

The Balance of Terror: An Alternative Mechanism for Competitive Trade-Offs and Its Implications for Invading Species

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ABSTRACT: This article uses models to propose an explanation for three observations in community ecology: the apparent overreaction of prey to attack by specialist predators, the existence of a common trade-off among components of competitive ability in communities of unrelated competitors, and the ability of invading species to break the native trade-off. Strategies that increase resource collection ability are assumed to increase vulnerability to attack by specialist consumers according to a vulnerability function. If competitors compete for a common resource and share the same form of the vulnerability function, then they are favored to converge on the same evolutionarily stable level of competitiveness or trade-off curve even if the parameters describing their specialized consumers differ. The position of the common strategy or trade-off curve depends on the whole guild, with more speciose guilds tending to favor higher levels of competitiveness. Invaders can break the native trade-off if they come from a guild with a higher trade-off curve, an effect possibly enhanced evolutionarily by escape from specialist consumers.

Keywords: competition, defense, invading species, trade-offs.

This article proposes a testable explanation of three perplexing observations in communities of competing organisms. Each is exemplified by the behavior of ants.

Apparent Overreaction to Attack by Specialist Parasitoids. An entire colony of native fire ants, *Solenopsis geminata*, will cease food collection when confronted by even a single phorid fly parasitoid (Feener and Brown 1992). It is un-

clear what sort of cost-benefit analysis would be appropriate to assess this response (Abrams 1993).

Common Trade-Off among Components of Competitive Ability. Both Fellers (1987) and Holway (1997) have shown that species of native ant follow the same trade-off between different components of resource-gathering ability, such as exploitation and interference competition. It seems unlikely that a common constraint, such as resource allocation, would produce the same trade-off curve across unrelated species.

Ability of Invading Species to Break the Native Trade-off. That the trade-off curve is not universal has been repeatedly demonstrated by highly successful invading species that can "break the rules." Both the Argentine ant *Linepithema humile* (Holway 1997 and in press) and the imported fire ant *Solenopsis invicta* are superior to native ants in both exploitation and interference ability. Why have none of the native ants found the secret to success (Davidson 1998)?

The models presented here propose that evolutionary responses to specialist predators or parasitoids (hereafter referred to as consumers) explain these patterns. Many observations and models show that trade-offs between resource collection and surviving predation can support intermediate strategies (Lima and Dill 1990; Abrams 1993; Houston et al. 1993). When a single species is faced by a single consumer, the exact intermediate strategy favored depends on the efficiency and fecundity of that consumer. The models proposed here place species in a competitive context and show that appropriate symmetries in the interaction between competitors and their consumers lead to a convergence of competitor strategies.

The models have three main structural components. All species compete for a common pool of resources (and are thus members of the same "guild"), have specialist consumers, and use a common set of strategies to exploit those resources. Strategies that make a species an effective competitor make it more vulnerable to attack by its specialist consumer. The "vulnerability function," relating vulner-

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ability to competitive ability, has the same form for each species, although the specific parameters can differ. With these conditions, the evolutionarily stable strategy (ESS) for coexisting competitors converges on a common shared strategy (when the strategy space is one-dimensional) or a common trade-off curve (when the strategy space is two-dimensional). The position of this common strategy or trade-off curve depends on the properties of the entire community of competitors and consumers. I term this shared strategy the "balance of terror" because species remain in balance in response to their terror of being eaten.

Background

The models consider three primary issues: coexistence, invasions, and trade-offs between foraging and predation. I review literature on these three topics in turn and then discuss related models.

Coexistence

Three general mechanisms promote coexistence of species that share a habitat. First, competitors might have specific niches, such as specialized predators or resources, that regulate populations independently (Holt and Lawton 1994). Second, there might be a trade-off between different modes of habitat exploitation, such as competitive ability and dispersal, guaranteeing that no one species is the best at everything (Bengtsson et al. 1994). Third, species might be sufficiently similar that processes excluding a particular species are too weak or slow to overcome stochasticity (Hubbell and Foster 1986). The last two mechanisms depend on some sort of character convergence (Vadas 1990), either to a common trade-off curve or a common suite of traits. The coexistence in this article assumes that a specialist consumer defines the niche for each competitor.

Invasions

Invading species show that trade-off curves are not universal. Some invaders can join a community by exploiting empty niches or by leaving their specialist consumers behind (Williamson 1996). Others can destroy a native guild by breaking the rules and freeing themselves from trade-offs that constrain natives (Davidson 1998). For example, Holway (in press) has shown that Argentine ants are superior at both exploitation and interference competition in a native community, lying above the native trade-off curve (Fellers 1987). Similarly, nonnative grasses have highly successful water-use strategies that are not exploited by natives (Baruch and Fernandez 1993; Williams and Black 1994; Holmes and Rice 1996).

Foraging/Predation Trade-Offs

Many studies have shown a trade-off between resource collection and surviving predation. Lima and Dill (1990) review the many changes in behavior induced by predation risk, and Houston et al. (1993) review models used to find optimal behaviors in the presence of such a trade-off. Foragers must choose speed (Werner and Anholt 1993) and patches (Mangel and Clark 1988; Kennedy et al. 1994) based simultaneously on food and danger levels. Plants must choose levels of costly defense (Coley et al. 1985; Mole 1994). Brawling birds and fish must face up to the fact that escalated fighting behavior increases predation risk (Jakobsson et al. 1995). Shapely, rapidly growing bacteria are more vulnerable to predators (Nakajima and Kurihara 1994).

