

# Definitions

Ecology the study of interactions between organisms and their biotic and abiotic environments

Evolution change in heritable characteristics of populations over successive generations

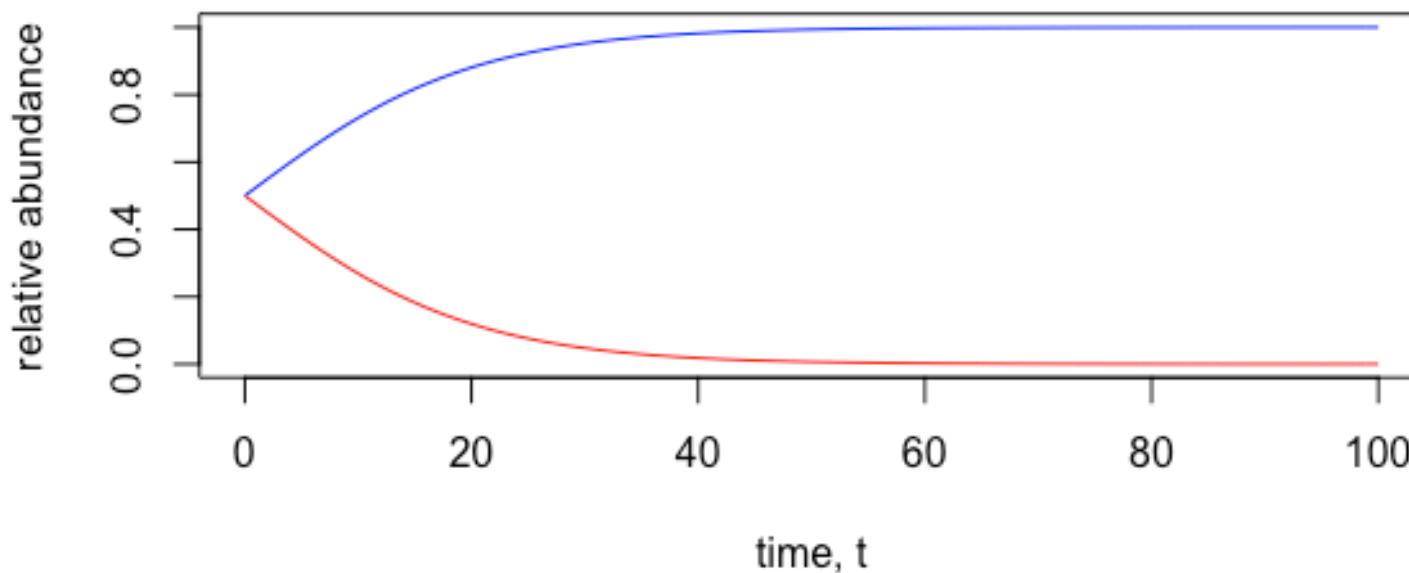
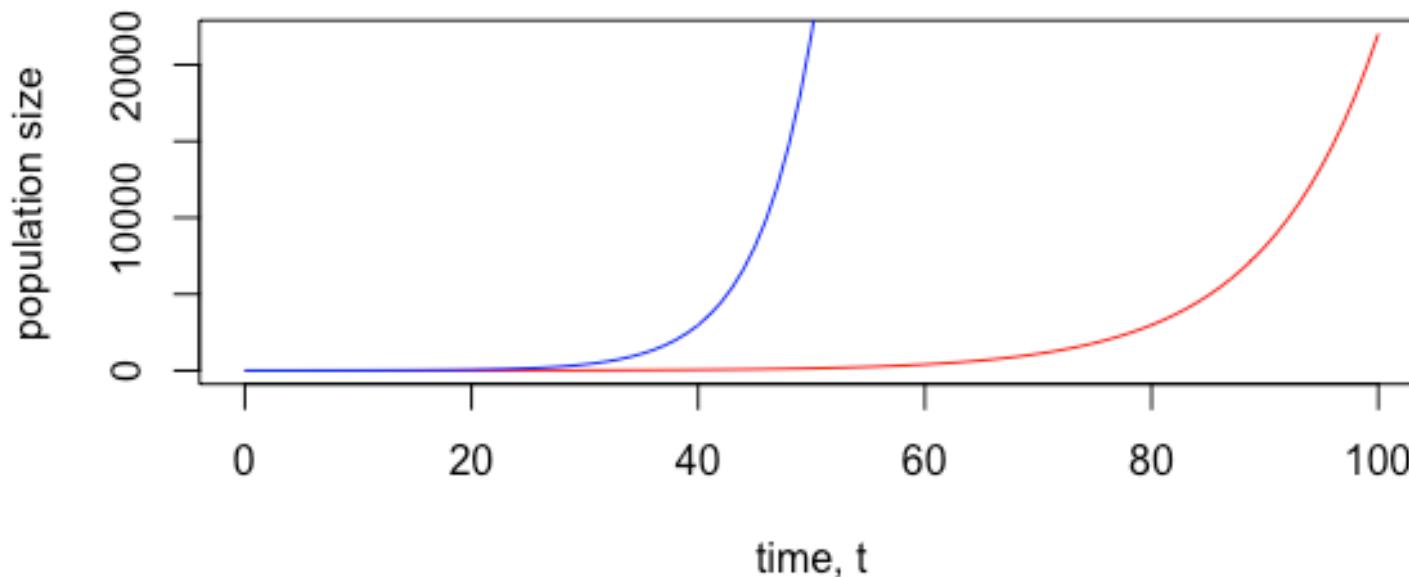
Fitness average contribution to the gene pool by individuals with a given genotype or phenotype

