowing an intermediate level of coupling (which is probably most realistic). This could be done in a number of ways, for example, by including other prey species in the model in addition to the focal prey, making the death rate of the predators density dependent, or including some density-independent immigration of the predators. At some point, as the coupling becomes very weak, we would expect the predictions to shift from those of the dynamic predator to those of the static predator. But it would be useful to know how sensitive life-history evolution is to this coupling as one moves along this continuum.

It would also be useful to examine different assumptions regarding the way in which size structure is incorporated into the model. One interpretation of the form of size-structured dynamics in equations (1–4) is that individuals spend a random (and exponentially distributed) amount of time in the small size class before moving to the large one. Although such models are often used, another possibility is that individuals spend a fixed amount of time in the small size class before moving to the large one (effectively making it an age-structured model). The extent to which this would alter our conclusions is unclear, but it is an interesting subject for future research because reality likely lies somewhere between these two extremes.

To our knowledge there is not yet any empirical data that clearly addresses the predictions of the theory presented here, but Chase's (1999b) study is one suggestive example. As noted in the introduction, one of the more interesting findings of this study was the result that snails did not alter their life histories plastically in response to different levels of resource unless a predator was present. At first glance, this result fits nicely with the predictions of the theory presented above if we suppose that the predator in question is tightly coupled to the snail. In this case, when predators are present we have a dynamic predator and our results predict that higher resource levels should lead to greater growth into the size refuge. However, when predators are absent, this is equivalent to the static predator scenario, and our results predict that

there should then be no response to resource levels. However, this simple match between theory and data should be interpreted with some caution. For this kind of life-history plasticity to evolve, snails in natural populations would need to have some chance of developing in a predator and a non-predator environment, and where predators are present, they must be strongly coupled ecologically to the snail prey. The extent to which this is likely (or even possible) will depend on many factors, including the spatial scale of movement of predator and prey. Consequently, a more explicit model of this situation would be required before one could say with confidence that the mechanism described here is a plausible explanation for the evolution of this life-history plasticity.

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APPENDIX

Here we derive the main analytical results of the article. The calculations are presented for the case in which predator density is dynamic, but the calculations for the static predator case are virtually identical and produce the same results. Denoting the mutant consumer strategy and densities by \hat{g} , \hat{N}_s , and \hat{N}_b , respectively, the augmented dynamical system is given by

$$\frac{dR}{dt} = \rho R \left(1 - \frac{R}{K} \right) - a_s N_s R - a_b N_b R - a_s \hat{N}_s R - a_b \hat{N}_b R, \quad (\text{A1})$$

$$\frac{dN_s}{dt} = a_s N_s R b_s(g) - g g_{\max} a_s N_s R - d_s N_s + b_b a_b N_b R - s_s P N_s, \quad (\text{A2})$$

$$\frac{dN_b}{dt} = g g_{\max} a_s N_s R - d_b N_b, \quad (\text{A3})$$

$$\frac{dP}{dt} = \beta s_s P N_s + \beta s_b P \hat{N}_s - \mu P, \quad (\text{A4})$$

$$\frac{d\hat{N}_s}{dt} = a_s \hat{N}_s R b_s(\hat{g}) - \hat{g} g_{\max} a_s \hat{N}_s R - d_s \hat{N}_s + b_b a_b \hat{N}_b R - s_s P \hat{N}_s, \quad \text{and} \quad (\text{A5})$$

$$\frac{d\hat{N}_b}{dt} = \hat{g} g_{\max} a_s \hat{N}_s R - d_b \hat{N}_b. \quad (\text{A6})$$

