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Density-Dependent Selection

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Abstract

Density-dependent selection, which promotes contrasting patterns of trait means at different population densities, has a long history in population genetics and ecology. The unifying principle from theory is that density-dependent selection operates on phenotypic traits whose values counter the effects of whatever ecological agent is limiting population growth, be it resource competition, predators, or pathogens. However, the complexity inherent in density dependence means that the same selective process can generate multiple outcomes, depending upon the details of how population density affects vital rates and the age or size structure of a population. Failure to appreciate the potential for multiple outcomes confounded many early studies of the process. Nonetheless, careful empirical work in laboratory studies, long-term field studies, and studies of sexual selection demonstrates the wide reach of density-dependent selection. The inconsistent outcomes observed in these studies call for renewed research into how the details of density dependence channel adaptive responses.

1. INTRODUCTION

Density-dependent selection, which promotes contrasting patterns of trait means at different population densities, has long been common ground for population geneticists and ecologists (Mallet 2012). For population geneticists, density-dependent selection offered insights into the relationship between natural selection and population dynamics (Anderson 1971), the connections between demography and fitness (Charlesworth & Giesel 1972), the maintenance of genetic polymorphisms (Roughgarden 1971), and the reduction of genetic load in polymorphic populations (Clarke 1973). For ecologists, density-dependent selection offered a hypothesis for regular oscillations in population density (Chitty 1967), a mechanism for ecological character displacement (Bulmer 1974), and the potential to explain associations of trait variation, particularly life-history traits, with different regimes of population density (Pianka 1970, Grime 1977).

With such early promise, one might expect density-dependent selection to have been a central subject in evolutionary and ecological research. It is not clear that this has been so. For example, a search on the key phrase "density dependent selection" in Web of Science on December 18, 2022, for papers published between 1981 and 2020 returned 2,555 publications in the top ten life science subject areas (e.g., ecology, evolutionary biology, genetics/heredity). By contrast, a search with the same parameters using the key phrase "sexual selection" returned 24,672 publications.

The comparative lack of attention to density-dependent selection is not because the raw material for it is lacking. Many sets of natural populations display substantial, consistent differences in density regimes (Harrison et al. 2015, Soderquist et al. 2020). Ecological studies have suggested that population density affects the positions of adaptive peaks for many traits (Einum et al. 2008). In this light, the relative lack of attention to the process is striking.

It is even more striking, given how pervasive the influence of density-dependent selection might be. Older reviews stressed the importance of density-dependent selection in many areas of evolutionary biology and ecology (Antonovics & Levin 1980). The rise of community genetics (Whitham et al. 2006) promoted the importance of density-dependent selection for understanding species interactions. There are many behavioral processes for which variation in population density is considered a driving force, e.g., mating systems and sexual selection (Kokko & Rankin 2006), dispersal patterns (Matthysen 2005), and habitat selection (Webber & Vander Wal 2018).

Density-dependent selection has certainly not been neglected. Recent theoretical work has offered new insights (Lande et al. 2009, Engen et al. 2020, Coulson et al. 2022), and recent work in natural populations has demonstrated density-dependent selection for life-history traits (Saether et al. 2016, Reznick et al. 2019, Kentie et al. 2020), color morphs (Kvalnes et al. 2022), and phenotypic plasticity (Donohue et al. 2000). Our argument is that density-dependent selection demands even more investigation.

Here, we restore density-dependent selection to its rightful place as a central issue in evolutionary biology and ecology. We do so by showing how the principles of density-dependent selection apply across a range of empirical situations. We first review the theory of density-dependent selection, showing that it applies broadly to regulated populations no matter the agent of regulation. We then review the empirical evidence that the raw material for density-dependent selection is widespread, namely genotypic variation for norms of reaction of vital rates or key traits relative to density. Following that, we review laboratory and field studies of density-dependent natural and sexual selection. We conclude by synthesizing our observations and pointing to the profitable directions of future research.

2. CONCEPTS AND THEORY

2.1. Density-Dependent Population Dynamics

In 1798, Malthus (1798) observed that as food production increased, so did human population size. He argued that this pattern could not continue indefinitely because resource production must eventually plateau. As a consequence, a population dependent on the resource would cease growing as mortality rates increased or reproductive rates decreased. Verhulst (1838) formalized these arguments with the logistic equation, which coupled slowing population growth with increasing population size, thereby initiating the study of density-dependent population dynamics. Malthus' argument for population limitation was based on food production so, as a result, density-dependent dynamics were all too often equated with resource limitation. A more expansive view is that density-dependent dynamics emerge through any process that couples the rate of population growth with population size, be it resource availability, predation, or pathogen infection (Turchin 2003).

