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Evolution in Population Parameters: Density-Dependent Selection or Density-Dependent Fitness?

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ABSTRACT: Density-dependent selection is one of earliest topics of joint interest to both ecologists and evolutionary biologists and thus occupies an important position in the histories of these disciplines. This joint interest is driven by the fact that density-dependent selection is the simplest form of feedback between an ecological effect of an organism's own making (crowding due to sustained population growth) and the selective response to the resulting conditions. This makes density-dependent selection perhaps the simplest process through which we see the full reciprocity between ecology and evolution. In this article, we begin by tracing the history of studying the reciprocity between ecology and evolution, which we see as combining the questions of evolutionary ecology with the assumptions and approaches of ecological genetics. In particular, density-dependent fitness and density-dependent selection were critical concepts underlying ideas about adaptation to biotic selection pressures and the coadaptation of interacting species. However, theory points to a critical distinction between density-dependent fitness and density-dependent selection in their influences on complex evolutionary and ecological interactions among coexisting species. Although density-dependent fitness is manifestly evident in empirical studies, evidence of density-dependent selection is much less common. This leads to the larger question of how prevalent and important density-dependent selection might really be. Life-history variation in the least killifish *Heterandria formosa* appears to reflect the action of density-dependent selection, and yet compelling evidence is elusive, even in this well-studied system, which suggests some important challenges for understanding density-driven feedbacks between ecology and evolution.

Keywords: competitive ability, density-dependent selection, eco-evo interactions, ecological genetics, evolutionary ecology, *Heterandria formosa*.

Introduction

The rate at and manner through which fitness responds to population density is an especially interesting subject

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in the examination of reciprocity between ecology and evolution for several reasons. Density-dependent selection is the simplest form of feedback between an ecological effect of an organism's own making (crowding due to sustained population growth) and the selective response to the resulting conditions. In addition, density-dependent selection is one of the earliest topics of joint interest between ecologists and evolutionary biologists and thus occupies an important position in the histories of these disciplines (Birch 1955; MacArthur 1962; Haldane and Jayakar 1963; MacArthur and Wilson 1967).

In this article, we explore two themes. Our first theme is historical and traces how the study of reciprocal interactions between ecology and evolution at the community level has emerged from combining the questions of evolutionary ecology with the assumptions and approaches of ecological genetics. In particular, we argue that density-dependent fitness and density-dependent selection emerge from this history as the fundamental concepts for understanding adaptation to biotic selection pressures. Our second theme is contemporary and follows the argument about the importance of density-dependent selection to crystallize some fundamental issues in the study of reciprocity between ecology and evolution. In particular, we focus on the important distinction between density-dependent fitness (the general effect of density on absolute fitness) and density-dependent selection (genotypes that are favored at low density differ from those favored at high density). We use our studies of the least killifish *Heterandria formosa* to illustrate how elusive the evidence for density-dependent selection can be, even when the natural history strongly suggests that it has occurred. In this light, there are some difficult challenges for understanding how density-driven feedbacks create the density-dependent selection necessary for genuine reciprocity between ecology and evolution. We conclude by suggesting how those challenges might profitably be addressed.

The Pedigree of Reciprocity: The Confluence of Evolutionary Ecology and Ecological Genetics

Although it was difficult for the pioneers of evolutionary biology to consider evolution without thinking about ecology, it was not difficult for the earliest ecologists to consider ecology divorced from evolution. Elton (1938, p.127) outlined why:

Ecologists ... have inclined to believe that evolution was long and ecology was short ... one of the assumptions made in most ecological work is that the species will remain constant.

Of course, evolution was never completely out of ecologists' minds. Adaptive evolution was acknowledged as the ultimate cause of a species' features that determined its ecological niche (Grinnell 1924). Even so, with a view that the evolution of those features occurred only very slowly (Grinnell 1928), practicing ecologists and evolutionary biologists could safely assume that the influence of either set of processes on the other was imperceptible.

Ecologists interested in biotic interactions, such as competition, predation, and parasitism (rarely mutualism), exhibited a sharper focus on evolution, which reflected their predilection to see features of organisms as adaptations to biotic forces. This focus led to the development of evolutionary ecology (Lack 1965; Harper 1967). Evolutionary ecologists employed "selection thinking" (*sensu* Charnov 1982) and asked how ecological patterns at the population or community level might emerge from the biotic selective pressures acting on individuals. Selection thinking led to enormous advances, from early theories of optimal foraging (Emlen 1966; MacArthur and Pianka 1966) and habitat selection (Fretwell 1972) to a general theory of sex allocation (Charnov 1979, 1982).

Although the injection of evolution into ecology was implicit in selection thinking, the practice of evolutionary ecology was consistent with the assumption that ecological and evolutionary processes occurred on different timescales. Two subjects pushed back at this assumption. The first was character displacement, which is the evolution of trait differences between competitors that allowed coexistence where their distributions overlapped (Brown and Wilson 1956). Character displacement requires that two species exert reciprocal selection pressures on each other to generate divergence in resource use at a rate sufficient to preclude one species' competitively excluding the other (Slatkin 1980; Taper and Case 1985). The second subject was the taxon cycle, which is the hypothesis that species occupying islands and archipelagoes moved through cycles of invasion, expansion, adaptive differentiation, local extinction, and eventual endemism (Wilson 1961; Ricklefs and Cox 1972; Ricklefs and Bermingham 2001). Taxon

cycles occur through the joint dynamics of population size, geographic range, and genes and, by definition, require that evolution and ecology unfold on a common timescale.