In defense theory, trade-offs are often thought of as balancing costs and benefits (Coley et al. 1985). This article addresses costs that are expressed in a competitive context. Traits for which competitive success creates higher vulnerability to consumers (Levin and Paine 1974; Levin et al. 1977; Pacala and Crawley 1992; Holt et al. 1994; Hulme 1996) are referred to as competition for enemy free space (Jeffries and Lawton 1984). Bergelson (1994) reviews literature indicating that costs of defense are higher in stressful and competitive conditions.

Related Models

Many modelers have looked at the optimal trade-off between foraging success and predation (Houston et al. 1993). I review models here that have examined evolution when the costs and benefits of strategies are mediated through susceptibility to attack and success in competition.

Holt et al. (1994) study the conditions under which competitors can coexist when they also share a predator but do not include an evolutionary component. The models in this article consider the evolutionary response of prey. Several models have examined competition mediated through evolution of predator behavior (Williamson 1993; Moody et al. 1996). Brown and Vincent (1992) studied coevolutionary models of predator-prey interaction, finding the conditions under which a trade-off between competitive ability and susceptibility to attack can support communities with more than one species.

Several models track the evolutionary response of a single prey species to a consumer. Abrams (1992) showed that evolution might favor prey that overreact to attack, altering strategies so much that they have increased population size in the presence of predators. Similarly, Abrams (1993) showed that behaviors that trade-off surviving predation against foraging success will evolve to an intermediate level and that avoiding predators can diminish

population growth rates more than direct mortality (see also Werner and Anholt 1993). Abrams and Matsuda (1994) examined evolution of competitive characters that carry other costs, showing the possibility of oscillations between high and low levels of the competitive trait. As an even more extreme reaction, Matsuda and Abrams (1994) found that “timid consumers” could drive themselves to extinction by steadily evolving lower and lower foraging rates to avoid predation.

Basic Model

Overview

The basic community consists of a set of competitors, each beset by a specialist consumer (Grover 1994; fig. 1). There are N_i competitors of species i attacked by P_i specialist consumers. Competitor fitness has two components, resource collection and survivorship, linked by their common dependence on the competitiveness parameter c_i .

The vulnerability function h describes how vulnerability increases as a function of the competitiveness c_i . The overall vulnerability of competitor i depends on two properties of its specialist consumer: the area of discovery a_i that measures per capita consumer efficiency (Hassell 1978) and the consumer population P_i that depends on consumer fecundity. For example, if $h(c)$ is a linear function, each competitor will experience linearly increasing vulnerability to attack, although the slopes for different species can differ.

The three structural assumptions are as follows. The competitors compete for a common resource R , have specialist consumers, and share a common strategy for exploiting the resource. The increasing vulnerability function $h(c)$ quantifies how strategies that make a species an effective competitor make it more vulnerable to attack. All species share the same vulnerability function, even though the parameters determining area of discovery and consumer population dynamics can differ.

Because this model has n competitors interacting with $n + 1$ resources (the actual resource and the n specialist consumers), it is easy to find parameter values that produce coexistence (Levin 1970; Armstrong and McGehee 1980). Grover (1994) derived the general conditions for coexistence in models of this form. I will suppose that n species of competitors and their specialist consumers coexist.

Dynamics

Each competitor collects a share of the resource pool that is inversely proportional to the total competition T_i experienced by that competitor. The total competition de-

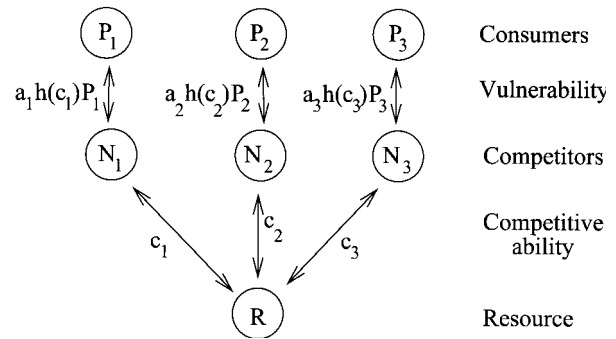


Figure 1: Basic connections in the model: N_i is the population of competitor i with competitiveness c_i (ability to collect the resource R). It is attacked by a population P_i of specialized consumers with area of discovery a_i . Vulnerability h describes how increased competitiveness leads to higher vulnerability to attack.

pends on the number and competitiveness through the sum

$$T_i = \sum_{j=1}^n f(c_i, c_j) N_j. \quad (1)$$

The function $f(c_i, c_j)$ describes the effect one individual with competitiveness c_j has on an individual with competitiveness c_i . It must be increasing in c_j and decreasing in c_i and has scaling $f(c, c) = 1$ for any value of c . A competitor with a larger value of c_i exerts more effect on other competitors. The sum acts as a surrogate for the resource (Adler 1990).

The fraction of competitors of species i that survive attack, g_i , depends on the competitiveness c_i through the vulnerability function h and the equation

$$g_i = F(a_i h(c_i) P_i). \quad (2)$$

The survivorship function F is a decreasing of its argument

$$x_i = a_i h(c_i) P_i, \quad (3)$$

termed the “vulnerability” of competitor i . The key assumption driving the analysis is that the vulnerability function h and the survivorship function F must be the same for each competitor, although the parameters describing their consumers can differ.

