VOL. 175, NO. 6 THE AMERICAN NATURALIST JUNE 2010 Ⓔ

Evolutionary Balancing of Fitness-Limiting Factors

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Submitted July 20, 2009; Accepted February 9, 2010; Electronically published April 16, 2010

Online enhancements: appendixes, zip file.

ABSTRACT: Debates concerning the roles of different factors that may limit an organism's reproductive success pervade evolutionary ecology. We suggest that a broad class of limiting-factors problems involving essential resources or essential components of reproductive effort can be analyzed with an evolutionary application of Liebig's law of the minimum. We explore life-history evolution using the metaphor of an organism that must harvest two essential resources (resources 1 and 2) from a stochastically varying environment. Our models make three predictions. First, organisms should overinvest, relative to the deterministic case, in harvesting the resource whose per-offspring harvest cost is smaller. Second, at the optimum, organisms balance multiple fitness-limiting factors rather than being consistently limited by one factor. Third, the optimal investment in harvesting a resource is directly linked to the probability that the organism's fitness will be limited by that resource. Under temporal variation, the optimal proportional investment in harvesting resource 1 is equal to the probability that resource 1 will limit fitness. Our results help to explain why the responses of populations to environmental perturbations are hard to predict: as an organism transitions between different limiting factors, its responses to perturbations of those factors will likewise change.

Keywords: limiting factors, Liebig's law of the minimum, life-history evolution, stochastic environments, ecological predictability.

Introduction

All organisms have the potential to produce descendants whose numbers grow exponentially but are eventually prevented from doing so by the action of various factors that limit survival and reproduction. The field of ecology is largely devoted to the study of these limiting factors. Debates concerning the relative importance of different potentially limiting factors for particular microbe, plant, and animal taxa pervade the evolutionary ecology literature (table 1). Important progress has been made in developing theory to resolve these debates in particular contexts (Haig and Westoby 1988; Kozlowski and Stearns 1989; Cohen and Dukas 1990; Kirkwood and Rose 1991; Burd 1995, 2008; Dawkins 1995; Ellers et al. 2000; Gardner et al. 2003; Gandon et al. 2009; Olofsson et al. 2009). However, theoretical treatments of fitness-limiting factors have been developed in isolation from one another, with little attempt to develop a more general approach. Perhaps as a consequence, debates on fitness-limiting factors have persisted and frequently have been contentious, often with opposing positions in which the primacy of a particular limiting factor is championed. The resolution of these debates is important for our understanding of ecology. A population of organisms whose fitness is consistently limited by one particular factor will respond predictably to perturbations of that factor. On the other hand, a population of organisms whose fitness is limited by different factors at different times or places will respond to perturbations less predictably.

We suggest that these seemingly disparate debates concerning limiting factors share a common logical structure. First, the focal organism inhabits a stochastic environment in which it faces more than a single potentially limiting factor. Most of the debates have been framed as the competing importance of two or three factors whose magnitude can vary in time or space (table 1). Second, the organism can allocate resources to ameliorate the impact of a particular potentially limiting factor. However, because resources are finite, an increased allocation to coping with limiting factor A must be traded off against a reduced allocation to coping with limiting factor B. Third, the organism has limited phenotypic plasticity or a limited ability to assess its environment, such that it cannot adjust its allocations to match perfectly its local circumstances. Thus, organisms are faced with an evolutionary problem of how best to allocate finite resources to cope with the impact of multiple limiting factors whose anticipated magnitudes are uncertain.

In this study, we focus on a class of limiting-factors problems that involve essential (nonsubstitutable) resources or essential components of reproductive effort (table 1). These

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Am. Nat. 2010. Vol. 175, pp. 662–674.
DOI: 10.1086/652468

Table 1: Prominent debates in the evolutionary ecology literature framed explicitly as examinations of the relative importance of different fitness-limiting factors

Taxon and limiting factors	References
1. Limiting factors interact as described by Liebig's law of the minimum to shape fitness:	
Any:	
Environmental mortality versus intrinsic mortality (evolution of senescence)	Kirkwood and Rose 1991; Kirkwood 2008
Physical wear of different critical parts of the body	Cartar 1992; Dawkins 1995; Nussey et al. 2007; Carranza and Pérez-Barbería 2007
Carbon versus nitrogen versus phosphorus in the food supply	Bloom et al. 1985; Elser et al. 2000; Sterner and Elser 2002; Elser et al. 2007; Kaspari et al. 2008
Production of zygotes versus production of fully provisioned offspring	Kozlowski and Stearns 1989; Mock and Forbes 1995
Various (protozoan parasites, beetles, wasps):	
Production of daughters versus production of sons (sex allocation under local mate competition)	Heimpel 1994; Nagelkerke and Hardy 1994; Hardy et al. 1998; West et al. 2002; Gardner et al. 2003
Marine phytoplankton:	
Iron versus macronutrients	Boyd et al. 2007
Plants:	
Ovules versus pollination	Burd 1995; Burd et al. 2009
Pollination versus resources for provisioning seeds or maturing fruits	Haig and Westoby 1988; Cohen and Dukas 1990; Ashman et al. 2004; Knight et al. 2005; Aizen and Harder 2007; Burd 2008
Seeds versus availability of animal seed dispersers	Vander Wall et al. 2005; Hampe 2008
Insect herbivores, parasitoids:	
Eggs versus hosts	Rosenheim 1996; Sevenster et al. 1998; Ellers et al. 2000; West and Rivero 2000; Rosenheim et al. 2008; Gandon et al. 2009
Birds and bats:	
Calcium versus energy availability during reproduction	Barclay 1994; Graveland et al. 1994; 2002; Booher 2008
Birds:	
Eggs versus incubation versus provisioning young	Monaghan and Nager 1997; Williams 2005
2. Limiting factors interact multiplicatively to shape fitness:	
Any:	
Natural enemies versus food resources (top-down vs. bottom-up population regulation)	Walker and Jones 2001; Borer et al. 2006; Gruner et al. 2008
Density-dependent mortality factors (generally biotic) versus density-independent mortality factors (generally abiotic)	Turchin 1995
Plants:	
Seeds versus establishment	Moles and Westoby 2002; Clark et al. 2007; Poulsen et al. 2007
Animals:	
Number of offspring versus competition of offspring for a key resource (hosts, nest sites, territories, mates)	Creighton 2005; Goubault et al. 2007; Olofsson et al. 2009
Broadcast-spawning marine invertebrates:	
Sperm limitation versus polyspermy versus resources for provisioning eggs	Styan 1998; Podolsky 2004; Levitan 2006; Bode and Marshall 2007
Nest-building wasps and bees:	
Food resources for offspring versus nest sites versus parasites	Steffan-Dewenter and Schiele 2008