Selection differential fecundity and survival due to differences in phenotype

# Learning goals

- Understand how evolution and population dynamics are linked via mathematical models

# Evolution in populations with no density dependence



```
Evolution_No_Density_Dependence.R *
```

Source on Save

```
1 # EVOLUTION WITH NO DENSITY DEPENDENCE IN POPULATION DYNAMICS
2
3 # Remove all objects - always start with this
4 rm(list=ls())
5
6 # times
7 t = seq(0,100)
8 # intrinsic growth rates for genotype 1 and 2
9 r1 = 0.1
10 r2 = 0.2
11 # initial population size for genotypes 1 and 2
12 n10 = 1
13 n20 = 1
14 # population size for genotypes 1 and 2
15 n1 = n10*exp(r1*t)
16 n2 = n20*exp(r2*t)
```

# **Evolution when population dynamics are density-independent are not very interesting**

- The choice of the trait that evolves is obvious/doesn't matter
  - Trade-offs between life history components don't matter/aren't interesting
  - There is no interaction between genotypes
  - The evolutionary dynamics are unsurprising
- Let's consider evolution when population dynamics follow continuous time logistic growth!

# Learning goals

## Evolution in populations with density dependence

- Argue a hypothesis relating to offspring number and quality given density-dependent population growth
- Appreciate the importance of assumptions concerning which traits can evolve
- Appreciate the bias introduced from the logistic equation parameterization
- Describe an experimental set-up that might test a hypothesis

# Evolution in populations with density-dependent population growth

## Hypothesis

- at low density, genotypes that produce many offspring are selected (r-selected)
- at high density, genotypes that produce high quality offspring (strong competitors) are selected (K-selection)
- Trade-off between number of offspring and quality

MacArthur and Wilson (1967) coined the terms “*K*-selection” and “*r*-selection” for these two kinds of selection, which are clearly not restricted to the tropics and the temperate zones (*K* refers to carrying capacity and *r* to the maximal intrinsic rate of natural increase [ $r_{\max}$ ]). To the extent that these terms invoke the much overused logistic equation, they are perhaps unfortunate. However, it is clear that there are two opposing kinds of