The population N_i' of competitors in the following generation is

$$N'_i = \frac{N_i}{T_i} g_i. \tag{4}$$

The ratio N_i/T_i is the fraction of total available resources captured and converted into next year's population of competitor i . This population is multiplied by the survivorship g_i . These dynamics are coupled to those of the consumers, which need not be specified explicitly.

Evolution

Each competitor experiences a trade-off between resource acquisition and vulnerability to consumer attack. We can thus look for the ESS level of c_i (Maynard Smith 1982; Vincent and Vincent 1996). Suppose a new variant of competitor i arises with competitiveness \hat{c}_i and population size \hat{N}_i . Because it shares consumers with the resident, the population in the next generation is

$$\hat{N}'_i = \frac{\hat{N}_i}{\hat{T}_i} \hat{g}_i,$$

where

$$\hat{T}_i = \sum_{j=1}^n f(\hat{c}_i, c_j) N_j$$

and

$$\hat{g}_i = F(a_i h(\hat{c}_i) P_i)$$

when the invader is rare. The strategy of the resident appears in the total competition \hat{T}_i and in the consumer population P_i .

The framework of this model matches that underlying the ESS maximum principle (Vincent and Vincent 1996). The invader will succeed if its per capita reproduction exceeds that of the resident, which is 1 at equilibrium. A particular strategy c_i^* is uninvadible if all invaders with $\hat{c}_i \neq c_i^*$ have per capita reproduction < 1 . When the resident strategy and its consumer are at dynamic equilibrium, the ESS occurs where the per capita reproduction g_i/T_i takes on its maximum for the values of P_i and N_j established by the resident strategy.

Existence of a Shared ESS with One-Dimensional Strategy Set

In the simplest model of exploitation competition, the per capita effect is given by the ratio

$$f(c_i, c_j) = \frac{c_j}{c_i}. \tag{5}$$

In this case, c_i might represent the per capita time spent foraging by competitor i . The total competition T_i experienced by competitor i is

$$T_i = \sum_{j=1}^n \frac{c_j}{c_i} N_j = \frac{T}{c_i}, \tag{6}$$

where $T = \sum_{j=1}^n c_j N_j$. The fraction of resources collected by competitor i is thus

$$\frac{N_i}{T_i} = \frac{c_i N_i}{T},$$

meaning that each competitor species receives a fraction of food proportional to its own total competitiveness.

This model of exploitation competition assumes that the resource pool is divided up entirely among the members of the guild even when population sizes are small. This might be an appropriate model for a resource like space that gets filled every generation or for highly fecund organisms that quickly reach a resource-limited carrying capacity. A more general model, consistent with slower population dynamics, includes resource depletion from other sources. A simple version represents depletion with the parameter β and takes the form

$$N'_i = \frac{c_i N_i}{\beta + T} g_i.$$

Because the qualitative results of the analysis are unchanged with this more realistic form, the following analysis is based on the case with $\beta = 0$.

Particular forms of the vulnerability and survivorship functions simplify the analysis. Assume that

$$h(c_i) = c_i^m \tag{7}$$

for some positive power m , the same for each competitor. The value $m = 1$ is appropriate when c_i represents time spent foraging.

A simple survivorship function F is based on the negative binomial distribution (Hassell and May 1973), used to avoid the unstable dynamics associated with the simpler Nicholson-Bailey model (Hassell 1978), and has the form

$$F(x) = \frac{1}{[1 + (x/k)]^k}, \tag{8}$$

where k is the negative binomial parameter. In general, the equilibrium tends to be stable for lower values of k

that aggregate attacks on competitors (Hassell and May 1973).

With exploitation competition (eq. [5]), the ESS is the strategy that maximizes $c_i F(x_i)$ because this is proportional to the per capita reproduction. Using $h(c_i) = c_i^m$ (eq. [7]), the derivative is

$$\begin{aligned} \frac{d}{dc_i} c_i F(x_i) &= F(x_i) + c_i \frac{dF}{dx_i} m a_i c_i^{m-1} P_i \\ &= F(x_i) + m x_i \frac{dF}{dx_i} \\ &= F(x_i) \left[1 - \frac{m x_i}{1 + (x_i/k)} \right]. \end{aligned}$$

This equation depends only on x_i and is equal to 0 when

$$x_i = x^* = \frac{k}{km - 1} \Rightarrow g^* = F(x^*), \quad (9)$$

as long as $km > 1$. If $km < 1$, the cost of higher competitive ability resulting from increased vulnerability never outweighs the benefit, and all competitors would evolve to ever increasing values of c_i in the absence of other constraints. I consider only the case $km > 1$.

Equation (9) indicates that the common vulnerability and survivorship functions favor strategies that lead to equal vulnerability x^* and equal survivorship g^* for each competitor. The ESS competitiveness c_i for competitor i is found by solving $x^* = a_i h(c_i) P_i$, or

$$c_i = \left(\frac{x^*}{a_i P_i} \right)^{1/m}.$$

The ESS strategy of each competitor depends on the area of discovery a_i and equilibrium population size P_i of its consumers. Those blessed with inefficient or infrequent consumers can apparently use a higher value of c_i .