To determine if the mutant type can invade, we linearize the above system at the equilibrium with the mutant absent (i.e., $\hat{N}_s = \hat{N}_b = 0$). This results in a Jacobian matrix of the form

$$\begin{bmatrix} \mathbf{R} & \mathbf{A} \\ \mathbf{0} & \mathbf{M} \end{bmatrix}, \quad (\text{A7})$$

where $\mathbf{0}$ is a 2×4 matrix of zeros and \mathbf{R} , \mathbf{A} , and \mathbf{M} are 4×4 , 4×2 , and 2×2 matrices, respectively. Because the Jacobian (A7) is an upper triangular matrix, its eigenvalues are those of the submatrices \mathbf{R} and \mathbf{M} . Given that the resident type reaches an equilibrium in the absence of the mutant, the submatrix \mathbf{R} has eigenvalues whose real parts are negative. Therefore, the invasion of the mutant is completely determined by the eigenvalues of the submatrix \mathbf{M} . The dominant eigenvalue, λ , is given by

$$\lambda(\hat{g}, g) = \frac{1}{2}(a_s b_s(\hat{g})R^* - d_b - d_s - a_s \hat{g} g_{\max} R^* - s_s P^* + R), \tag{A8}$$

where

$$R = [Z^2 - 4(d_b(d_s + a_s \hat{g} g_{\max} R^* + s_s P^*) - a_b a_s b_b \hat{g} g_{\max} R^{*2} - a_s d_b b_s(\hat{g})R^*)]^{1/2} \tag{A9}$$

$$Z = (d_b + d_s + a_s \hat{g} g_{\max} R^* + s_s P^* - a_s b_s(\hat{g})R^*), \tag{A10}$$

and R^* and P^* are the resource and predator densities at equilibrium in the absence of the mutant consumer (which are determined, in part, by the strategy, g , of the resident type). We also have that $\lambda(g, g) = 0$ for all g because, when the mutant and resident consumer have the same strategy, the mutant will be exactly neutral with respect to its ability to invade (technically, it is possible that this condition need not hold if R is imaginary, but it is possible to prove that this cannot happen in the present model). As a result, we can use the fact that

$$d_b + d_s + a_s \hat{g} g_{\max} R^* + s_s P^* - a_s b_s(\hat{g})R^* = R \tag{A11}$$

to simplify the following calculations.

Condition (8)

The first-order condition is given as

$$\left. \frac{\partial \lambda}{\partial \hat{g}} \right|_{\hat{g}=g^*} = \frac{1}{2} \left(a_s \frac{db_s}{d\hat{g}} R^* - a_s g_{\max} R^* - s_s P^* + \frac{dR}{d\hat{g}} \right) \Bigg|_{\hat{g}=g^*}, \tag{A12}$$

which, using (A9) and (A11), can be simplified to

$$\frac{a_s R^* \left(a_b b_b g_{\max} R^* + d_b \left(\frac{db_s}{dg} - g_{\max} \right) \right)}{d_b + d_s + a_s \hat{g} g_{\max} R^* + s_s P^* - a_s b_s R^*}. \tag{A13}$$

Setting this equal to zero gives condition (8) of the text.

Condition (7)

The second-order condition is given as

$$\left. \frac{\partial^2 \lambda}{\partial \hat{g}^2} \right|_{\hat{g}=g^*} = \frac{1}{2} \frac{\partial}{\partial \hat{g}} \left(a_s \frac{db_s}{d\hat{g}} R^* - a_s g_{\max} R^* - s_s P^* + \frac{dR}{d\hat{g}} \right) \Bigg|_{\hat{g}=g^*}, \tag{A14}$$

which, using (A9), (A11), and condition (8) can be simplified to

$$\frac{a_s d_b R^*}{d_b + d_s + a_s \hat{g} g_{\max} R^* + s_s P^* - a_s b_s R^*} \frac{d^2 b_s}{dg^2}. \tag{A15}$$

The denominator of (A15) is positive (from equality A11), and therefore the second-order condition is given by (11) of the text.

Condition (6)

The convergence condition is found by differentiating (A13) with respect to g before evaluating it at $g = g^*$. Using condition (8) in this calculation gives

$$\left. \frac{d}{dg} \frac{\partial \lambda(\hat{g}, g)}{\partial \hat{g}} \right|_{\hat{g}=g} = \frac{a_s R^* \left(a_b b_b g_{\max} \frac{dR^*}{dg} + d_b \frac{d^2 b_s}{dg^2} \right)}{d_b + d_s + a_s \hat{g} g_{\max} R^* + s_s P^* - a_s b_s R^*}. \tag{A16}$$

Noting that the denominator of (A16) is positive (from equality A11) results in condition (10) of the text.