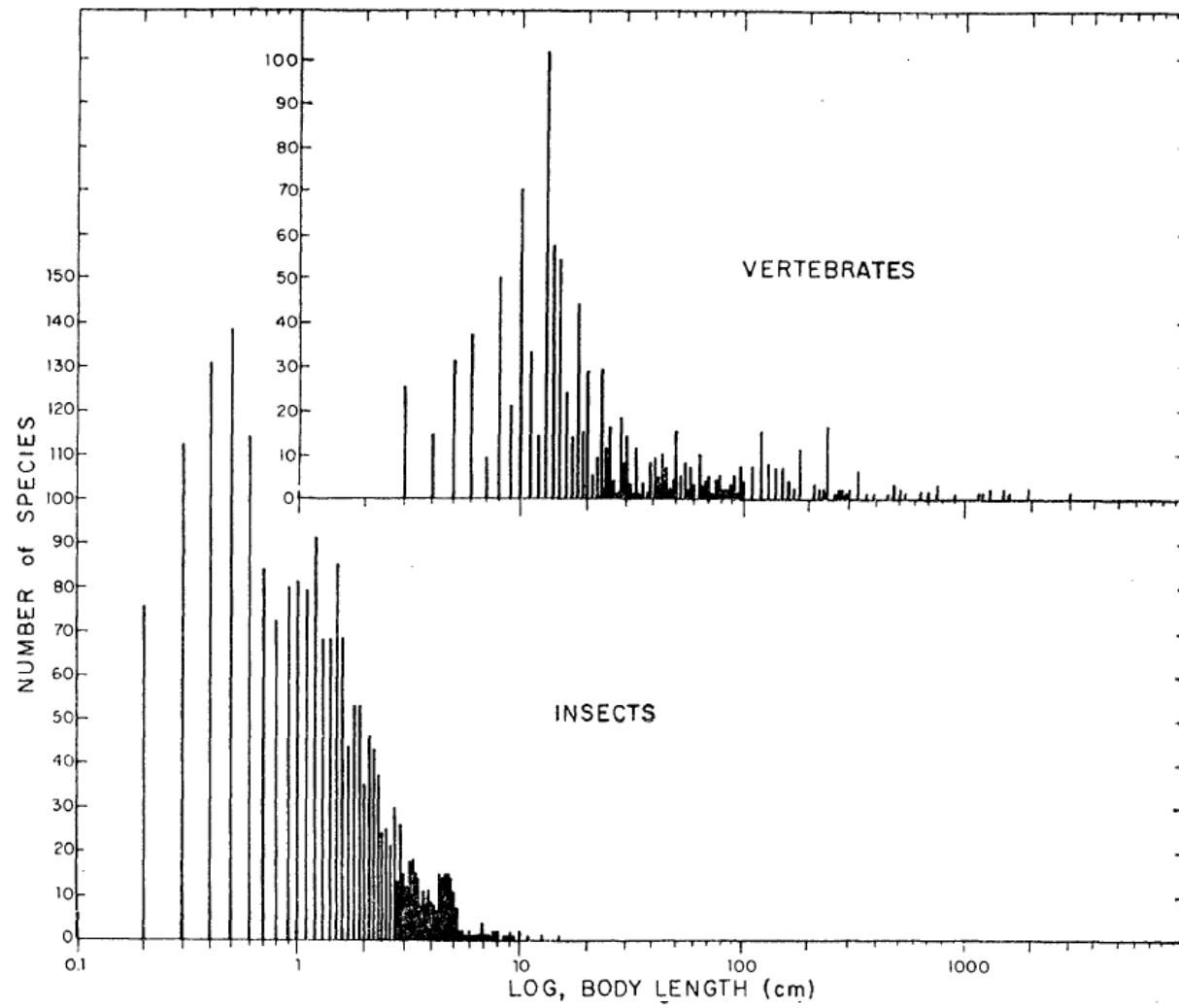
TABLE 1  
SOME OF THE CORRELATES OF *r*-AND *K*-SELECTION

	<i>r</i> -Selection	<i>K</i> -Selection
Climate . . . . .	Variable and/or unpredict- able: uncertain	Fairly constant and/or pre- dictable: more certain
Mortality . . . . .	Often catastrophic, nondi- rected, density-independent	More directed, density-de- pendent
Survivorship . . . . .	Often Type III (Deevey 1947)	Usually Type I and II (Deevey 1947)
Population size . . . . .	Variable in time, nonequilibr- rium; usually well below carrying capacity of en- vironment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year	Fairly constant in time, equi- librium; at or near carry- ing capacity of the environment; saturated communities; no recolon- ization necessary
Intra- and interspecific competition . . . . .	Variable, often lax	Usually keen
Relative abundance . . . .	Often does not fit MacArthur's broken stick model (King 1964)	Frequently fits the Mac- Arthur model (King 1964)
Selection favors . . . . .	<ol style="list-style-type: none"> <li>1. Rapid development</li> <li>2. High <math>r_{\max}</math></li> <li>3. Early reproduction</li> <li>4. Small body size</li> <li>5. Semelparity: single repro- duction</li> </ol>	<ol style="list-style-type: none"> <li>1. Slower development, greater competitive abil- ity</li> <li>2. Lower resource thresholds</li> <li>3. Delayed reproduction</li> <li>4. Larger body size</li> <li>5. Iteroparity: repeated re- productions</li> </ol>
Length of life . . . . .	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to . . . . .	Productivity	Efficiency

along it. The  $r$ -endpoint represents the quantitative extreme—a perfect ecologic vacuum, with no density effects and no competition. Under this situation, the optimal strategy is to put all possible matter and energy into reproduction, with the smallest practicable amount into each individual offspring, and to produce as many total progeny as possible. Hence  $r$ -selection leads to high productivity. The  $K$ -endpoint represents the qualitative

extreme—density effects are maximal and the environment is saturated with organisms. Competition is keen and the optimal strategy is to channel all available matter and energy into maintenance and the production of a few extremely fit offspring. Replacement is the keynote here.  $K$ -selection leads

One whole class of terrestrial organisms (vertebrates) seems to be relatively  $K$ -selected, while another large group (most insects, and perhaps terrestrial invertebrates in general) apparently is relatively  $r$ -selected.