This analysis, however, neglects the second key structural component of the models; all competitors coexist on a single resource. The population in the next generation is

$$N_i' = \frac{N_i}{T_i} g_i = \frac{c_i N_i}{T} g_i$$

(eqq. [4] and [6]). If the competitors coexist at an equilibrium,

$$\frac{c_i g_i}{T} = 1.$$

Suppose that each competitor is using its ESS strategy. Then $g_i = g^*$ for each i . Combining these equations implies that

$$c_i = \frac{T}{g^*} = c^* \quad (10)$$

for each i . Each competitor in a guild of competitors coexisting on a single resource will evolve to share the same strategy.

Because each competitor has the same value of c^* and x^* ,

$$a_i P_i (c^*)^m = x^* \Rightarrow a_i P_i = \frac{x^*}{(c^*)^m} = P_a^*,$$

where P_a^* is the consumer pressure. At equilibrium, more efficient consumers must have lower population sizes (or they would have driven their food to extinction).

It might seem unlikely that the system would balance itself in this way. To see that it is possible, assume a specific dynamic for the consumers,

$$P_i' = \lambda_i N_i (1 - g_i) \quad (11)$$

(Hassell 1978). The consumer fecundity λ_i can differ for each species, and P_i appears implicitly in g_i . At the ESS, the equilibrium (N_i^*, P_i^*) satisfies

$$P_i^* = \lambda_i N_i^* (1 - g^*).$$

Multiplying both sides by a_i and using the fact that $a_i P_i = P_a^*$,

$$P_a^* = a_i P_i = a_i \lambda_i N_i (1 - g^*) \Rightarrow N_i^* = \frac{1}{a_i \lambda_i} \frac{P_a^*}{1 - g^*}.$$

The equilibrium population of competitor i is smallest for those competitors attacked by highly efficient or highly fecund consumers. Equilibrium values for both N and P are decreasing functions of area of discovery a when all consumers have the same fecundity λ (fig. 2A). When all consumers instead have the same area of discovery, equilibrium values for P are constant and equilibrium values of N are decreasing functions of fecundity (fig. 2B).

The exact value of the ESS competitive ability can be found by substituting the solution for N_i into the equilibrium condition. At the ESS,

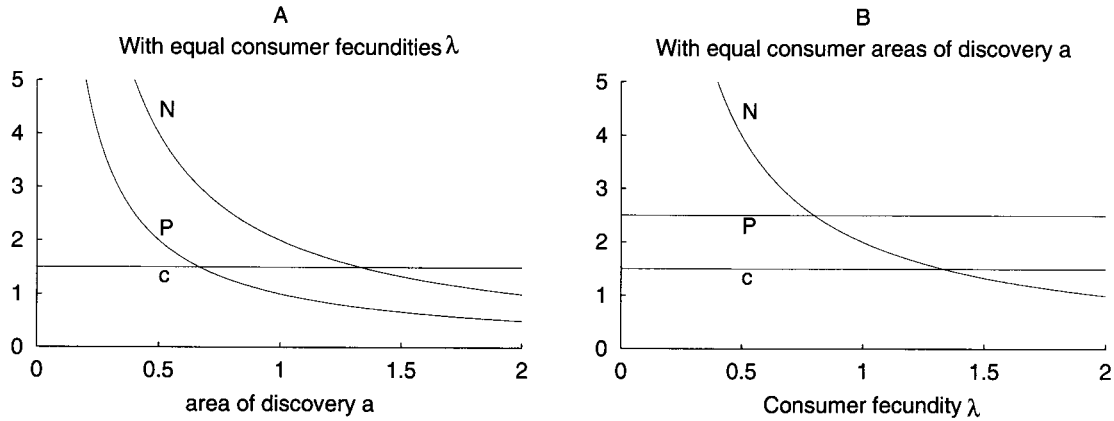


Figure 2: Dependence of competitor equilibria (N), consumer equilibria (P), and optimal strategy (c) on the area of discovery a (A) and the fecundity λ (B).

$$T = \sum_{i=1}^n c^* N_i^* = c^* \sum_{i=1}^n \frac{1}{a_i \lambda_i} \frac{P_a^*}{1 - g^*}.$$

Using the fact that $T = c^* g^*$, and the equation for P_a^* , the ESS value c^* is

$$c^* = \left[\frac{Ax^*}{g^*(1 - g^*)} \right]^{1/m}, \tag{12}$$

where

$$A = \sum_{i=1}^n \frac{1}{a_i \lambda_i}.$$

The shared value of c^* is thus larger when there are more competitors in the guild or when the consumers are either less efficient or less fecund on average (with the appropriate average being the harmonic mean of the product). If one competitor is blessed with extremely feeble consumers, the whole guild responds with higher competitiveness.

The results presented here carry over to more general forms of F and h and to forms of f that model interference competition (results not shown). In these cases, the dynamics can become unstable, but the basic result of convergence to a common strategy holds with unstable dynamics as long as the competitors coexist.

Results When Vulnerability Functions Differ

If the competitors do not share the same vulnerability function, they will not share the same ESS strategy. However, if they share the same survivorship function F , the

structure of the model still imposes a relationship among the ESS competitor strategies.