However, one might argue that character displacement and taxon cycles, although they require a common timescale, do not require a rapid one. Arguing for a common but slow timescale presumes that the biotic forces driving these processes are sufficiently weak that they alter population densities and gene frequencies slowly. This presumption is at odds with repeated experimental demonstrations that manipulations of one species' density can quickly produce substantial changes in the density of another (Hairston 1989).

Such a common, rapid timescale for ecological and evolutionary dynamics also implies strong selection, which is the hallmark tenet of ecological genetics (Ford 1975). In classical population genetic theory, selection is assumed to be sufficiently weak that the dynamics of allelic variation, as governed by relative fitness, can be studied independently of the dynamics of density (Crow and Kimura 1970). When selection is strong, differences among genotypes in fitness affect demography noticeably, and the joint dynamics of numbers and alleles follows accordingly (Champagnat et al. 2006).

The possibility for such joint dynamics motivated the earliest topic on which ecologists and evolutionary biologists found explicit common ground, density-dependent selection. Haldane (1953) was among the first to suggest that, when absolute fitness decreased with an increase in population density, natural selection would maximize population density. MacArthur (1962) formalized this argument and demonstrated that, if competing genotypes with similar innate growth rates varied markedly in their response to density limitation, then the fitness of each genotype would be indicated by its carrying capacity. Selection would favor the genotype with the highest carrying capacity, and as a result, adaptive evolution would often, although not always, maximize population density (a result demonstrated empirically soon thereafter by Ayala 1965). MacArthur (1962) also pointed out that, more generally, when there was a genetic trade-off between fitness at low density and fitness at high density, it would be possible for density-dependent selection to favor different genotypes under different density regimes. Subsequent work summarized by Charlesworth (1994) refined these ideas into more precise predictions, especially in the context of age-structured populations and the evolution of life histories, where the joint dynamics of numbers and genes can produce a variety of outcomes that depend upon the precise nature of density dependence.

The consequences of density-dependent fitness (defined here as occurring when absolute fitness is a function of population density) and density-dependent selection (de-

fined here, following MacArthur's discussion, as occurring when the rank order of genotypes with respect to absolute fitness changes as population density changes) attracted both ecologists and evolutionary biologists. Ecologists were drawn to density-dependent selection because it provided a mechanism through which individuals, especially their life-history traits, could adapt to characteristically different density regimes (Pianka 1970; Boyce 1984). Evolutionary biologists looked at density-dependent selection as a potential vehicle for protecting adaptive polymorphisms and as a means through which theories of evolution could become more ecologically realistic (Prout 1980; Mueller 1997).

Density-dependent selection is the simplest example of reciprocity between evolution and ecology. There is feedback from ecology to the evolutionary process as increased density changes the milieu of natural selection. Chitty's hypothesis for population cycling in microtine rodents was one of the earliest explicit invocations of reciprocity to explain an ecological pattern (Chitty 1967). Chitty began with the same premise as MacArthur (1962), that different genotypes would have higher fitness values in different ranges of population density. He expanded on this idea to posit that the success of genotypes favored at low density would cause a rapid increase in density; the resultant high densities would favor different genotypes, which could tolerate those high densities. As the "high density" genotypes increased in frequency, they would create ecological conditions leading to a population crash and the low densities that would, in turn, favor "low density" genotypes (see Abrams and Matsuda 1997 for a different perspective on this hypothesis).

Ongoing reciprocity at the community level can be initiated when the agent of density regulation is another species, such as a pathogen, predator, or competitor. This was the foundation of Pimentel's (1961, 1968) "genetic feedback" hypothesis for antagonist coadaptation in predator-prey and plant-herbivore systems that would regulate both populations and drive joint dynamics of numbers and genes. This hypothesis extended the concept of density-dependent fitness to interspecific density dependence and inspired formal models by Łomnicki (1971, 1988) and Levin (1972) and extensions by Leon (1974), Roughgarden (1976), and Levin and Udovic (1977).

The articles by Roughgarden (1976) and Levin and Udovic (1977) bound ecology and evolution inextricably. These articles showed that the explicit inclusion of genetic dynamics and interspecific density dependence could generate remarkably different patterns in multispecies systems than would emerge from purely ecological models without evolutionary components. The wider range of possible outcomes is a direct result of the higher dimensionality of the integrated system. In a single-species model of density-

dependent selection, that species' own population density is the only feedback onto fitness; in multispecies models, feedback onto fitness in each species can be a function of its own density, the density of other species, and the effects of specific genotypes of those other species on the fitness of the genotypes in the focal species. The more parameters necessary to describe the network of feedbacks, the higher the dimensionality of the system and the more complex its overall behavior can be (Metz et al. 1996; Heino et al. 1997, 1998).