problems can be analyzed with an evolutionary application of Liebig's law of the minimum (Brock 2002). As originally framed, Liebig's law of the minimum states that the rate of plant growth is defined by the single nutrient that is most scarce in relation to the needs of the plant. Here we define a factor (e.g., an essential resource, x) as limiting to fitness (F) if a small increase in the availability of that factor increases realized reproductive success (i.e., $dF/dx > 0$). When this definition is applied to individual organisms faced with a Liebigian limiting-factors problem, we can usually identify a single factor that acts as the limit to fitness (for all other factors, $dF/dx = 0$); however, multiple factors can act simultaneously as limits when the problem is viewed at the population level or at the community level (e.g., Danger et al. 2008).

To the best of our knowledge, the literature on limiting factors has never been synthesized. Here, to motivate our attempt to produce a more general treatment of life-history evolution under multiple potentially limiting factors, we briefly examine previous models of the various context- or taxon-specific expressions of Liebigian limiting-factors problems to ask what predictions have been made regarding (i) the optimal allocations to coping with different potential limitations and (ii) the resulting probabilities that a particular factor will emerge as the limit to fitness.

How should organisms change their allocations to coping with different potentially limiting factors in unpredictable environments? Early models predicted that environmental stochasticity favored increased investment in the less expensive early stages of reproduction (e.g., eggs for birds or insects, ovules for plants; Temme and Charnov 1987; Kozlowski and Stearns 1989; Burd 1995; Sevenster et al. 1998; Ellers et al. 2000) or the less expensive offspring gender in species with local mate competition (Green et al. 1982; Heimpel 1994; Nagelkerke and Hardy 1994; West et al. 2002; Gardner et al. 2003). Later models, however, predicted instead either overinvestment or underinvestment in the initial stages of reproductive effort (Cohen and Dukas 1990; Sakai 1996, 1997; Burd 2008) and highlighted the discrepancy with earlier results. A likely contributor to the lack of consensus is that the subliteratures have not communicated with each other; however, even within the well-integrated literature on plant reproduction, authors have emphasized the divergent predictions of different models (Sakai 1996, 1997; Burd 2008).

Similarly, there has been little agreement on the frequencies with which different factors should be expected to emerge as limits to fitness in stochastic environments. Early analyses, not based in mathematical modeling, led to suggestions that particular factors should function as consistent limits to reproductive success while other factors should be relatively unimportant (e.g., Janzen 1977; Willson and Burley 1983; Godfray 1990; Hardy and Godfray 1990; see reviews in Elser et al. 2000; Sterner and Elser 2002; Williams 2005; Rosenheim et al. 2008). Dawkins (1995), however, considering the functional morphology of organisms, argued that natural selection would never favor a design in which a particular component consistently emerged as the weak link in the organism's physical durability. Such a design, he noted, implied that all other parts were overbuilt. Dawkins (1995, p. 124) argued that a "proper balance" of different limitations should instead be favored by natural selection. Indeed, predictions of preeminent roles for single limiting factors have almost universally failed to be supported when the question of competing limitations has been explored mathematically. Models have suggested instead that organisms should evolve life histories under which the probability of an individual's fitness being limited by any particular factor, P, is intermediate ($0 < P < 1$; Haig and Westoby 1988; Cohen and Dukas 1990; Kirkwood and Rose 1991; Heimpel 1994; Burd 1995; Rosenheim 1996).

But what should the proper balance be? Here there has been less progress. Some authors have suggested that realistically high levels of environmental stochasticity can push life histories very close to the case where one factor is the universal limit (e.g., Begon and Parker 1986; Sevenster et al. 1998; Ellers et al. 2000). Other authors have suggested that the proper balance of two limitations occurs when each is expressed 50% of the time (Thomson 2001). Several models have yielded analytical solutions for expected frequencies with which particular factors will emerge as limits to fitness (Kozlowski and Stearns 1989; Cohen and Dukas 1990; Burd 1995; Rosenheim 1996; Sakai 1996, 1997; Sevenster et al. 1998; Ellers et al. 2000), but simple biological interpretations for the derived expressions have been elusive.

Our goals are to see whether a generic model of life-history evolution under multiple potential limiting factors can lead to simple and readily interpreted predictions for (1) how stochasticity shapes optimal investment in coping with different limiting factors and (2) what the resulting expectations are for the probabilities of being limited by particular factors. Although previous authors have often discussed spatial and temporal stochasticity together, nearly all the models have analyzed spatial variation only (exceptions include Temme and Charnov 1987; Cohen and Dukas 1990). Our final objective is therefore to examine temporal and spatial stochasticity separately and to contrast their effects.

Models

Limiting Factors in a Deterministic Environment

We introduce here the biological metaphor, chosen for its transparency, that we will employ throughout. As a key benchmark, we begin with the case of an organism that lacks phenotypic plasticity and that occupies a deterministic environment. Assume that a hypothetical organism makes copies of itself using just two resources, resources 1 and 2. It harvests these resources from the environment, where they are present in concentrations x and y, respectively, constant over time and space. Our organism allocates proportions u and v from an internal metabolic pool of some constant size to produce pumps for resources 1 and 2, respectively. The central allocation trade-off is

$$u + v = 1. \tag{1}$$

In a key simplifying assumption, we let the harvest of resources be linearly related to the investment in pumps. We let the cost per pump for the two pump types be equal and assume that the pumps have the same inherent capacity (these two assumptions could trivially be relaxed); thus, the lifetime harvests of resources 1 and 2 are proportional to ux and vy, respectively. For simplicity, we assume that the constant of proportionality is 1 in both cases. We denote the amounts of resources 1 and 2 needed to produce a single offspring as a and b, respectively. Thus, the offspring equivalents of resources 1 and 2 that are harvested are ux/a and vy/b, respectively, and the number of offspring that can be produced, a measure of fitness, F, is

$$F = \min\left(\frac{ux}{a}, \frac{vy}{b}\right). \tag{2}$$

Equation (2) is an application of Liebig's law of the minimum to lifetime reproduction. Our use of Liebig's law of the minimum incorporates the key assumptions that our two resources are nonsubstitutable and that one resource does not facilitate acquisition of the other.