Suppose that competitors interact through the exploitation competition (eq. [5]), that survivorship follows the negative binomial (eq. [8]), and that vulnerability follows a power rule as in equation (7) but with a different exponent m_i for each competitor, or

$$h_i(c_i) = c_i^{m_i}. \tag{13}$$

The optimum vulnerability x_i of competitor i is, as in equation (9),

$$x_i^* = \frac{k}{km_i - 1}. \tag{14}$$

The survivorship $g_i^* = F(x_i^*)$ does differ for different competitors but depends only on the shape parameter m_i and not on the consumer properties a_i or P_i . Using the equilibrium condition $c_i g_i^* = T$, we can solve for c_i^* as a decreasing function of m_i . A competitor with a less steep vulnerability function (smaller m_i) should adopt a higher value of c_i and ends up with lower survivorship (fig. 3).

An alternative model has competitors sharing the same vulnerability function as before, so that $x_i = a_i P_i c_i^m$, but obeys

$$N_i' = \frac{c_i N_i}{T} s_i F(x_i),$$

where s_i is a survivorship factor that could be different for each competitor species. As before, each competitor shares the same optimal $x_i = x^*$ (eq. [9]), but now c_i^* is inversely proportional to s_i . A competitor with a low value of s_i must

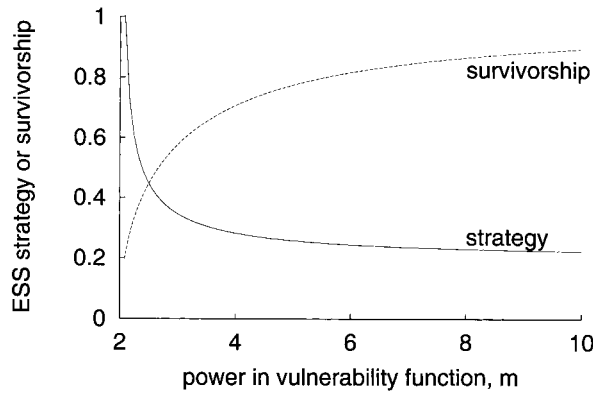


Figure 3: Response of competitiveness and survivorship when the value of m_i in the vulnerability function $h(c) = c^m$ differs for each species in the guild. Mortality follows the negative binomial with $k = 0.5$. Values shown assume a total competitiveness $T = 5$.

adopt a more competitive strategy to compensate and pays with lower overall survivorship as before.

Multiple Competitor Strategy Dimensions

When competitors have a single strategy dimension, the evolutionary dynamics push all competitors toward the same strategy, independent of the parameters describing the individual consumer. What happens when the strategy space is higher-dimensional? A two-dimensional model is diagrammed in figure 4. Competitor i has two strategies, b_i and c_i , each of which may increase vulnerability to its consumer. In general, set the survival g_i of competitor i to be

$$g_i = F(y_i, x_i), \quad (15)$$

where

$$y_i = \tilde{a}_i h_b(b_i) P_i \quad \text{vulnerability due to strategy } b$$

$$x_i = a_i h_c(c_i) P_i \quad \text{vulnerability due to strategy } c.$$

Again, competitors share the vulnerability functions h_b and h_c and the survivorship function F but can have different consumer parameters \tilde{a} , a , and P .

The competitiveness function $f(b_i, c_i, b_j, c_j)$ is also a function of both strategies, again describing the effect of one individual with competitiveness (b_j, c_j) on an individual with competitiveness (b_i, c_i) . The total competition experienced by competitor i is

$$T_i = \sum_{j=1}^n f(b_i, c_i, b_j, c_j) N_j. \quad (16)$$

Because I have been unable to obtain general results, the analysis in this section is restricted to a special case. However, I have not found any case, either analytically or through computer experimentation, that behaves qualitatively differently. Suppose that survivorship takes the negative binomial form

$$g_i = F(y_i, x_i) = F(y_i + x_i) = \frac{1}{\{1 + [(y_i + x_i)/k]\}^k} \quad (17)$$

(as in eq. [8]), that h_b and h_c are power functions

$$h_b(b) = b^{m_b}, \quad h_c(c) = c^{m_c}, \quad (18)$$

and that the competitive effect is

$$f(b_i, c_i, b_j, c_j) = \frac{b_j}{b_i} + \sigma \frac{c_j}{c_i}, \quad (19)$$

where σ can take on any positive value.

The per capita reproduction of competitor i is g_i/T_i , where

$$T_i = \sum_{j=1}^n f(b_i, c_i, b_j, c_j) N_j = \frac{T_b}{b_i} + \sigma \frac{T_c}{c_i}$$

for

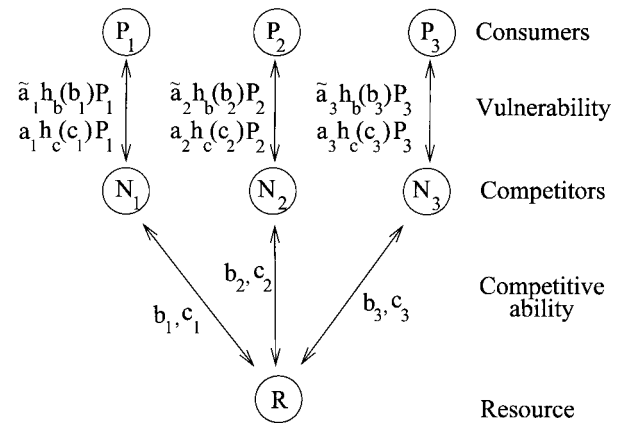


Figure 4: Connections in the general model with two strategic dimensions. Each competitor has two strategies, b_i and c_i , that increase vulnerability to attack through the vulnerability functions h_b and h_c , respectively.