Complexity through reciprocity and feedback are not merely theoretical curiosities. Yoshida et al. (2003) demonstrated that when experimental populations of a green alga were allowed to evolve in response to grazing by a rotifer, all of the parameters that specified the population dynamics of the rotifer and the alga (damping of oscillations, amplitude, period, and degree to which cycles of rotifer and alga density are offset from one another) changed dramatically from the dynamic patterns when the prey were not allowed to evolve.

Yoshida et al. (2003) also illustrates the influence of ecological genetics on the emergence of research on ecological and evolutionary reciprocity. To be sure, the initial literature on laboratory experiments that explored density-dependent selection is firmly in the tradition of experimental population genetics (reviewed in Mueller 1997). However, there is an older literature on the influence of genetic variation on the outcome of interspecific interactions (Park and Lloyd 1955; Lerner and Ho 1961; Lerner and Dempster 1962). By definition, these experiments were looking for the signature of strong selection on numerical dynamics and, as such, sit securely within the paradigm of ecological genetics. Subsequent descriptions of fast-paced, joint dynamics of numbers and genes through pairwise species interactions (e.g., Goodnight 1990; Bohannan and Lenski 2000; Yoshida et al. 2003) also sit firmly in this paradigm, as does the burgeoning literature on the prevalence of rapid adaptive evolution in natural populations (e.g., Carroll et al. 2007). Thus, we argue that the tenets of ecological genetics, applied to ideas about biotic selection pressures emerging from evolutionary ecology, lead directly to community genetics and the current explorations of reciprocity between ecology and evolution (Antonovics 2003; Whitham et al. 2006; Fussmann et al. 2007; Schoener 2011).

Density-Dependent Selection or Density-Dependent Fitness?

Density-Dependent Evolution

Density-dependent evolution is the lynchpin concept governing reciprocity between ecology and evolution via in-

terspecific interactions. This follows from two points. First, all ecological models of interacting species depict pairwise interactions as functions of population density. Second, when biotic interactions matter, fitness, which is the contribution of an individual to population growth measured in offspring, must be an explicit function of intra- and interspecific density. We argue that the challenge in understanding the reciprocity between ecology and evolution is distinguishing density-dependent selection from density-dependent fitness (Prout 1980).

To appreciate this point, consider that the carrying capacity of a genotype in simple models of density-dependent fitness actually involves more than just its sensitivity to the depressant effects of density, which is what many verbal models assume implicitly. For example, in a logistic model of population growth with the form

$$\frac{(1/N)dN}{dt} = a - bN, \quad (1)$$

the carrying capacity is a/b , and the most successful genotype could achieve a higher carrying capacity by having either a higher value of a (the innate growth rate) or a lower absolute value of b (the sensitivity to the depressant effects of density; see Charlesworth 1994 for a mathematically complete argument in place of this heuristic).

The feature(s) that are expected to evolve from this process depend on the evolvability of a and b and on which traits are associated with changes in each parameter. If competing genotypes differ more in traits affecting their values of b than their values of a , then variation in b will dominate the response to selection. We would then see not only the evolution of a higher equilibrium density as genotypes displaying smaller absolute values of b increase in frequency but also the evolution of greater tolerance to the depressant effect of density. Another way to express this evolution in b is that adaptive evolution alters the interactions among individuals to reduce the effect of density on fitness and allows a higher number of individuals to coexist. Of course, if competing genotypes differ more in traits associated with their values of a , then adaptive evolution increases the equilibrium size without changing the sensitivity to the depressant effects of density; MacArthur (1962) illustrated this point clearly.

Figure 1 is a graphical depiction of the distinction between density-dependent fitness and density-dependent selection. The scenario that has intrigued ecologists is depicted in figure 1A, the classic scenario for density-dependent selection in which there is a genetic trade-off between fitness in different ranges of population density. If ecological forces keep different populations at different ends of the density gradient, different genotypes predominate, and different features emerge via density-dependent