Diagnosing this density dependence, regardless of cause, requires recognizing that natural populations are subject to demographic and environmental stochasticity (Tuljapurkar 1990). Stochastic effects make population dynamics an interplay between density-dependent and stochastic processes (Coulson et al. 2001) in which populations fluctuate in time within a stochastic equilibrium described by a stationary distribution of population sizes. The signature of density dependence is a set of fluctuations around a mean abundance whereby when a population is observed to be large, it is likely to be small when next sampled, and vice versa.

This more realistic view of population dynamics led to the recognition that density-dependent dynamics are widespread (Bonenfant et al. 2009). It also prompted a renewed focus on understanding the mechanisms of density dependence. On the theoretical side, this meant building demographic models of births and deaths in limiting environments (Charlesworth 1994, Lande et al. 2009, de Roos 2021, Coulson et al. 2022). These models led to a renewed interest in density-dependent selection, the driver of adaptation to a limiting environment.

2.2. Density-Dependent Selection

The earliest mathematical theory for density-dependent selection examined how the parameters of the logistic equation could describe fitness in contrasting situations (MacArthur 1962, Boyce 1984, Mueller 1997). The common formulation of the logistic equation in either discrete or continuous time has two parameters, r and K. The first of these is the maximum rate of population increase in the absence of any factor that limits the population's growth, while the second is the equilibrium population size, often called the carrying capacity, reflecting Malthus' enduring influence. The seminal paper of MacArthur (1962) argued that, in unregulated populations, a genotype's value of r would reflect its relative fitness, while in regulated populations, a genotype's carrying capacity would reflect its relative fitness. This argument led to the prediction that density-dependent selection would increase the equilibrium population size, a result that linked ecological and evolutionary dynamics.

In general, adaptation to a particular environment is all about competitive exclusion. The fittest strategy, be it a genotype in models like that of MacArthur (1962) or a phenotype in many of the models we discuss below, is the one that is the most competitive in that environment. In an unlimited environment, the fittest strategy is the one that grows most quickly, eventually displacing all others. In a limiting environment, the fittest strategy is the one that can persist at the highest density of the limiting factor. When a resource is limiting, the fittest strategy is the one that drives the resource to the lowest level, thereby persisting at a higher population density at that resource level than other strategies. In ecology, this principle, applied to species instead of strategies, is termed R* theory (Tilman 1982). Related logic can be used for predator-limited populations; the fittest strategy is the one that can persist at the highest predator density (Holt & Bonsall 2017).

One of the challenges in studying density-dependent selection is that it can generate different outcomes from the same process, depending upon biological details. Imagine a monomorphic population with a resident life-history strategy. On average, each individual replaces itself, and the population is stationary. A mutant arises that is more efficient at using resources, so it converts them more effectively into offspring. This mutant is fitter than the resident and, eventually, displaces it. Its greater efficiency at using resources produces the increased equilibrium population size predicted by theory.

Now imagine a different scenario with the same initial resident, but in this case, a mutant arises with a fitter life history because it is better at finding resources. As a consequence, this mutant drives those resources to lower abundance. The resources are so scarce that the resident life history strategy cannot replace itself, and it is replaced by the mutant. However, because the mutant life history has driven the resource to a lower abundance, there are fewer total resources, and the average population size of the mutant may be less than that of the resident it has replaced. This does not contradict MacArthur's (1962) result. The lower equilibrium size is driven by the lower resource levels; all else being equal (that is, for a given resource level), the mutant strategy has the higher equilibrium size. Mueller (1988) developed this argument in his mathematical model of density-dependent selection in *Drosophila*.

The importance of biological detail is evident in another context. MacArthur & Wilson (1967) suggested that traits associated with higher values of r would be associated with lower values of K and vice versa. This suggestion led many ecologists to assume that density-dependent selection would be reflected, invariably, in a trade-off between the two parameters themselves. In fact, this trade-off occurs only under specific conditions.