lenged, there are a number of reasons to believe it is real. For instance, figure 1 shows the distribution of body lengths for a wide variety of terrestrial insects and vertebrates from eastern North America. Body length is far from the most desirable measurement to demonstrate the polarity, but the strong inverse correlation of  $r_{\max}$  with generation time and body size (below) suggests that, when frequency distributions for the former two parameters become available, a similar bimodality will emerge.

time. Smith pointed out that  $r_{\max}$  measures the rate at which an organism can fill an ecologic vacuum (at zero density); it is therefore one of the better indices of an organism's position on the  $r$ - $K$  continuum. He also noted that  $r_{\max}$  was inversely related to body size (i.e., that larger organisms are usually more  $K$ -selected than smaller ones). Now,  $r_{\max}$  is inversely

prevail at a given locality. An organism which lives less than a year encounters only a portion of the total annual range of conditions. The latter usually survive the harshest periods by forming resting eggs or pupae. Their

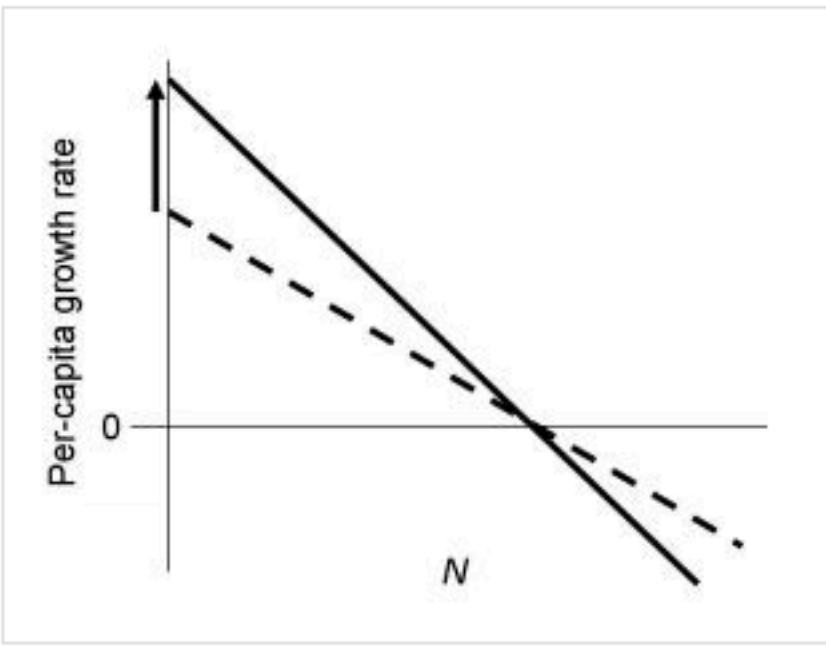
# Zombie ideas in ecology: r and K selection

For instance, consider the familiar logistic equation:

$$dN/dt=rN(1-N/K) \quad (1)$$

Now consider a second, less familiar model

$$dN/dt=rN-aN^2 \quad (2)$$



In reality, the y-intercept increased, which is what you wanted. And the x-intercept remained unchanged, which is what you wanted. *And the slope of the line became more negative, indicating stronger intraspecific competition on a per-capita basis.* Is that what you wanted? When you think of "*r*-selected" species, do you ordinarily think of species in

you wanted? When you think of "*r*-selected" species, do you ordinarily think of species in which intraspecific competition is strong on a per-capita basis, so that adding a single individual to the population takes a big bite out of the population growth rate? Do you ordinarily think of environments which select for "high *r*" (e.g., disturbed environments, newly-colonized islands) as "selecting" for stronger intraspecific competitive ability? Do you ordinarily even think of *r*-selection as having the "side effect" of strengthening intraspecific competition? If you're like most people, you probably don't. For instance, *r*-selected species are classically thought of as small-bodied (Pianka 1970), and you'd think that adding a small individual to the population shouldn't reduce population growth rate as much as adding a large individual would.

# Logistic equation: traditional formulation

- No parameter associated with competitive ability (related to the strength of density dependence)
- So then high quality offspring are suggested to have higher K.
- Parameters related to intraspecific competition between genotypes are missing
  - Motivation for density dependence was limiting resources

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

Joseph Travis,<sup>1,\*</sup> Jeff Leips,<sup>2</sup> and F. Helen Rodd<sup>3</sup>

## 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.

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).

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

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. In-

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).