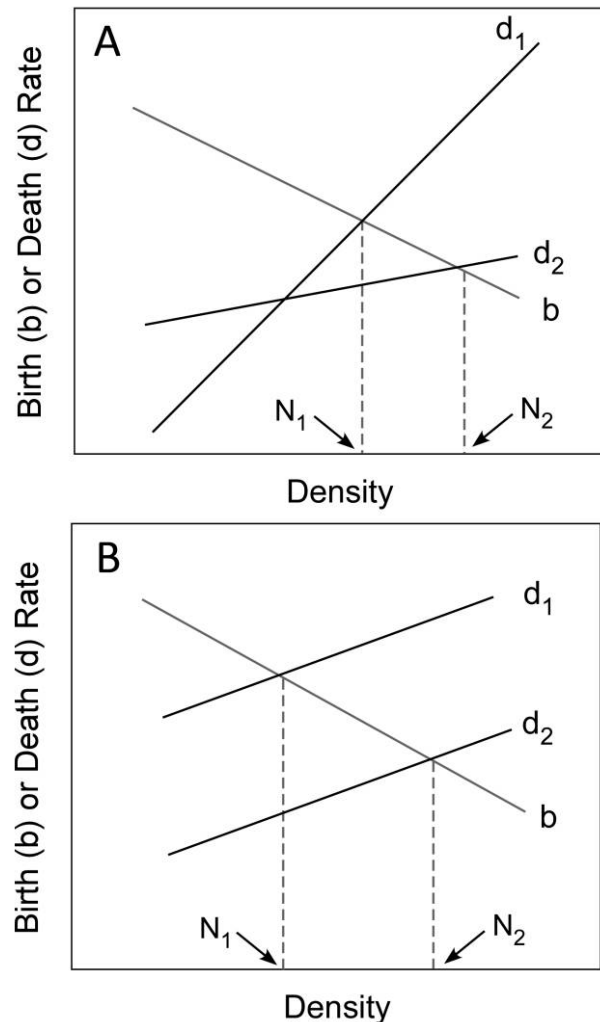


Figure 1: Graphical depiction of fitness components, birth rate (b) and death rate (d), as functions of density. Each cartoon depicts two genotypes with equal birth rate functions but different death rate functions. Fitness is determined by the excess of birth rates over death rates at any given density. In growing populations at low densities, the fittest genotype is that with the largest excess; in regulated populations near their equilibrium, when birth rates are balanced by death rates, the fittest genotype will often be the one for which the intersection of b and d functions produces the highest equilibrium density. *A*, The classic scenario for density-dependent selection, in which the fittest genotype at low densities is not fittest at high densities. *B*, A scenario in which fitness is strongly density dependent but selection is not, because one genotype is fittest throughout the range of densities.

selection. Without a genetic trade-off (fig. 1B), fitness may vary sharply with density, but the competing genotypes will respond similarly to the same density gradient; fitness is density dependent, but selection is not, and populations whose steady states fluctuate in different regions of the density gradient will be genetically similar (fig. 1B).

The distinction between density-dependent fitness and density-dependent selection and identifying the target of any density-dependent selection becomes more critical when we extend our thinking to interspecific interactions. To illustrate, we expand equation (1) to two competing species:

$$\begin{aligned}\frac{(1/N_1)dN_1}{dt} &= a_1 - b_{11}N_1 - b_{12}N_2, \\ \frac{(1/N_2)dN_2}{dt} &= a_2 - b_{21}N_1 - b_{22}N_2,\end{aligned}\quad (2)$$

where the subscript refers to species identity and b_{ij} is the per capita depressant effect of an individual of species j on species i . Consider a heuristic example of two genotypes for species 1 that differ in their values of b_{11} and b_{12} (fig. 2). Genotype A is more sensitive to intraspecific density (the slopes of the lines in the plane; N_1 , fitness), but genotype B is more sensitive to interspecific density. Which genotype is favored by selection depends upon how influential the interspecific interaction is in determining where the population of species 1 is typically found in the (N_1 , N_2) plane. However, that, in turn, can depend on how individuals of species 1, in their turn, affect the fitness of individuals in species 2, which is reflected in the values of b_{21} . Of course, if there is no meaningful genetic variation in any of the parameters describing intra- and interspecific interactions (the various b parameters), there will be no density-dependent selection and no opportunity for reciprocity between ecology and evolution even when there is a strong effect of density on fitness.

Although the importance of the distinction between density-dependent fitness and selection may seem obvious, the importance of understanding the target of any density-dependent selection is not. There are many potential targets for selection, even in a two-species interaction. For example, the targets of interspecific density-dependent selection on species 1 could be traits that affect either b_{12} or b_{21} , depending upon the indirect effects in the community (Miller and Travis 1996). Adaptive evolution of traits associated with these different parameters will create different feedbacks to the interaction between the species. To see this, consider that evolution in species 1 could lessen its susceptibility to competition from species 2 by decreasing b_{12} (e.g., character displacement, which might not affect the density of species 2 appreciably) or increase its impact on species 2 by increasing b_{21} (e.g., interspecific aggression, which would likely affect the density of species 2). Hairston (1980) described an empirical illustration of each of these evolutionary outcomes in the same two-species interaction as they played out in different geographic areas. The likely differences in the effect of adaptive evolution on N_1 and N_2 produced by selection on the different parameters can