To see this, consider the model

$$\begin{aligned}\frac{1}{R}\frac{\mathrm{d}R}{\mathrm{d}t} &= r_R\left(1-\frac{R}{K_R}\right)-\gamma C\\ \frac{1}{C}\frac{\mathrm{d}C}{\mathrm{d}t} &= \delta\gamma R-\mu\end{aligned}, \qquad 1.$$

where r_R, K_R, and R are the intrinsic rate of increase, carrying capacity, and population size of the resource, respectively, and γ, δ, μ, and C are the feeding rate, conversion efficiency, mortality rate, and population size of the consumer, respectively. Assuming a timescale difference between the resource and the consumer, the consumer–resource model can be rewritten as the logistic equation (MacArthur 1970):

$$\frac{1}{C}\frac{\mathrm{d}C}{\mathrm{d}t} = \delta\gamma K_R-\mu-\frac{\delta\gamma^2K_R}{r_R}C, \qquad 2.$$

which has the general form of the logistic equation,

$$\frac{1}{C}\frac{\mathrm{d}C}{\mathrm{d}t} = r_C-\alpha C, \qquad 3.$$

where $r_C = \delta\gamma K_R-\mu$ and $\alpha = \frac{\delta\gamma^2K_R}{r_R}$, or the more familiar

$$\frac{1}{C}\frac{\mathrm{d}C}{\mathrm{d}t} = r_C-\frac{r_C}{K_C}C, \qquad 4.$$

with $K_C = \frac{r_R(\delta\gamma K_R-\mu)}{\delta\gamma^2K_R}$.

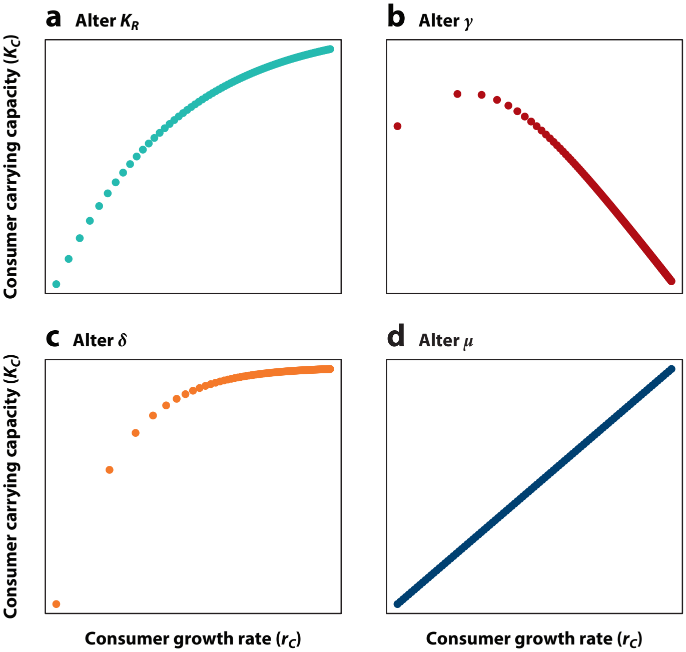

Figure 1

Relationships between consumer growth rate and consumer carrying capacity in the model described in Equations 1–4. Each graph shows the relationship across variation in one of the biological parameters underlying both growth rate and carrying capacity. (*a*) Effect of altering carrying capacity of the resource. (*b*) Effect of altering consumer feeding rate. (*c*) Effect of altering consumer conversion efficiency. (*d*) Effect of altering consumer mortality rate. Abbreviations: γ, feeding rate; δ, conversion efficiency; μ, mortality rate; *C*, population size of the consumer; K_R, carrying capacity of the resource; *R*, population size of the resource; r_C, intrinsic rate of increase of the consumer.

Notice that the intrinsic rate of increase (r_C) and the carrying capacity of the consumer (K_C) in the logistic equation share nearly all the same underlying parameters. The details of how the underlying ecological parameters contribute to *r* or *K* determine whether the relationship between *r* and *K* is positive or negative. In this model, changes in all of the parameters, except the feeding rate of the consumer (γ), generate positive covariance between r_C and K_C but even then only over some range of values (**Figure 1**). A negative covariance emerges only through changes in the consumer feeding rate.