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

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

$$\frac{dN}{dt} = aN - bN^2$$

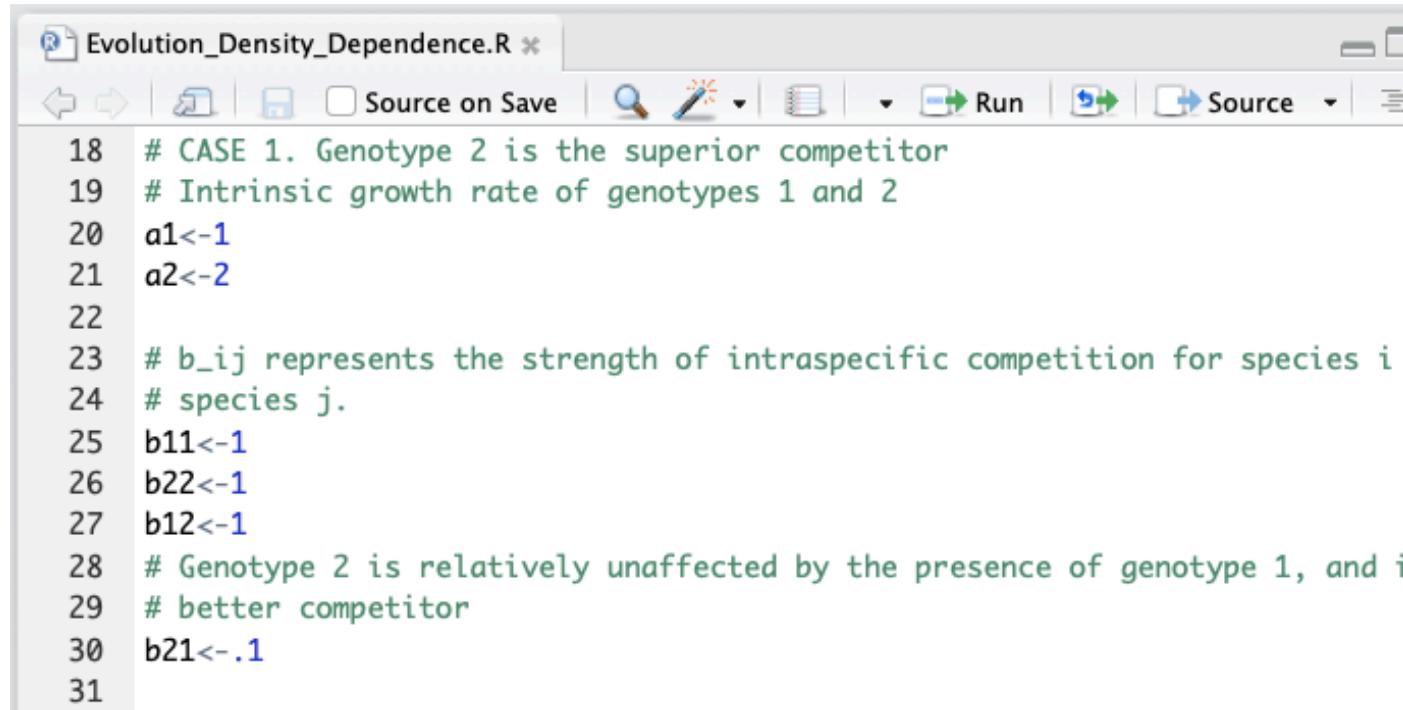
$$= aN \left( 1 - \frac{b}{a}N \right)$$

$$K = \frac{a}{b}$$

- Carrying capacity,  $K$ , is linked to  $a$ , and
- Positive relationship between  $K$  and  $a$ .

$$\frac{(1/N_1)dN_1}{dt} = a_1 - b_{11}N_1 - b_{12}N_2, \quad (2)$$

$$\frac{(1/N_2)dN_2}{dt} = a_2 - b_{21}N_1 - b_{22}N_2,$$



```

R Evolution_Density_Dependence.R ×
Source on Save | Run | Source | 
18 # CASE 1. Genotype 2 is the superior competitor
19 # Intrinsic growth rate of genotypes 1 and 2
20 a1<-1
21 a2<-2
22
23 # b_ij represents the strength of intraspecific competition for species i
24 # species j.
25 b11<-1
26 b22<-1
27 b12<-1
28 # Genotype 2 is relatively unaffected by the presence of genotype 1, and is
29 # better competitor
30 b21<-.1
31

```

Genotype 1 (red)