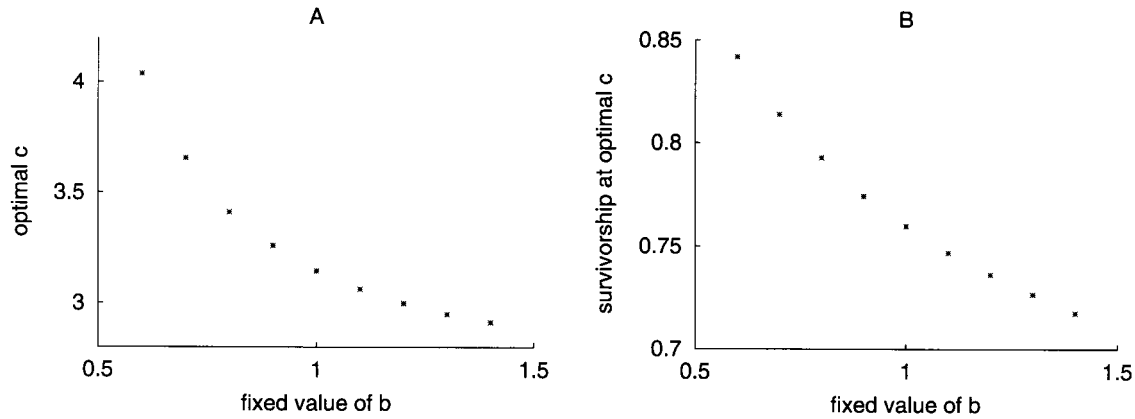


Figure 5: ESS strategies (A) and survivorships (B) of 10 different species when b_i is a fixed value and only c_i affects vulnerability to consumers. Parameters are $\sigma = 2.0$, $k = 0.5$, $m_c = 3.0$. Parameter values for the 10 species are $\lambda = 2.3, 1.9, 1.8, 2.1, 2.4, 2.5, 1.7, 1.9, 1.4, 2.3$; $a = 0.9, 1.2, 1.3, 0.7, 0.8, 1.1, 1.0, 0.6, 1.4, 1.3$; and $b = 1.3, 0.7, 0.8, 1.1, 1.0, 0.6, 1.4, 1.3, 0.9, 1.2$.

$$T_b = \sum_{j=1}^n b_j N_j, \quad T_c = \sum_{j=1}^n c_j N_j.$$

Character Convergence with a Joint Vulnerability Function

Before addressing the truly two-dimensional case, suppose that survivorship is filtered through a single vulnerability function according to

$$x_i = a_i h(b_i, c_i) P_i, \quad g_i = F(x_i).$$

For example, assume that

$$h(b_i, c_i) = (b_i c_i)^m,$$

a reasonable form if c_i is fraction of time spent foraging and b_i is apparency while foraging. We can maximize the per capita reproduction by taking the partial derivatives with respect to b_i and c_i and setting them equal to 0. After some algebra, we find

$$x_i = \frac{k}{2km - 1}.$$

As before, identical values of x_i lead to values of $b_i = b^*$ and $c_i = c^*$ that are identical for each competitor. This apparently two-dimensional model behaves like a one-dimensional model because the vulnerability is one-dimensional.

Evolution to Constraint Curve When Competitors Differ Intrinsically

This section treats the case where strategy b_i is not linked to increased vulnerability and has evolved to some optimal value for each competitor as a result of other constraints. The following section allows both b_i and c_i to evolve when each creates increased vulnerability.

In the case at hand, strategy b_i does not affect vulnerability, meaning that $\tilde{a}_i = y_i = 0$ for each i . Because b_i is fixed, we maximize only over c_i . Taking the derivative of the per capita reproduction with respect to c_i and setting it equal to 0 leads to

$$\sigma \frac{T_c}{c_i} = m_c \left(1 + \frac{x_i}{k} \right) x_i \left(\frac{T_b}{b_i} + \sigma \frac{T_c}{c_i} \right).$$

The equilibrium condition $T_i = g_i$ implies

$$\frac{T_b}{b_i} + \sigma \frac{T_c}{c_i} = g_i.$$

Subtracting from the previous equation gives

$$\frac{T_b}{b_i} = g_i \left[1 - m_c x_i \left(1 + \frac{x_i}{k} \right) \right].$$

For a given value of b_p , we can solve for the vulnerability x_i and thus the survivorship g_i . These different values can be substituted into the equilibrium condition to solve for c_i in terms of b_p , leading to a trade-off where those competitors with higher values of b_i have lower values of c_i (fig. 5A).

The resulting survivorships are shown in figure 5B. Those competitors favored with a higher level of the intrinsic parameter b_i are willing to suffer lower survivorship, matching the pattern found when vulnerability functions differ (fig. 3). Strategy c shows the opposite pattern; competitors with high values of c_i have higher survivorship.