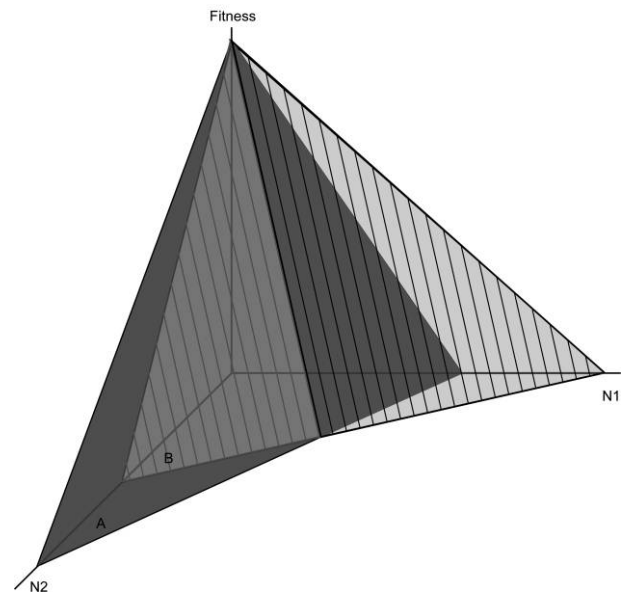


Figure 2: Graphical depiction of fitness of two genotypes, A and B, as functions of the population density of their own species, N_1 , and the population density of a competing species, N_2 . For both genotypes, fitness decreases as the density of either species increases; genotype A is more sensitive to intraspecific density, whereas genotype B is more sensitive to the density of the other species. Which genotype might prevail will depend on the region in the N_1 , N_2 plane in which the population is typically found.

produce different effects on the ecosystem (Miller and Travis 1996; Boots et al. 2009), which in turn would create different distributions of new selection pressures on these two species.

Although these simple models cannot fully describe nature, they identify the issues with which empirical work must grapple. In particular, they draw our attention to the importance of understanding the distinction between density-dependent fitness and density-dependent selection. Empirically, the prevalence and importance of the former is manifestly obvious; the prevalence and thus the importance of the latter is not (Prout 1980; Travis and Mueller 1989; Mueller 1997; Leips et al. 2000). To be sure, evidence for genotypic variation in the norm of reaction of fitness to density in laboratory systems dates from Dobzhansky and Spassky (1944) and Lewontin (1955), and there is clear evidence that density-dependent selection in laboratory populations influences the evolution of several organismal features (reviewed in Mueller 1997). However, there are very few convincing demonstrations that density-dependent selection has molded contrasting patterns of trait variation in nature (Law et al. 1977; Sinervo et al. 2000; Bradshaw et al. 2004; Levitan and Ferrell 2006).

The obvious reason for the dearth of evidence for den-

sity-dependent selection in natural populations is the difficulty of obtaining it (Mueller 1997). To demonstrate adaptation to different density regimes, one needs a set of populations that display long-term differences in density regime, that exhibit genetically based differences in features associated with fitness, and whose representatives will demonstrate differences in fitness as a function of density that are aligned with their long-term density distributions. Of course, one must be able to distinguish the signature of selection via population density from that of other potential agents of selection whose incidence may covary with density regime because they themselves affect density, such as the intensity of predation on a focal species. This is a tall order, even when the natural history of a species points clearly to the potential importance of density-dependent evolution. We illustrate this challenge by summarizing our studies of the least killifish *Heterandria formosa* in north Florida.

Density-Dependence in the Least Killifish

The least killifish is a small (~15–25-mm body length), short-lived (~140-d maximum female life span in nature) denizen of the shallow littoral zone of springs, rivers, lakes, and marshes in northern Florida. These habitats differ in a host of features, from thermal regime and water chemistry to density of aquatic vegetation and predation levels (descriptions in Leips and Travis 1999 and Richardson et al. 2006). Population densities vary by orders of magnitude (fig. 3), are associated with different levels of heterozygosity at neutral genetic markers (Soucy and Travis 2003; Schrader et al. 2011), and we and our colleagues have been documenting these patterns for almost 20 years. In general, sites with more predators and reduced amounts of aquatic vegetation cover have lower densities. There is considerable evidence that these populations are regulated around different density levels, although the strength of that regulation is different in different locations (Leips and Travis 1999; Richardson et al. 2006).

There are many phenotypic differences among these populations. The most obvious ones are in life history: the mass of the average female varies by almost 50% between populations, and after adjusting for differences in female size, the average fecundity can vary by fourfold, and average offspring mass can vary by over twofold (Leips and Travis 1999; Schrader and Travis 2005, 2012; Leips et al. 2009). There is also significant, albeit less substantial, variation among populations in the age at maturity, male body shape, and thermal tolerance (Forster-Blouin 1989; Baer et al. 2000; J. Landy and J. Travis, unpublished data; J. Travis, unpublished data).

Many of these differences are associated with variation in ecological parameters (Travis 1994; Schrader and Travis