Liebig's law of the minimum is a heuristic model for many, but not all, limiting-factor debates (see table 1). In particular, Liebig's law can be applied to two types of limiting-factors debates. First, Liebig's law can be applied to organisms that must harvest from the environment multiple essential resources that are then packaged together when making offspring. For this case, our verbal metaphor is directly appropriate. Second, Liebig's law can be applied to organisms that must make multiple reproductive allocations, without any of which the entire reproductive endeavor fails. This applies to cases where reproduction involves a temporally distinct sequence of allocations (e.g., for plants: allocations first to securing pollinations, then to provisioning seeds, and, finally, to maturing fruits; for birds: allocations first to producing eggs, then to incubating eggs, and, finally, to feeding chicks) or where reproduction requires production of different types of offspring (e.g., both males and females for species with obligate sib mating). In these cases, a different verbal metaphor is needed (investments are no longer made in resource pumps but rather in the different required reproductive allocations), but the mathematical formulation is the same.

We note two important cases in which alternate model formulations may be more useful. First, for some organisms, and especially long-lived and iteroparous organisms, the factor that limits reproductive output may vary over time across successive bouts of reproduction. In this case, lifetime reproductive success for an individual is limited jointly by multiple factors, and a different modeling framework that explicitly considers age-specific mortality and reproduction is needed (e.g., Tuljapurkar et al. 2009). Second, some limiting-factors debates, such as the debate concerning whether population regulation acts via top-down versus bottom-up mechanisms or debates involving the size versus the quality of individual offspring (table 1), involve competing factors that interact multiplicatively to define individual fitness rather than in the complementary manner represented by equation (2).

As shown in figure 1 (*top*), F in equation (2) is maximized with respect to u under the constraint of equation (1) in a deterministic environment at u_{d}^*, given by

$$u_{\mathrm{d}}^* = \frac{a/x}{a/x + b/y}. \tag{3}$$

The numerator of equation (3) represents the costliness of harvesting one offspring equivalent of resource 1, whereas the denominator represents the costliness of harvesting one offspring equivalent of both resources. Thus, the optimal allocation to pumps for resource 1 is equal to the proportion of total harvest costs contributed by the cost of harvesting resource 1. At this optimal allocation, the offspring equivalents of resources 1 and 2 harvested are equal ($ux/a = vy/b$); this is a perfectly balanced harvest, with no excess or waste of either resource. This solution is directly analogous to the threshold element ratios of ecological stoichiometry (Sterner and Elser 2002) and the symmorphosis condition of functional morphology (Weibel et al. 1991). If ux/a were less than vy/b, the organism would have harvested an excess of resource 2, resource 1 would be defined as limiting, and fitness would be enhanced by allocating less to pumps for resource 2 and more to pumps for resource 1. The reverse is true when $ux/a > vy/b$. At the perfect balance, we cannot define a single limiting factor; instead, both factors are simultaneously limiting (fig. 1). This creates both perfect ecological predictability and an asymmetry: increasing the harvest of either resource 1 or resource 2 alone will not

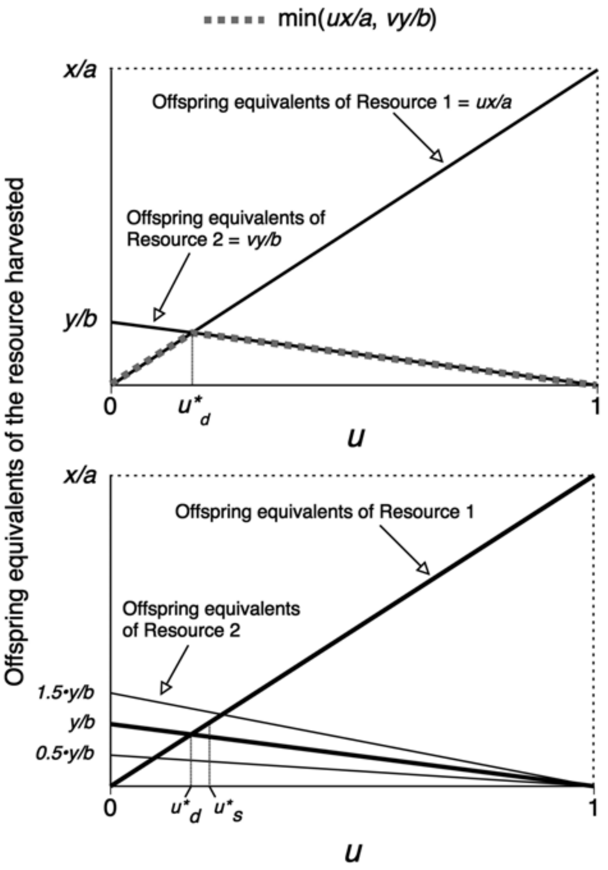

Figure 1: *Top*, limiting factors in a deterministic environment. Under the central allocation trade-off, $u + v = 1$, the optimal allocation to pumps for resource 1, u^*_d, maximizes the function $\min(ux/a, vy/b)$. As shown here, this occurs when $ux/a = vy/b$. Note that the per-offspring harvest cost of resource 1 is smaller than the per-offspring harvest cost of resource 2 (i.e., $x/a > y/b$). *Bottom*, limiting factors in a stochastic environment. The environmental availability of resource 2 is unpredictable, such that the maximum harvest possible varies following a uniform distribution between $1.5y/b$ and $0.5y/b$. A value of u slightly greater than u^*_d produces an expected gain in fitness; a large potential gain, realized when resource 1 is limiting and the fitness returns are defined by the steep slope of the resource 1 harvest function, more than offsets the small potential loss, incurred when resource 2 is limiting and fitness returns are defined by the shallow slope of the resource 2 harvest function. Thus, selection favors $u > u^*_d$ under stochasticity (i.e., overinvestment in the harvest of the resource whose per capita harvest costs are lower). In the example shown here, $x/a = 5 \cdot y/b$, from equation (3) we obtain $u^*_d = 0.167$, and simulations show that the optimal allocation to harvesting resource 1 in a temporally stochastic environment, u^*_s, is 0.205.

increase fitness, but decreasing the harvest of either will decrease fitness (Haig and Westoby 1988; Cohen and Dukas 1990; Burd 2008). For this reason, at this hypothetical optimum and in the strict absence of phenotypic plasticity, natural selection, curiously, is unable to favor mutants with more efficient pumps for resource 1 or resource 2, that is, pumps that cost the same but that would harvest more of resource 1 or resource 2 over the organism's lifetime (e.g., Partridge and Gems 2006); only a mutation that simultaneously enhanced pumping efficiency for both resources would be favored. Thus, under this solution we have a population whose ecology is perfectly predictable and whose evolution is highly constrained.