Evolution to a Constraint Curve When Both Strategies Can Evolve

Suppose that b_i affects vulnerability through the function h_b and is free to evolve. We maximize the per capita reproduction by taking its derivatives with respect to b_i and c_i and setting them equal to 0,

$$\sigma \frac{T_c}{c_i} = m_c T_i \frac{x_i}{1 + [(y_i + x_i)/k]}, \quad (20)$$

$$\frac{T_b}{b_i} = m_b T_i \frac{y_i}{1 + [(y_i + x_i)/k]}. \quad (21)$$

Adding and dividing by T_i ,

$$1 + \frac{y_i + x_i}{k} = m_b y_i + m_c x_i. \quad (22)$$

Suppose b_i takes on some value. Equations (21) and (22) are two equations for the two unknowns x_i and y_i . Solving does not depend on the parameters a_i or \tilde{a}_i . These solutions can then be substituted into equation (20) to give c_i as a function of b_i . Again, the strategies fall along a trade-off curve even though the consumers of the two competitors differ (fig. 6A). The exact position of a competitor on the trade-off curve is determined by the properties of its consumers.

If $m_b = m_c$, equation (22) can be solved for $y_i + x_i$, meaning that every competitor will have the same survivorship. Otherwise, competitors associated with a high value of the strategy with a lower value of m will have a higher survivorship (fig. 6B).

Discussion

Trade-offs between competitive ability and vulnerability to attack favor the evolution of intermediate trait levels (Abrams 1993). This article argues that a guild of competitors, each competing for the same resource and each beset by a specialist consumer, will evolve to a common level of competitiveness independent of the particular parameters describing the consumer. The assumption required to maintain this balance of terror is that competi-

tors share the same vulnerability function, the functional form translating increased competitive ability into increased vulnerability. When vulnerability functions differ, species with flatter vulnerability function evolve higher competitiveness and lower survivorship than the rest of the guild. Although there was not space to include the analysis, the general result holds when consumers are not exact specialists as long as each competitor is attacked by the same effective number of consumers or when the resource is simultaneously consumed by other organisms.

These results propose explanations for the three observations laid out in the introduction. First, overreaction, perhaps measured by a species giving up more biomass in lost foraging opportunity than in avoidance of predation, makes sense only in the competitive context of that species. In the presence of specialist consumers, a competitor with the potential for dominance may lower its resource gathering effort to match the rest of its guild.

Second, when competitors have two strategy dimensions, at least one of which produces increased vulnerability, evolution pushes them to fall along a common trade-off curve. Trade-off curves are often thought of as a range of solutions to a common allocation constraint (Johnson et al. 1987; Stearns 1992; Mole 1994). The mechanism proposed here is fundamentally different, with allocation decisions constrained by ecological circumstances rather than resource limitation. The common allocation constraint is perhaps most likely to explain a trade-off curve when the competitors are phylogenetically related.

Finally, there is nothing to stop invaders that have left their specialist consumers behind from breaking free from the balance of terror and evolving steadily higher levels of competitiveness. Furthermore, the position of the trade-off curve might be different in the invader's native habitat (fig. 7). If that guild contains a larger number of competitor species or a less fecund or efficient array of consumers, the trade-off curve will be higher. Such invaders will have an immediate advantage, which provides a possible explanation for the phenomenon of biotic resistance, where more diverse communities are less susceptible to invasion (Case 1991).

The generality of these results depends on whether real populations of competitors are attacked either by specialist consumers or in the appropriate symmetrical way, and whether they truly compete for one or a few resources. Few communities have been studied in sufficient detail to check the assumptions (Pacala and Crawley 1992; Goldberg 1996). Where it has been studied, the community structure of consumers can be highly complicated (Hawkins 1994; Memmott et al. 1994).

The models could be extended in several ways. If species compete for several resources, will they still find a common trade-off? It is possible that the behavioral options opened

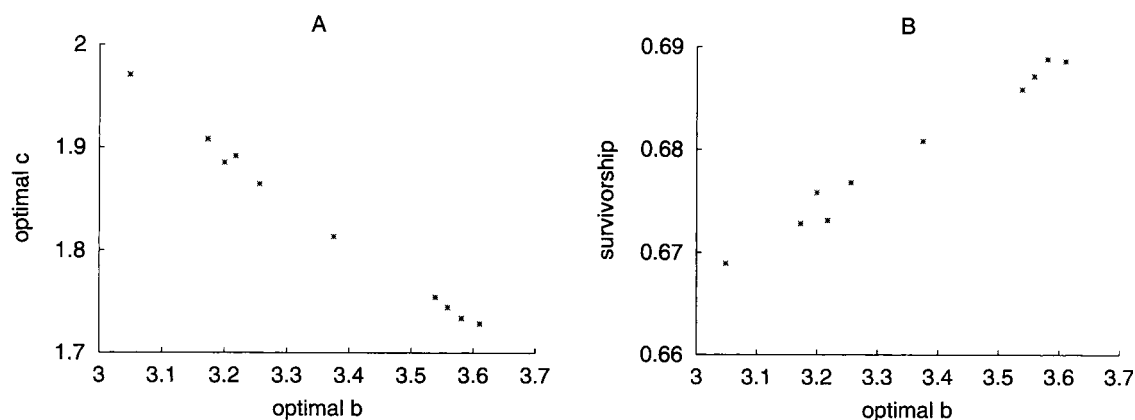


Figure 6: ESS strategies (A) and survivorships (B) of 10 different species when b_i and c_i appear in different functions h_b and h_c . Parameter values are $m_b = 2.5$, $m_c = 5.0$, $k = 2.0$, $k = 0.5$. Species-specific parameters match those in figure 5, with the values for b from figure 5 used as values of \bar{a} . Results are from a simulation.

up in this situation would break the pattern observed here. Patch selection often creates a trade-off between resource exploitation and attack by consumers. Would a model that explicitly included patch choice preserve the symmetry observed here?