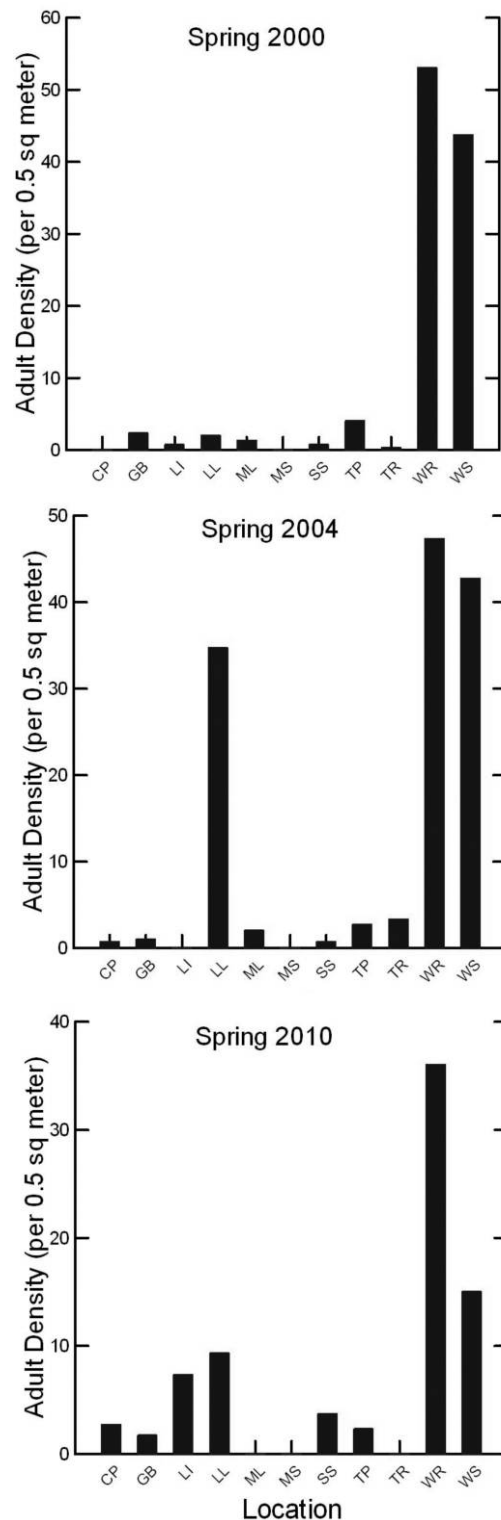


Figure 3: Variation in average adult density (number per 0.5 m²) in 11 populations of the least killifish in northern Florida at three points in time between 2000 and 2010.

Table 1: Comparison of population densities and selected life-history traits between Trout Pond and Wacissa River populations between 2000 and 2010

Feature	10-year average value (minimum–maximum yearly average)	
	Trout Pond	Wacissa River
Adult density (no. per 0.5 m ²)	3.9 (.1–12.3)	43.8 (2.3–175.3)
Mature female body length (mm)	18.0 (13.4–22.1)	16.8 (15.2–21.0)
Total no. of embryos carried by a female	11.4 (1.6–20.0)	5.0 (2.7–12.0)
Dry mass of offspring ready for parturition (mg)	.49 (.40–.65)	.68 (.57–.87)

2012; J. Landy and J. Travis, unpublished data). Higher densities are associated with lower female body size, lower size-adjusted fecundities, larger offspring sizes, and an anterior shift in the position of the intromittent organ in males. Populations in rivers have more streamlined males and produce larger offspring than populations in lakes. Populations with higher predation levels have males with wider caudal muscles and produce more and smaller offspring than those with lower predation levels. However, the ecological conditions covary with one another; higher predation levels are characteristic of lakes and are associated with lower densities. Nonetheless, partial correlation analyses show that the basic associations between density and fecundity and between density and offspring size persist even after taking each variable's association with predation level into account (Schrader and Travis 2012).

Although we have not demonstrated that every population-level distinction in average trait values, across the 15 northern Florida populations that we have surveyed, has a genetic basis, we know that reproductive traits, especially offspring size, are heritable within a population (Henrich and Travis 1988) and the differences in reproductive traits among some pairs of populations are genetically based (Leips et al. 2000; Schrader and Travis 2009). Some of the variation in male shape seen among three populations is maintained in F_1 fish raised in a common environment (J. Landy and J. Travis, unpublished data).

Almost every feature of *H. formosa* displays phenotypic plasticity with respect to density (Leips et al. 2000, 2009; J. Landy and J. Travis, unpublished data; J. Travis, unpublished data). Juveniles grow more slowly at higher densities, females are smaller in body size and harbor reduced lipid levels, and reproductive allotment (the proportion of total dry mass bound in reproductive tissues) and fecundity are lower. Offspring size varies with density, but the pattern varies with the amount of food available to the dam. At a constant total level of food resources, higher densities cause females to make smaller offspring, although the effect is seen only over a large gradient in density. If per capita food level is kept constant, higher densities cause females to make larger offspring.

These patterns—long-term differences in density, consistent associations of trait variation with density even in the face of correlated factors, and genetically based differences in at least some of these traits—suggest the strong possibility that density-dependent selection could be responsible for molding some of the population-level variation in the features of least killifish. The questions to answer are (i) whether there is evidence for genetically based trade-offs in fitness as a function of population density that could reflect the signature of density-dependent selection and (ii) whether the adaptive significance of traits that vary concomitantly with density can be shown to depend on density regime. Here we focus solely on the first question.

We focus our discussion on a comparison between two populations, Trout Pond (T) and Wacissa River (W). We have studied these populations for many years, because they represent typically low- and high-density populations, respectively, and display a number of differences in key life-history traits (table 1). Leips et al. (2000) constructed five F_4 stocks from crosses between them, representing an allelic series: TTTT, TTTW, TTWW, TWWW, and WWWW. Each of these stocks was used to found six replicate experimental populations, each in separate 800-L cattle-watering tanks. Rates of early population growth differed significantly among stocks and reflected what one might expect from density-dependent selection; TTTT replicates showed the highest rates of growth and attained apparent carrying capacity most quickly, TTTW replicates were next highest, and so on, down to WWWW stocks, which showed the lowest rate of growth and longest time to attain apparent carrying capacity (fig. 1 in Leips et al. 2000). There were no statistically significant differences among the five stocks in their average densities at the apparent steady state.