The deterministic logistic equation offers limited insight into density-dependent selection. This is because it collects the demography of populations, which are the rates of survival, growth, and reproduction, into two summary parameters. Those rates are the building blocks of fitness, and a more detailed approach to understanding fitness, especially in stochastic environments, is necessary.

Fitness is a central but slippery concept. Simply defined, fitness is genetic representation within a population at some arbitrary point in the future. It is not easy to transform this definition into something that can be quantified. In terms of alleles, fitness is simply a change in frequency with time and is determined by the birth and death rates of individuals that carry the allele (Charlesworth 1994). For genotypes and phenotypes, change in frequency is also a measure of fitness, but because these entities do not make replicates of themselves in sexual populations, the definition of fitness using frequency becomes increasingly fraught as there is no single measure of their increase in abundance over time.

A convenient simplification for advancing mathematical theory is to assume clonal reproduction, in which a life history—a strategy described by rates of survival, growth, and reproduction—is described with a set of parameters that are passed faithfully from parent to offspring (Metz et al. 1995). This approach can describe the evolutionary end of point of selection by identifying the evolutionarily stable life-history strategy (ESS), which is one that cannot be invaded by any other. In a stochastic, density-independent environment, the fittest strategy is the one with the highest long-run stochastic growth rate (Tuljapurkar & Orzack 1980, Childs et al. 2004).

One way to make this approach tractable for density-dependent selection is to assume that the dynamics of the limiting factor do not change with evolution of the focal population. This assumption allows fitness to be described by the mean population size at equilibrium, or something similar such as a weighted of sum of individuals in different age or stage classes (Coulson et al. 2022). In models of density-dependent stochastic environments, assuming that each strategy competes equally against every other strategy, the contrast between the mean population size of residents and mutants when each is the only extant strategy perfectly predicts the ESS (Charlesworth 1994, Kentie et al. 2020). This means that, in theory, the outcome of density-dependent selection can be assessed by the stationary distributions of population sizes of each of the competing strategies.

With this result in hand, we can ask in more detail why different strategies achieve different population sizes and thus different levels of relative fitness. Equilibrium population size, when the population growth rate between times t and $t + 1$ equals 1, is determined by (*a*) the strength of density dependence in vital rates and (*b*) the value of demographic rates that are not influenced by density. We can examine this by assuming a very simple example with just two rates that we analyze at equilibrium:

$$1 = S_x + R_x\,(k_x), \qquad 5.$$

where 1 is the population growth rate at equilibrium, S_x is the survival rate of strategy x, $R_x(k_x)$ is the density-dependent reproductive rate of strategy x, and k_x is the population size of strategy x at equilibrium. If we assume that one individual of strategy A is competitively equivalent to one individual of strategy B, then A is the evolutionarily stable strategy when $k_A > k_B$ and vice versa. Next, assume that the function $R_x(N_x)$ is identical between strategies A and B such that $R_x(N_x) = e^{\beta_0+\beta_1 N_x}$ where the βs are parameters and $\beta_1 < 0$, meaning that increasing the population size of x dampens its rate of population increase.

As S_x increases, then $R_x(k_x)$ must decrease to maintain the identity in Equation 5, and this requires an increase in k_x. The fittest strategy is consequently the one with the highest value of the density-independent rate S_x, the smallest value of $R_x(k_x)$, and the largest value of k_x, which is the equilibrium population size (Charlesworth 1994).

The next step is to incorporate phenotypic traits explicitly into these models. In Equation 5, $R_x(k_x)$ and S_x negatively linearly covary, and runaway selection results in $k_x \to \infty, R_x(k_x) \to 0$, and $S_x \to 1$. Metabolic scaling and genetic constraints prevent this from happening; nonetheless, values of S_x and $R_x(k_x)$ can change when traits that influence them evolve. We can extend Equation 5 to make survival and reproduction functions of phenotypic traits z_1 and z_2:

$$1 = S_x\,(z_1) + R_x\,(k_x, z_2). \qquad 6.$$

Evolution of z_1 increases the value of the density independent rate, and the trait is said to be *r*-selected. In contrast, evolution of z_2 increases the value of $R_x(k_x, z_2)$, which in turn requires an increase in the value of k_x in order to balance Equation 6. A life history that evolves predominantly by increasing density-independent rates is said to be *r*-selected, while one that evolves by increasing k_x is said to be *K*-selected (MacArthur 1962). In stochastic environments, in which populations fluctuate, both *r*-selected and *K*-selected life history strategies can coexist, but this does not always appear to happen. Kentie et al. (2020) reported models where the ESS in a deterministic density-dependent environment was also the ESS in a stochastic environment.