The models presented here do not explicitly model behavioral response to the presence of specialized consumers. The competitive trait studied here can be thought of as the flip side of a constitutive defense. Would a model with optimal inducible responses (Adler and Karban 1994) show similar behavior? When consumer populations are roughly constant, the constitutive response modeled here approximates the average behavioral response to encounters with consumers and should provide a good approximation of competitive success in exploitation competition.

The dynamics of consumer-resource interaction are sensitive to the behavior of consumers (Abrams 1986, 1989). When consumers can choose among several competing species, each with its own strategy and level of vulnerability, the functional response to those species strongly determines the selective forces. More sophisticated responses might significantly alter the results. Alternatively, the reproductive system in the competitors could alter evolution (for a discussion of the potential interaction between competitive environments and mating systems, see Proulx 1999).

Finally, the models neglect evolution of consumers (Brown and Vincent 1992). Because competitors evolve to a common trade-off curve even when consumers are described by different parameters, changes in those parameters over time might adjust only the position of the common trade-off curve. However, if consumers evolve at

different rates or evolve different vulnerability functions, the pattern might break down.

The operation of the balance of terror depends on the existence and similarity of the vulnerability function for different competing species. To my knowledge, the function connecting a particular competitive strategy with the risk of attack it engenders has not been measured in any system. Measurements of the costs and benefits of defenses (Karban and Baldwin 1997) can show a trade-off between growth rate and level of attack but have yet to estimate the shape of the resulting curve. If such curves could be feasibly measured in a single guild, the theory predicts that the guild will lie along a trade-off curve and that competitors should avoid strategies capitalized on most effectively by their particular consumers.

If measurements of vulnerability functions reveal sufficiently similar forms among competitors, what predictions does the theory make? First, the model predicts that the responses of competitors to consumer attack, such as those of the native fire ant (Feener and Brown 1992), act to lower the resource gathering potential of this species to match those in the surrounding guild. Colonies from areas with more species of competitor should not respond as much to the threat of attack. Second, when there are two strategy dimensions, survivorship should be higher for those competitors that have high values of the strategy associated with the flatter vulnerability curve.

Invading species should rapidly evolve more competitive traits that make them more susceptible to the consumers they left behind (Blossey and Notzold 1995). As long as the consumers are absent, the native species suffer from the “double whammy” of a nonnative competitor that has been released both numerically and evolutionarily from

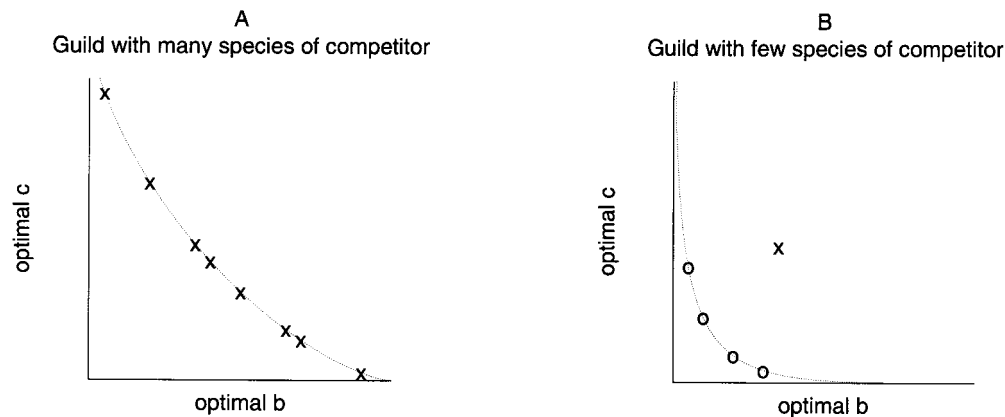


Figure 7: A, Trade-off curve in a hypothetical guild with many species. Each cross represents the ESS strategy of one consumer species. B, Trade-off curve in a hypothetical guild with few species (circles). An invader from the speciose guild (cross) would lie well above the local trade-off curve.

attack. The evolutionary response of the invaders to this release is sure to take some time, perhaps explaining the observation that many invaders expand their range rapidly only after an initial period of slow growth (Veit and Lewis 1996).

However, this evolutionary response might make invaders highly vulnerable to biological control. In particular, if invaders come from a community where the balance of terror favors relatively high competitive levels, the initial response to attack in a new community might be insufficient, leading to extremely high mortality. More speculatively, it is possible that the evolution of the highly successful polygynous form of the imported fire ant in North America (Porter et al. 1988) is only possible because it has escaped from some unknown pathogen. These colonies reproduce by budding rather than through a single queen and should thus be more susceptible to transmission of pathogens. Were the pathogens to be introduced, the more competitive polygynous form might no longer succeed.

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