Limiting Factors in a Stochastic Environment

We now introduce environmental stochasticity. Many organisms exhibit phenotypic plasticity and can continuously change their allocations in response to local conditions. Thus, building on the deterministic model, an organism may make its initial allocations u and v in response to the long-term average availabilities of resources 1 and 2. If it then finds itself in an environment where resource 1 is less abundant than average, it can reallocate by tearing down some pumps for resource 2 and building more pumps for resource 1 (e.g., Bloom et al. 1985; van den Berg et al. 2002; Klausmeier et al. 2007).

Although phenotypic plasticity is broadly important in this context, there are limits to what it can accomplish. Organisms often must allocate resources at different times to cope with different potential limiting factors. For example, plants often allocate first to ovules, then to pollinator attraction, then to seed provisioning, and, finally, to fruit maturation. In such cases, early allocations must be made before the conditions are known under which subsequent allocations will occur, and only a perfect forecasting ability would allow phenotypic plasticity to achieve an exactly balanced allocation.

Here, therefore, we focus on the case without phenotypic plasticity (we return to plasticity in the "Discussion"). We assume that organisms inhabiting a stochastic environment can make only a single, irreversible allocation. We further assume that the probability distributions of availabilities of resources 1 and 2 have median values equal to the deterministic case values. One possible scenario is that our focal organism could continue to express the allocation that was optimal for the deterministic case. It would then experience a 50% probability of being limited by resource 1 and a 50% probability of being limited by resource 2. Is this optimal?

Temporal Stochasticity

Temporal and spatial heterogeneity often have different effects on life-history evolution (Roff 2002); thus, we will treat them separately. To study evolution in a temporally variable environment, we use the standard approach (e.g., Roff 2002) of maximizing the natural log of the geometric mean of the per-generation fitness.

As a special case of temporal (between-generation) heterogeneity that is amenable to analytic solution, assume that resource availabilities, (x, y), are uniformly distributed with probability density $p(x, y) = 1/XY$, where X and Y are the maximum possible concentrations of resources 1 and 2, respectively. As we did for the deterministic case, we will first identify the optimal allocations to harvesting resources 1 and 2 and then determine how these allocations influence the likelihood that fitness will be limited by resource 1 or resource 2. We wish to find $u = u^*$ such that the temporal case fitness, denoted $\langle \ln F \rangle$ and defined by

$$\langle \ln F \rangle = \int_0^X \int_0^Y p(x, y) \ln \min\left(\frac{ux}{a}, \frac{vy}{b}\right) dx dy, \tag{4}$$

is maximal under the constraint (eq. [1]) of fixed total allocation to pumps. In appendix A in the online edition of the *American Naturalist*, we show that

$$u^* = \frac{(1/2)\left[\sqrt{1 + 8(aY/bX)} - 1\right]}{1 + (1/2)\left[\sqrt{1 + 8(aY/bX)} - 1\right]} \tag{5}$$

for $Y/b \geq X/a$ and

$$u^* = \frac{1}{1 + (1/2)\left[\sqrt{1 + 8(bX/aY)} - 1\right]} \tag{6}$$

for $Y/b < X/a$. The optimal strategy is to overinvest, relative to the deterministic case, in pumps for the resource whose harvest, on average, is less costly per offspring produced (i.e., that has the larger value, comparing X/a with Y/b) and to underinvest in pumps for the resource whose harvest is more costly per offspring (fig. 2).

Can we understand intuitively why it should be optimal to overinvest in harvesting the less expensive resource? We suggest two lines of reasoning. The first is a verbal argument: if an organism starts at the deterministic solution and then reallocates a unit of investment from harvesting the more costly component to the less costly component, the result is a greater proportional increase in supply of the less costly component compared to a smaller proportional decrease in supply of the more costly component. For example, if the deterministic solution is to allocate 1% to harvesting resource 1 and 99% to harvesting resource 2, then in a stochastic environment increasing the allocation to 2% for harvesting resource 1 doubles the harvest of resource 1 while sacrificing only one-ninety-ninth of the harvest of resource 2. Therefore, the reallocation is favored (Sevenster et al. 1998; Ellers et al. 2000).