$$a_1 = 1$$

$$b_{11} = 1$$

$$b_{12} = 1$$

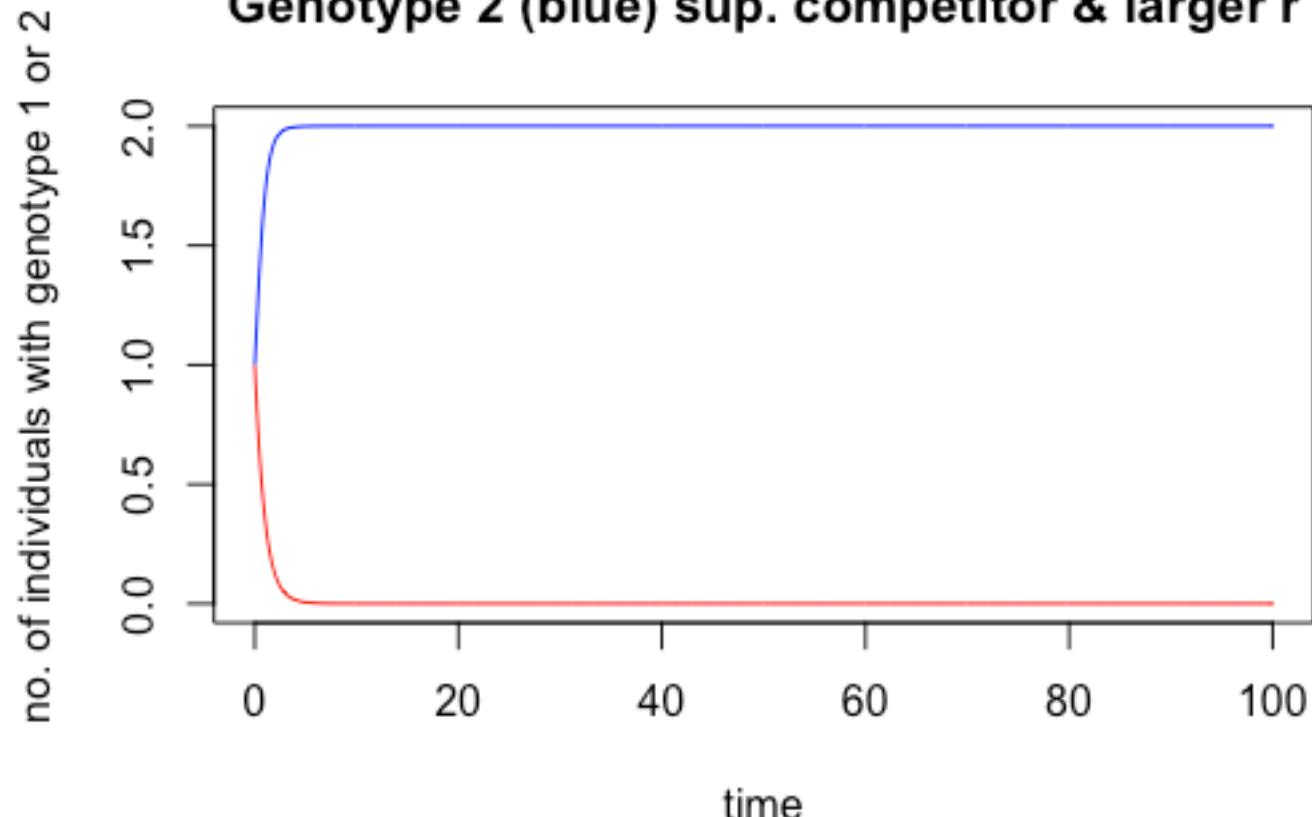
Genotype 2 (blue)

$$a_2 = 2$$

$$b_{22} = 1$$

$$b_{21} = 0.1$$

**Genotype 2 (blue) sup. competitor & larger r**



Genotype 1 (red)