These patterns in numerical dynamics do not reflect what the simplest heuristic models like equation (1) lead us to expect, which is that the WWWW stocks should at least have a higher carrying capacity in pure culture than the TTTT stocks. However, recall that even our heuristic model produces this prediction only under the assumption that competing genotypes differ much more in the b pa-

parameter of equation (1) than the a parameter. In this case, it is evident that TTTT and WWWW stocks differ substantially in population growth rate, or the equivalent of the a parameter of equation (1). For the pure cultures to have the same carrying capacity in the face of this difference (i.e., to have similar values of a/b), there must be a compensatory difference in b , meaning that TTTT stocks must have a greater sensitivity to the depressant effects of density, a de facto signature of density-dependent selection. Although we illustrate this argument with our heuristic model, the basic deduction, which is that equal carrying capacities in the face of unequal growth rates at low density requires some form of differential density dependence, is quite robust (see Lloyd 1968 for an analogous argument in a laboratory flour beetle system).

The direct evidence for differential density dependence is equivocal. On the one hand, it is clear that the average reproductive rate of the TTTT stocks decreased by a greater proportion between low and high densities than did that of the WWWW stocks. On the other hand, mark-recapture studies in each replicate population indicated that, although adult survival and recruitment decreased with increasing density, there were no detectable differences among stocks after adjusting for density or in the relationships of those rates to density (Leips et al. 2000). Of course, in an experiment of this size (six replicate populations per stock), our statistical power to detect any but the most striking differences was low.

The argument for a signature of density-dependent selection would be more convincing if accompanied by direct evidence for fitness differences between TTTT and WWWW that change in different ranges of population density. There is evidence for this point if we examine reproductive rate, measured by the number of offspring carried by a female in a single brood (fig. 9 in Leips et al. 2000). In the early phase of population growth (low density), there were no significant differences among stocks in measurable reproductive rate, although the rank order of that rate (highest for TTTT and lowest for WWWW) matched the rank order of population growth rate. At the high-density steady state, even small differences in density were associated with significant decreases in reproductive rate. After adjusting for the effects of local density and female body size (females were smaller in replicates with higher densities), there were substantial, significant, additive genetic differences among stocks in reproductive rate; the rank order of reproductive rate was reversed from the low density phase, with WWWW displaying the highest rate and TTTT displaying the lowest.

These results would also not convince the skeptic. First, they rely on the reversal in the rank order of reproductive rate between low and high densities and ignore the lack of statistically significant differences at the low densities.

Second, the long-term steady state period indicates that the reproductive rate of the TTTT populations was at or close to replacement because there was no statistically significant change in population density for a long period after the carrying capacity was attained. Given that the reproductive rate of the TTTT populations was significantly lower than that of WWWW populations, either there must have been differences among stocks in other components of fitness or the population size in the TTTT stocks would have decreased. As noted above, we failed to find evidence for differences among stocks in adult survival or recruitment rate after adjusting for density and were unable to make direct tests of juvenile survival rate. An examination of the data indicates that there was long-term trend toward decreased densities in the TTTT populations, but, as noted, this was not statistically significant.

We have to conclude that the evidence for the signature of density-dependent selection from these data is, at best, equivocal. The critical piece of missing evidence is a direct demonstration that some component of fitness is more sensitive to the depressant effect of density in the T genotypes than the W genotypes. In a separate study, we compared juvenile performance of W and T fish across a range of densities, in enclosures in mesocosms (800-L cattle tanks) with either fish from their own population or when in competition with fish from the other population (J. Leips, F. H. Rodd, and J. Travis, unpublished data). We quantified juvenile growth rates and ages and sizes at maturity of F_2 fish from both populations as part of a larger experiment on maternal effects (table 2). When we measured these traits in pure cultures, we found that, although quadrupling offspring density reduced the average juvenile growth rate by 50%, there was no evidence that juvenile growth rates differed between these populations. There was also no differential sensitivity to the depressant effects of population density for age and size at maturity. However, when W and T fish were allowed to interact, we discovered that the competition between F_2 fish from the different populations was decidedly asymmetric (J. Leips, F. H. Rodd, and J. Travis, unpublished data; table 2). The presence of W fish caused T fish to mature at later ages than in pure stocks, especially at high density, but the presence of T fish had no effect on the age at maturity of W fish. These results indicate that W fish are superior competitors to T Pond fish and are thereby more able to cope with the competitive environments of high densities where they naturally occur. This is precisely what one might expect as a signature of density-dependent selection, even when selection does not maximize the population size in pure culture (Mueller 1988).