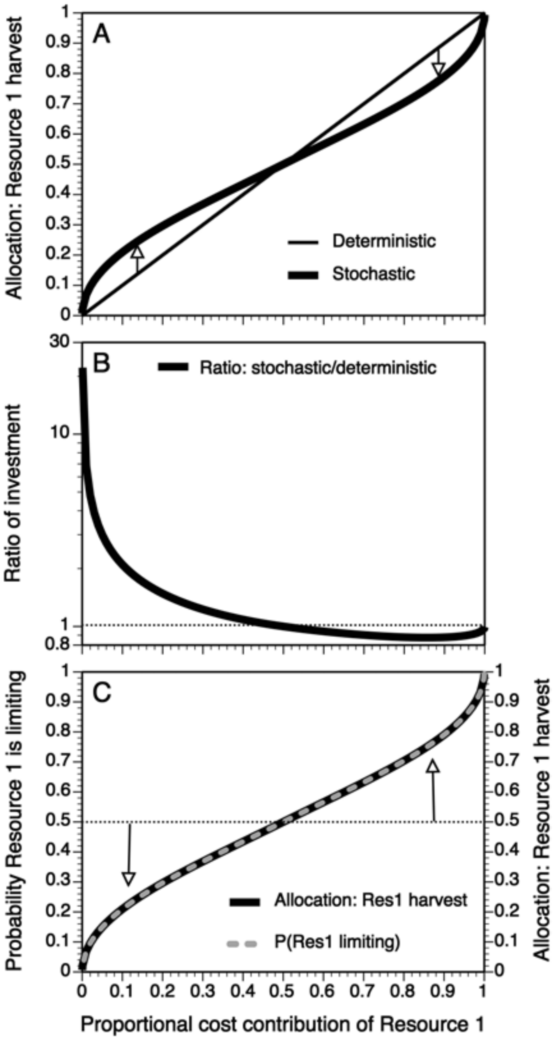

Figure 2: Limiting factors in a temporally stochastic environment. The X-axis is the proportional cost contribution of resource 1 to the total cost of producing an offspring, $(a/X)/[(a/X) + (b/Y)]$. *A*, Optimal proportional allocation to pumps for the harvest of resource 1, u^*. Shown is a comparison of the optimal allocation when resources 1 and 2 are present at a fixed concentration in the environment ("deterministic") and when their concentrations are variable, following the uniform probability density ("stochastic"). The optimal strategy is to overallocate, relative to the deterministic case, to the harvest of the cheaper resource (ratio >1.0) and underallocate to the harvest of the more expensive resource (ratio <1.0; see arrows). *B*, Ratio of optimal investment in the harvest of resource 1, stochastic/deterministic. The dotted line where the ratio of investment = 1 is indicated as a benchmark. *C*, Probability that reproduction is limited by resource 1, P_1, given the optimal allocation for the stochastic case. If the allocation that was optimal for the deterministic case were retained in the stochastic setting, the outcome would be $P_1 = 0.5$ (*dotted line*). Note that the shifted allocation depresses the probability that fitness will be limited by the cheaper resource and elevates the probability that fitness will be limited by the more expensive resource (see arrows). Shown for comparison is the optimal allocation to pumps for resource 1, u^*. Note that the two functions are equal.

We can also provide a graphical explanation (fig. 1, *bottom*) that will be helpful later when we consider nonlinear harvest functions (see "Discussion"). We continue with the example introduced in figure 1, in which resource 1 is the less expensive component of reproduction (i.e., $x/a > y/b$, and therefore, the absolute value of the slope of the resource 1 harvest function is greater than the absolute value of the slope of the resource 2 harvest function). Consider the simple case where the availability of resource 1 in the environment remains fixed but the environmental availability of resource 2 is unpredictable, following a uniform distribution between 1.5 and 0.5 of its mean availability. The slope of the resource 2 harvest function can now fall anywhere between the two thin lines shown in figure 1 (*bottom*). If we consider values of u close to u_d^*, then we expect fitness to be limited by the harvest of resource 1 half the time; in this case, fitness payoffs associated with any strategy u are defined by the harvest function for resource 1. Of course, in the remaining half of the time, resource 2 will be limiting, and fitness payoffs are defined by the harvest function for resource 2. Consider, then, a strategy of choosing u slightly smaller than u_d^*. When fitness is defined by the resource 1 harvest, the new strategy suffers a large decrease in fitness compared to the strategy u_d^* because the slope of the harvest function for resource 1 is steep. When fitness is defined by the resource 2 harvest, the new strategy benefits from a small increase in fitness because the slope of the harvest function for resource 2 is shallow. Averaging these two effects, we see that $u < u_\mathrm{d}^*$ is not favored. In contrast, values of $u > u_\mathrm{d}^*$ produce an expected gain in fitness: a large potential gain, realized when resource 1 is limiting, more than offsets the small potential loss incurred when resource 2 is limiting. Thus, some overinvestment in harvesting the less expensive resource is favored. As u increases further above u_d^*, the probability that fitness will be limited by the harvest of resource 1 decreases from 0.5 to 0.0, while the probability that fitness will be limited by the harvest of resource 2 increases from 0.5 to 1.0. Thus, with increasing u, an equilibrium is eventually reached at which further increases in u are no longer favored because a shrinking chance of a large payoff (on the steep resource 1 harvest curve) no longer offsets a growing chance of incurring a small cost (on the shallow resource 2 harvest curve). For the case depicted in figure 1, $u_\mathrm{d}^* = 0.167$, whereas the optimal allocation to harvesting resource 1 in a temporally stochastic environment, u_s^*, is 0.205. The graphical argument highlights that it is the relative slopes of the two harvest functions in the vicinity of the point where the two functions intersect that determine the optimal response to stochasticity.

Stochastic simulations (see Matlab code, available as a zip file in the online edition of the *American Naturalist*) suggest that the qualitative form of the optimal allocation curve shown in figure 2*A* is robust to different underlying distributions for the two resources (fig. D1 in the online edition of the *American Naturalist*). Simulations also demonstrate that the large proportional increase in the harvest of the less costly resource is favored because (i) it insures against reproductive shortfalls that can occur when the less costly resource is unusually rare and (ii) it ensures that the organism can capitalize on opportunities for reproductive bonanzas that can occur when the more costly resource is unusually abundant (fig. 3).

How does the optimal allocation to pumps (eqq. [5], [6]) in a temporally varying environment shape the probability that a given resource will limit an individual's fitness? The overallocation to harvesting the less costly resource depresses the probability that this resource will be limiting below 50% but not to 0 (fig. 2*C*), as has been implied in limiting-factors debates by positions favoring an exclusive role for a single limiting factor. Rather, as shown in appendix A, our central result is that the probability of being limited by a particular resource (here taken as resource 1), P_1, is equal to the cost of the optimal allocation made for its harvest:

$$P_1 = u^*. \tag{7}$$

Thus, whenever an organism must incur some cost to ameliorate the impact of a potentially limiting factor, our analysis suggests that natural selection favors a balancing of different limiting factors. Only free resources should never be limiting, and an organism whose fitness is never limited by a costly resource must be overinvesting in its harvest of that resource. That the equality described in equation (7) is robust to different assumptions regarding the underlying distributions of x and y is supported by a general analytic solution (see app B, eq. [B1], in the online edition of the *American Naturalist*).