$$a_1 = 1$$

$$b_{11} = 1$$

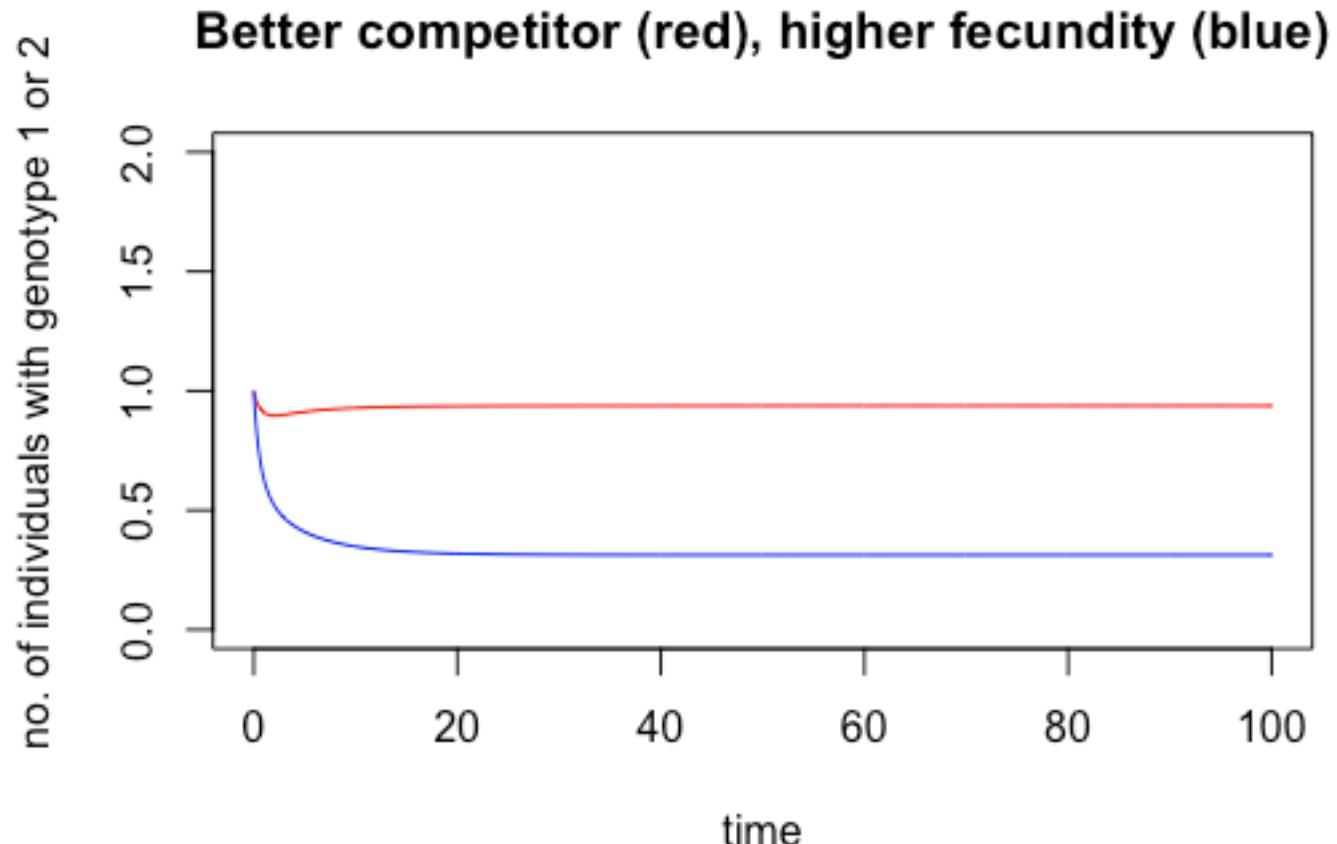
$$b_{12} = 0.2$$

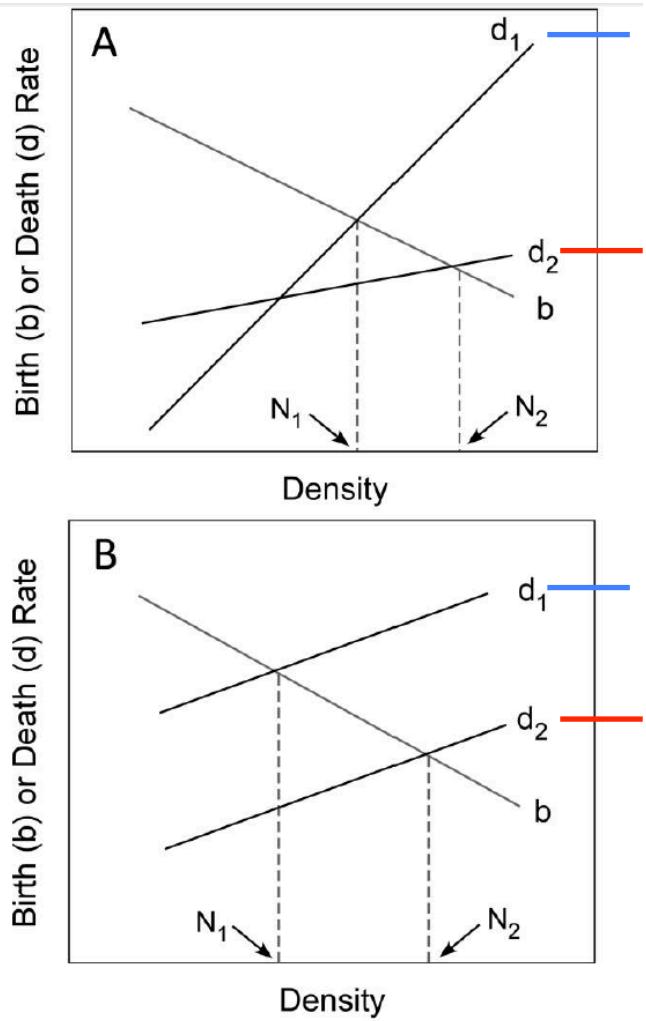
Genotype 2 (blue)