The lesson from this work is that the signature of density-dependent selection is not easy to find, even when the natural history suggests it. One reason for the difficulty is

Table 2: Juvenile growth rate and age at maturity under different experimental density conditions for F₂ fish from Trout Pond and Wacissa River populations

Trait	Mean value (± standard error)	
	Trout Pond	Wacissa River
Juvenile growth rate (mm/day):		
Pure stock:		
Low density	.10 (.02)	.09 (.01)
High density	.05 (.02)	.05 (.01)
Mixed stock:		
Low density	.12 (.02)	.10 (.01)
High density	.05 (.02)	.06 (.01)
Age at maturity (days):		
Pure stock:		
Low density	50 (2)	54 (3)
High density	50 (2)	50 (2)
Mixed stock:		
Low density	57 (6)	56 (4)
High density	61 (5)	52 (1)

Note: Age at maturity is the age of the first fish to mature in a replicate. Low density corresponds to 0.5 fish per liter, and high density corresponds to 2 fish per liter, both in outdoor enclosures. Pure stocks do not mix fish from different populations; mixed stocks are competition treatments with each stock at 50% relative frequency.

that density-dependent selection, as we have defined it, is a second-order phenomenon: two or more genotypes of genetic stocks must have different relationships of fitness with a gradient of density. It is much harder to distinguish two slopes than to distinguish two simple averages. In this light, one could argue that a much larger experiment than that reported in Leips et al. (2000) should have been conducted, although it is not obvious how this could have been done.

There is a second challenge that takes us beyond statistical issues of power and replication, which is whether studies of fitness and density in pure cultures are the correct context in which to seek evidence for density-dependent selection. Pure cultures eliminate interactions between individuals of different genotypes or from different genetic stocks. However, in nature, the ecological processes that unfold at high densities, such as intraspecific competition, involve either direct or indirect interactions among individuals. We can only know which genotype prevails under such conditions by performing experiments that mix those genotypes and allow them to interact. This is the paradigm described by models of “invasibility fitness,” which are designed precisely for scenarios with complex feedbacks between ecological variables and fitness; Bassar et al. (2012) illustrates how these models can guide the design and interpretation of empirical studies. In essence, one might argue that density-dependent selection

is difficult to detect because very few studies include the appropriate experiments.

Density-Dependent Evolution and the Larger Questions of Reciprocity

The most interesting issue in the study of reciprocity is whether it alters the outcome of evolution. It is important to be clear about this issue. Too often, discussions of reciprocity or “eco-evo interactions” become discussions of the ecological genesis of selective pressures on a focal species like the least killifish or, alternatively, discussions of how alternative phenotypes in a focal species like Trinidadian guppies produce different effects on ecosystem processes (Bassar et al. 2010). These factors are components of genuine reciprocity but are not the entire story. For reciprocity or evo-evo interactions to have meaning as a distinct class of hypotheses, we require (1) a focal organism to alter its environment as it responds successfully to some selective pressure; (2) the alteration in its turn to change the selective milieu for the focal organism; and, to complete the loop, (3) sufficient genetic variation in the focal organism, such that different genotypes or phenotypes succeed in the altered milieu than were favored in the original milieu. Put another way, the very success of one set of phenotypes sows the ecological seeds for their own eclipse at the hands, or genes, of alternative phenotypes.

The most interesting scenarios of density-dependent selection, as conceived by MacArthur (1962), illustrate this process. Population growth leads to increased density and crowding, with concomitant changes in ecological factors like per capita food availability, the aggregation of predators, or the transmission rate of pathogens, any or all of which in turn generate natural selection for different features than were favored at low densities, when population growth was relatively uninhibited. Given appropriate genetic variation, different genotypes are favored and eventually predominate in the high-density environments. Indeed, such a pattern has been demonstrated in laboratory populations of *Drosophila* (Borash et al. 1998).

We have discussed “population density” specifically, but conceptually, one could view density as a surrogate for any alteration in the environment produced by a focal organism, including effects on ecosystem variables. In this larger context, we might simply substitute “ecological state-dependent fitness” and “ecological state-dependent selection” for density-dependent fitness and selection, respectively. The detailed modeling of fitness as a function of an environmental factor will change, but the fundamental theory will not.

Expressed in these terms, reciprocity might seem inevitable: all organisms alter their own environments, and fitness is always context specific. However, reciprocity is

not inevitable. The key issues are (1) how distinct is the novel selective milieu created by the focal organism's impact on its own environment and (2) whether there is sufficient genetic variation for fitness in these different milieus to produce a different evolutionary outcome. The first of these is an ecological challenge, and the second is a genetic one. It is tempting to underestimate each challenge; we often presume that the context specificity of fitness is remarkably precise and that there will be additive genetic variance for fitness quietly awaiting a new selective milieu. Making either or both presumptions is a mistake.

Reciprocity, as we have described it, is a hypothesis for a very dynamic interplay between evolution and ecology and represents a modern focus of the traditional questions of ecological genetics and evolutionary ecology. It is a particularly exciting hypothesis, because it moves the interplay beyond phenomena like character displacement or other pairwise coevolutionary processes to a broader context that includes complex community and ecosystem processes, as described by other articles in this collection. We suggest that a focus on density-dependent fitness and density-dependent selection will offer as rich a set of insights in those contexts as it has done in studies of life histories and associated organismal features.

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