Can we understand intuitively why organisms faced with a Liebigian limiting-factors problem should always balance different limitations rather than being consistently limited by one factor? Here we extend the explanations provided by Dawkins (1995) and Rosenheim (1996). Consider an organism that requires two essential resources to reproduce, and assume that the per-offspring harvest costs for the two resources are equal (this assumption simplifies the logic and makes it clear that the balancing of limitations is unrelated to the overinvestment in the less expensive resource). Now, assume that all members of our population are consistently limited by their harvest of resource 1 and never limited by their harvest of resource 2. Can this be an optimal strategy? To evaluate the fitness of a mutant strategy that invested slightly less in the harvest of resource 2 and slightly more in the harvest of resource

1, we need to consider the benefits and costs of this new strategy. The benefits can be calculated as a product: (the probability of reaping a benefit) · (the expected magnitude of the benefit). Because the entire population is initially limited by resource 1, the probability of benefiting by increasing the harvest of resource 1 is ≈1.0. Let the magnitude of the benefit, in terms of the increase in the number of offspring equivalents of resource 1 harvested, be denoted as δ_1, where $\delta_1 \ll 1$. Thus, the overall benefit will be $\approx(1.0)\cdot(\delta_1) = \delta_1$. The costs of the new strategy can also be calculated as a product: (the probability of incurring a cost) · (the expected magnitude of the cost). Because no member of the population is initially limited by its harvest of resource 2, the probability δ_2 that a member of the population will incur any cost from a slight decrease in the harvest of resource 2 is very small: $\delta_2 \ll 1$. The magnitude of the expected cost for any individuals who become limited by resource 2 will be $\leq\delta_1$ because the per-offspring harvest costs of the two resources have been taken to be equal. Thus, the overall cost will be $\leq(\delta_2)\cdot(\delta_1)$. We see then that the benefits (δ_1) exceed the costs ($\leq\delta_2\delta_1$) because $\delta_2 \ll 1.0$. For this reason, natural selection will favor a reallocation of resources until at least some fraction of the population is limited by each resource, that is, until we have balanced limitations. In this example, it is easy to see that the reallocation will continue until 50% of the population is limited by each resource because it is at that point that the benefits of a further reallocation, (the probability of reaping a benefit) · (the expected magnitude of the benefit) ≈ $(0.5)\cdot(\delta_1)$, no longer exceed the costs, (the probability of incurring a cost) · (the expected magnitude of the cost) ≈ $(0.5)\cdot(\delta_1)$.

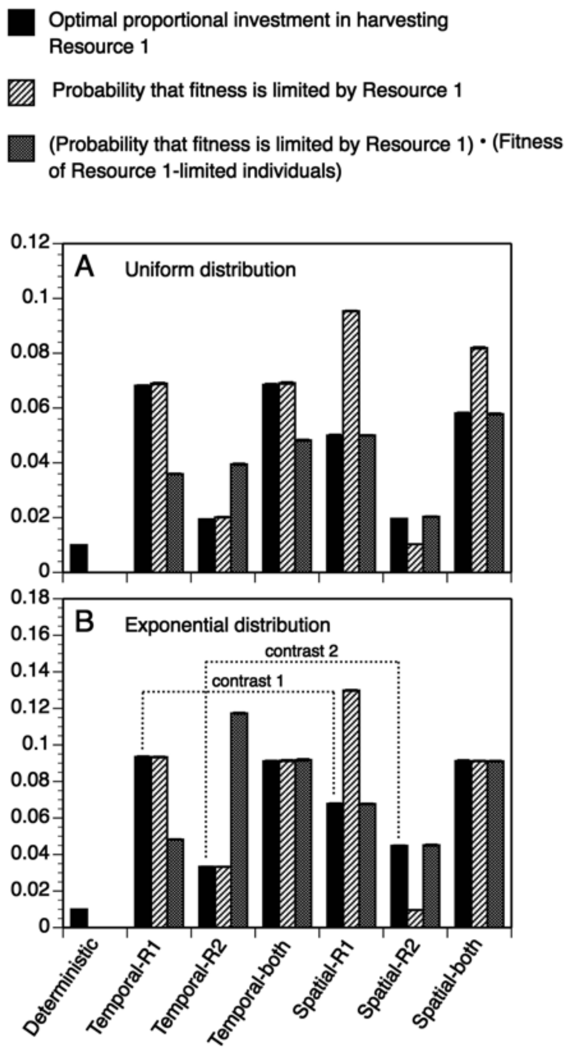

Figure 3: Limiting factors in a temporally or spatially stochastic environment. To isolate the influence of variability in resource 1 versus resource 2, simulations were conducted in which the availability of resource 1 only (*R1*), resource 2 only (*R2*), or both resources (*both*) were stochastic. Parameter values: mean environmental availabilities of resources 1 and 2 are assumed to be equal; the per-offspring requirement for resource 2 is 99 times greater than the per-offspring requirement for resource 1 ($a = 0.01$, $b = 0.99$). Resource concentrations follow the uniform distribution (*A*) or the exponential distribution (*B*). Overinvestment in the harvest of resource 1 is enhanced when the availability of only resource 1 is stochastic to insure against shortfalls of reproduction that occur when this resource is unusually rare. Overinvestment in the harvest of resource 1 is enhanced when the availability of only resource 2 is stochastic to capitalize on opportunities for high reproduction when resource 2 is unusually abundant. Note that under temporal stochasticity, the optimal investment in the harvest of resource 1, u^*, is equal to the probability that resource 1 is limiting, P_1, whereas under spatial variability, the optimal investment in the harvest of resource 1 is equal to the product (probability that resource 1 is limiting) • (fitness of individuals whose reproduction is limited by resource 1), $\tilde{P}_1 \cdot w_1$. Shown are means + 1 SE.

Spatial Stochasticity

We now treat the case of spatial heterogeneity. Here we maximize the spatial case fitness, denoted $\langle F\rangle$, which is the arithmetic mean reproduction,

$$\langle F\rangle = \int_0^X\int_0^Y p(x, y)\min\left(\frac{ux}{a}, \frac{vy}{b}\right)dxdy, \qquad (8)$$

where $\langle F\rangle$ is a heuristic fitness function that is suitable for populations with complete mixing and hard selection (i.e., selection can modify the proportional contribution of each location to the total offspring population). In appendix A we show that the optimal allocation to resource 1, denoted in the spatial case as $\tilde{u}$, is given by

$$\tilde{u} = \frac{\sqrt{1 + 3(aY/bX)} - 1}{\sqrt{1 + 3(aY/bX)}} \qquad (9)$$

for $Y/b \geq X/a$ and

$$\tilde{u} = \frac{1}{\sqrt{1 + 3(bX/aY)}} \tag{10}$$

for $Y/b < X/a$. Thus, spatial stochasticity also favors overinvestment in the harvest of the less costly resource (fig. D2 in the online edition of the *American Naturalist*). Temporal stochasticity produces especially strong penalties for generations with very low fitness and therefore favors heavier overinvestment, relative to the spatial case, in harvesting the less costly resource to reduce the impact of generations with extreme scarcity of that resource (e.g., fig. 3*B*, *contrast 1*). Spatial stochasticity, on the other hand, favors strategies that perform best in locations where fitness is particularly high and therefore favors stronger overinvestment, relative to the temporal case, in harvesting the less costly resource to capitalize on locations where the more costly resource is abundant (e.g., fig. 3*B*, *contrast 2*). Finally, as shown in appendix A, under spatial stochasticity the key relationship linking the probability of fitness being limited by resource 1, denoted $\tilde{P}_1$, and the optimal allocation $\tilde{u}$ to the harvest of resource 1 (cf. eq. [7] for the temporal case) now includes a weighting factor, w_1, which can be interpreted as the mean relative fitness of individuals whose reproduction is limited by resource 1, where the mean population fitness is taken as 1.0:

$$\tilde{P}_1 \cdot w_1 = \tilde{u}. \tag{11}$$

For some underlying distributions of resource availabilities, the relative fitness of individuals whose reproduction is limited by resource 1 is equal to the relative fitness of individuals whose reproduction is limited by resource 2 (i.e., $w_1 = w_2 = 1.0$), and equation (11) reduces to equation (7) (see fig. D3*B*, D3*D*, D3*E* in the online edition of the *American Naturalist*). In other cases, however, $w_1 \neq w_2$, and natural selection favors allocations that reduce the likelihood that fitness will be limited by the factor that constrains the more highly reproductive class of individuals (see figs. D2, D3*A*, D3*C*). We present a general analytical solution in appendix C in the online edition of the *American Naturalist* (eqq. [C1], [C2]), demonstrating that equation (11) is robust to different assumptions regarding the underlying distributions of x and y.

Discussion

Our results have the following implications. First, although we have focused on the problem of fitness-limiting factors, strong parallels exist with other problems of optimization under stochasticity that emerge in biology (e.g., quantitative evolutionary design; Alexander 1997; Diamond 2002; Salvador and Savageau 2006), in engineering (e.g., safety factors in design; Elishakoff 2004), and in economics (e.g., safety stocks in inventory control; Axsäter 2006; Teunter et al. 2010). We suggest that there are substantial opportunities to share insights across these problems.

Second, our results allow us to resolve some of the apparent contradictions emerging from models of optimal allocations for coping with limiting factors in stochastic environments. As reviewed in the "Introduction," several models have predicted that stochastic environments favor overinvestment in harvesting less expensive resources (Kozlowski and Stearns 1989; Cohen and Dukas 1990; Burd 1995; Alexander 1997; Ellers et al. 2000). However, other studies have predicted decreased investment in harvesting key resources as stochasticity increases, and their authors highlighted the apparent discrepancy with earlier results (Sakai 1996, 1997; Burd 2008). We can reconcile these views: the shift from overinvestment to underinvestment coincides with a shift in parameter values that renders the focal resource the more costly rather than the less costly contributor to offspring production. For example, in figure 2 of Sakai (1997), $a = 4.5$ renders flowers less expensive than fruits and, thus, increasing stochasticity favors overinvestment in flowers, whereas $a = 0.5$ renders flowers more expensive than fruits and, thus, increasing stochasticity favors underinvestment in flowers. Similarly, in figure 2 of Burd (2008), for the rich habitat, seed maturation is less costly than securing fertilization and, thus, stochasticity favors overinvestment in seeds, whereas for the poor habitat, seeds are more costly than fertilizations and, thus, stochasticity favors underinvestment in seeds. This helps to explain the paradoxical result discussed in this study. Another scenario that can explain the failure to observe overinvestment in the less expensive resource involves temporal stochasticity combined with unequal levels of uncertainty in the availability of different essential resources (a scenario not explored in this article). In this case, the need to bet-hedge to avoid extremely low fitness in some generations can lead to overinvestment in the more expensive resource when the availability of that resource is more highly variable (Cohen and Dukas 1990; J. A. Rosenheim, unpublished manuscript).

Third, our models predict that natural selection favors life histories that cope with multiple limiting factors in a way that links two levels of biological organization: (i) the internal world of physiological costs of resource allocations and (ii) the external world of ecological interactions with a stochastically variable environment. Equation (7) says that for an optimal life history in a temporally variable environment, the proportional allocation to the harvest of a particular potentially limiting resource (measurable in the physiology of the organism) is equal to the eventual likelihood that this resource becomes limiting to the organism's fitness (measurable in the ecology of the organism). Equation (11) says that in a spatially variable environment, the same link exists but now includes a weighting factor, the mean relative fitness of individuals whose reproduction is limited by a particular factor. For example, if individuals whose fitness is limited by resource 1 produce, on average, twice the number of offspring as individuals whose fitness is limited by resource 2, then it is optimal to double the allocation to the harvest of resource 1. We believe this study is the first to note these links between optimal allocations and the resulting likelihood of different limitations, although support for some kind of relationship between allocation costs and the likelihood of limitation by a given factor can also be obtained by rearranging analytical results given by Cohen and Dukas (1990), Burd (1995), and Rosenheim (1996; see also Kozlowski and Stearns 1989; Ellers et al. 2000). This mapping implies that at the optimum, an organism invests resources in direct proportion to the magnitude of the problem posed by a particular limiting factor. Thus, within an optimized life history, factors that are frequently limiting are major problems, and the organism invests heavily to ameliorate their impact; factors that are rarely limiting are minor problems, and the organism invests only lightly. This central prediction of our model should be readily testable. Although no tests of a link between physiological costs and the likelihood that fitness will be limited by a particular factor have been reported in the literature, research examining the relationship between limiting factors measured at the population level and per offspring allocation costs (e.g., with plant populations; Moles and Westoby 2002; Clark et al. 2007) suggests useful avenues for future work.

We note three important caveats. First, our model makes the conventional assumption that a trade-off exists between allocations to harvesting two essential resources (eq. [1]). In some cases, however, this trade-off need not operate. For example, many heterotrophs (phagotrophs) ingest multiple nutrients simultaneously when they feed rather than ingesting different nutrients separately from the environment. In this case, we may not observe the evolution of balanced limitations; instead, some factors may never be limiting. For example, phloem-feeding aphids may be limited by essential amino acids but virtually never by sugars, which they ingest in quantities that vastly exceed their metabolic requirements, only to be voided as honeydew (Douglas 2003). Balanced limitations thus flow from the assumption of harvest trade-offs.