$$a_2 = 1$$

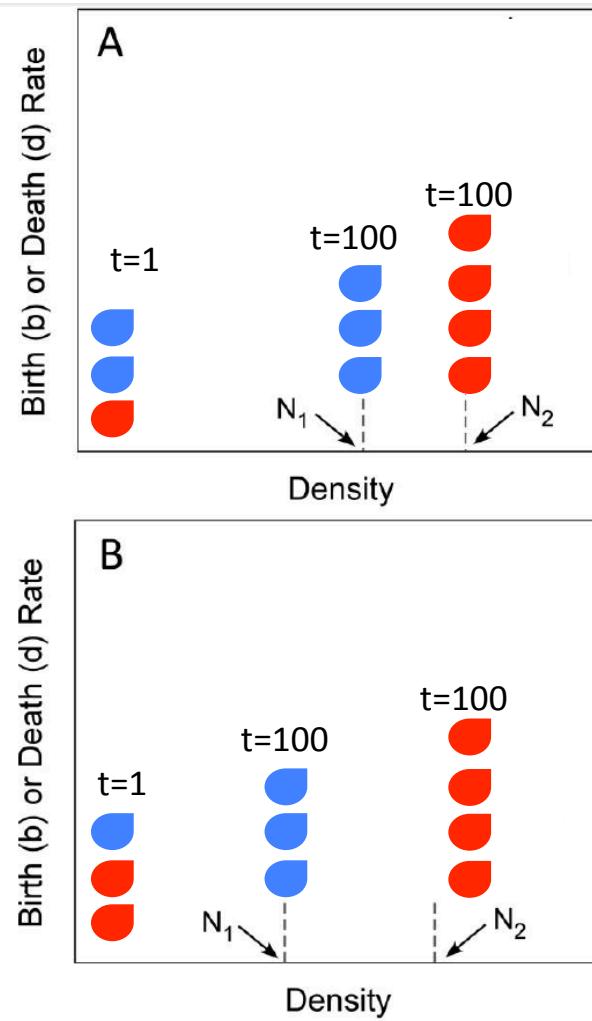
$$b_{22} = 1$$

$$b_{21} = 1.8$$

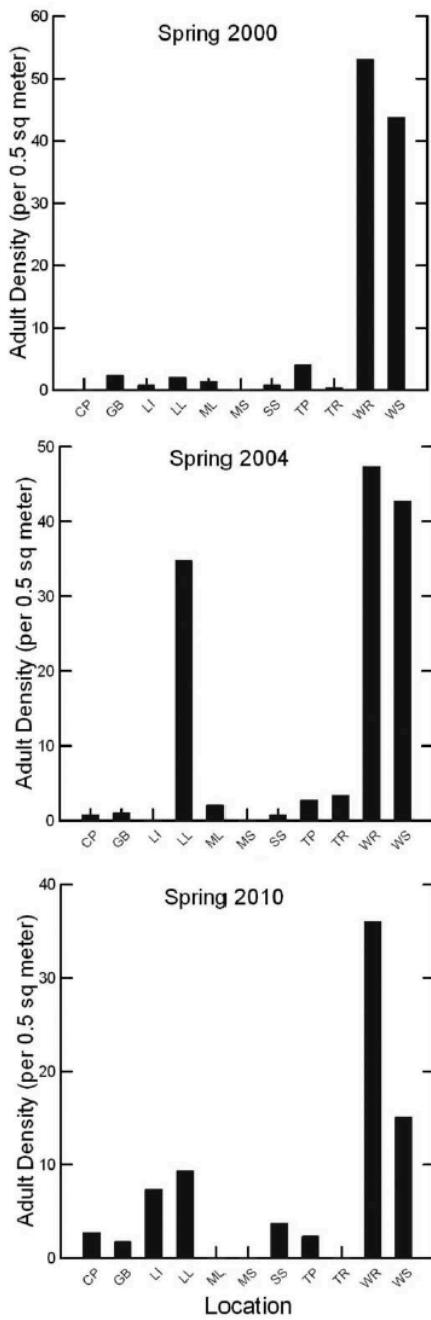




**Figure 1:** Graphical depiction of fitness components, birth rate (b) and death rate (d), as functions of density. Each cartoon depicts two genotypes with equal birth rate functions but different death rate functions. Fitness is determined by the excess of birth rates over death rates at any given 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 fitter genotype at low densities is not fitter 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. 1*B*), 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



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).

**Figure 3:** Variation in average adult density (number per 0.5 m<sup>2</sup>) 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 <sup>2</sup> )	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

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

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

ation 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.

Least killifish, *Heterandria formosa*



Brian Gratwicke [CC BY 2.0 (<https://creativecommons.org/licenses/by/2.0>)]



**Table 2:** Juvenile growth rate and age at maturity under different experimental density conditions for  $F_2$  fish from Trout Pond and Wacissa River populations

Trait	Mean value ( $\pm$ 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.

(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).

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.

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 heu-

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;

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

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

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