Second, the exact forms of equations (7) and (11) are sensitive to our assumption of a linear relationship between investment in pumps and the resulting amount of resource harvested. The linear case is useful, both because it will be appropriate in various biological applications and because it serves as a benchmark against which nonlinear cases can be compared. Although a full treatment of nonlinear harvest functions awaits further research, using figure 1 we can anticipate some likely results. As long as (i) the harvest of resource 1 is a strictly increasing function of investment in pumps for resource 1 and (ii) the harvest of resource 2 is a strictly decreasing function of investment in pumps for resource 1, the optimal allocation strategy for the deterministic case will be unique (i.e., the harvest functions will cross only once). Stochasticity will then favor overinvestment in harvesting the resource whose harvest function is the steeper in the vicinity of the deterministic optimum. This need not be the resource whose average per-offspring cost is the greater; instead, the focus now shifts to the marginal costs associated with harvesting an additional offspring's worth of each resource. As in the linear case, overinvestment in the harvest of a resource is expected to push below .5 the probability that this resource will emerge as the limit to fitness. Although the quantitative details will differ from those in equations (7) and (11), some linkage between physiological allocation costs and the likelihood that a factor is limiting appears likely to emerge in some settings with nonlinear harvest functions (e.g., sex allocation; J. A. Rosenheim, unpublished data), but in some—perhaps exceptional—cases this linkage may be broken (e.g., Rosenheim 1996).

Third, as noted in the "Introduction," our analysis considers evolutionary responses to stochasticity in the absence of phenotypic plasticity. How might our conclusions change if we allow evolutionary processes and plasticity to operate together? A full treatment of this question is beyond the scope of this article; however, preliminary analyses with a simulation model provide some initial hints (fig. D4). We modified our simulation model to allow pumps for whichever resource is harvested in excess to be torn down and the resulting molecular building blocks reassembled into pumps for the limiting resource; we assumed 50% efficiency (half of the initial allocation is lost during reallocation) and either limited or full plasticity (up to 20% or up to 100% reallocation allowed, respectively). The model continues to predict overinvestment in harvesting the less expensive resource relative to the deterministic case, even when plasticity is incorporated (fig. D4*A*); the overinvestment is stronger when plasticity is limited. Plasticity generates large changes in what factor(s) are predicted to emerge as limits to individual fitness (fig. D4*B*); in particular, plasticity allows many individuals to achieve the perfectly balanced harvest, under which fitness is simultaneously limited by both resources (e.g., multiple limitation [Rastetter and Shaver 1992; van den Berg et al. 2002] and colimitation [Klausmeier et al. 2007]). Nevertheless, at least for the less expensive resource, we continue to observe a positive relationship between optimal investment in pumps and the probability that the resource emerges as the sole limit to fitness (fig. D4*C*). Thus, even in the presence of plasticity, our central result, that the optimal investment in harvesting a resource is linked to the probability that the organism's fitness will be limited by that resource (eqq. [7], [11]), continues to be expressed, although the quantitative details are different.

Finally, our results suggest an explanation that complements other types of explanations (Benincà et al. 2008; Doak et al. 2008; Ives et al. 2008) for why researchers must often concede that the answer to many questions in ecology seems to be "It depends." Our analysis suggests that natural selection molds life histories to balance multiple limiting factors when these factors interact following Liebig's law to shape fitness. There will be no silver bullet in the ecology of a focal species that universally shapes individual reproductive success and hence population growth rates. Empirical evidence regarding the joint importance of multiple limiting factors in nature provides essentially universal support for this prediction (table 1). From the precarious perch on the knife edge of multiple limiting factors, an organism's responses to environmental perturbations will be fundamentally contingent on local conditions. When an organism is limited by factor A, it will respond predictably to perturbations of factor A but not to perturbations of factor B. When the organism is limited by factor B instead, sensitivity to small perturbations of factor A will disappear. This dependence on spatial and temporal variation in the environment renders the reproductive responses of populations hard to predict and is one reason that ecologists may search in vain for laws that are directly analogous to the deterministic laws of physics or chemistry. However, rather than viewing this as a shortcoming of ecology, we argue that the conditional dynamics of populations should be viewed as a fundamental feature of life histories shaped by organic evolution. At the same time, the balancing of different limiting factors broadens the range of efficiency-enhancing mutations that will be exposed to natural selection because an improved ability to cope with any of the balanced limiting factors will benefit at least some individuals occupying particular locations at particular times. In sum, our analysis suggests that optimal life histories lead ineluctably to contingent reproductive responses of populations while simultaneously expanding the purview of natural selection.

Acknowledgments

We thank R. Alexander, D. Harris, J. Kanda, S. Kaplan, N. Kashtan, A. Sih, and D. Woodruff for helpful discussions and R. F. Denison, R. Milo, B. Roitberg, S. Schreiber, and M. Turelli for comments on the manuscript. R. H. Teunter shared a very helpful unpublished manuscript. We gratefully acknowledge S. Schreiber for contributing the distribution-free derivation of equation (7) that is presented in appendix B in the online edition of the *American Naturalist*. J.R. acknowledges support from a Lady Davis Visiting Professorship, Hebrew University of Jerusalem, and a grant from the USDA National Research Initiative Competitive Grants Program (2001-35316-11013). U.A. and G.S. acknowledge support from the Kahn Family Foundation.

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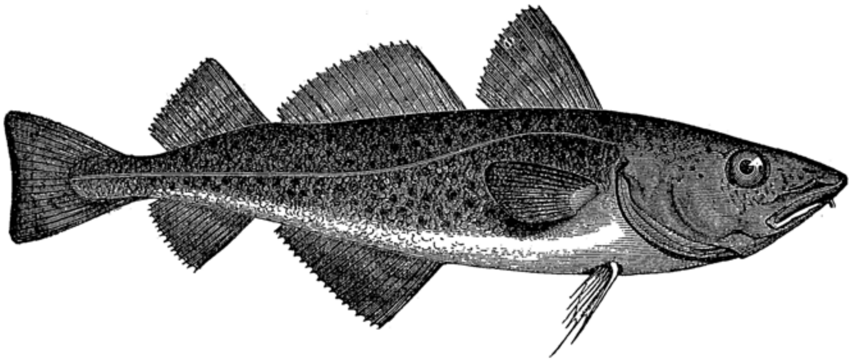

The codfish, *Morrhua americana.* “Codfish visit the shallow water of Massachusetts Bay to spawn about the first of November, and towards the last of this month deposit their eggs on the sandy banks and rocky ledges.” From “The Habits and Migrations of Some of the Marine Fishes of Massachusetts” by James H. Blake (*American Naturalist*, 1870, 4:513–521).