Pianka (1970) drew a list of traits he considered to be either *r*- or *K*-selected. His *r*-selected traits tended to be associated with species that could reproduce quickly, while his *K*-selected ones tended to be those found in long-lived species. Pianka consequently associated fast-lived species with being *r*-selected and slow-lived ones with being *K*-selected. However, we can see from Equation 5 that when density dependence operates via reproduction, then survival becomes the *r*-selected demographic rate. Pianka's list of *r*- and *K*-selected traits matched better with speed of life history, or what has subsequently become known as pace-of-life, rather than density-dependent selected characters.

Equations 5 and 6 are pedagogically useful but overlook much complexity. Natural populations are structured by age, stage, or body size, and these equations do not include that structure. Charlesworth (1994) and Lande et al. (2009) explored how density-dependent selection operates in age-structured populations, and others extended this work to stage-structured populations (de Roos 2021, Coulson et al. 2022). These models expand the range of phenomena that can be explored with density-dependent selection and also offer a clearer link to empirical work (Coulson et al. 2010).

To illustrate these points, we can expand Equations 5 and 6 to consider sexually immature and mature individuals. Writing mean population size as $\bar{N}$ and splitting the population into juvenile, j, and adult, a, classes, we can write

$$\bar{N} = \bar{N}_j S_j\left(\bar{N}\right) + \bar{N}_a\left(S_a + R_a\right). \qquad 7.$$

Here, mean population size is equal to the number of juveniles in the population multiplied by their survival rate plus the number of adults multiplied by the sum of their survival and reproductive rates. Juveniles are sexually immature and consequently do not have a reproduction term. Juvenile survival is the *K*-selected rate, and adult survival and reproduction are both *r*-selected. Dividing through by $\bar{N} = \bar{N}_j + \bar{N}_a$ gives

$$1 = \frac{\bar{N}_j}{\bar{N}} S_j\left(\bar{N}\right) + \frac{\bar{N}_a}{\bar{N}}\left(S_a + R_a\right). \qquad 8.$$

We can see from these equations that population structure matters, with the number (proportion) of juveniles and adults contributing to the dynamics. A challenge arises in that the asymptotic (deterministic environment) and stationary (stochastic) population structure are dependent on the demographic rates. If $S_j(\bar{N})$, S_a, or R_a evolves, then $\bar{N}_j$, $\bar{N}_a$, and $\bar{N}$ also change while maintaining the identity in Equation 6. For example, if S_a evolves to be larger, we might expect $\bar{N}_a$ to increase simply because adults now have an increased life expectancy. In addition, a greater of number of young might be born if $\bar{N}_a$ increases. However, an increase in S_a requires a lower value of $S_j(\bar{N})$ to maintain the identity, which in turn reduces the number of young surviving to become adults. The dependency between terms complicates the analysis of density-dependent models, with the maximization of mean population size requiring both values of rates and the population structure to be simultaneously optimized. General solutions for density-dependent selection are yet to be identified (Charlesworth 1994). Nonetheless, evolution for a decrease in a density-dependent per capita demographic rate, such as $S_j(\bar{N})$, frequently appears to occur in tandem with an increase in the number of individuals in that class (e.g., $\bar{N}_j$), with these two terms combining to determine the number of young that survive to adulthood (Charlesworth 1994, Coulson et al. 2022).

Equation 8 gives a very simple example of two classes, with only one class being influenced by density. In cases where multiple demographic rates are density dependent, evolution is expected to minimize the value of the per capita demographic rate that is most strongly influenced by density while acting to increase the number and proportion of individuals in that demographic class, a result analogous to that of MacArthur (1962). However, this result has not been mathematically proven (Charlesworth 1994).

Equation 8 can also offer insights into trait evolution under density-dependent selection. We can expand Equation 8 similarly to how we expanded Equation 5:

$$1 = \frac{\bar{N}_j}{\bar{N}} S_j\left(\bar{N}, z_1\right) + \frac{\bar{N}_a}{\bar{N}}\left(S_a\left(z_1\right) + R_a\left(z_1\right)\right). \qquad 9.$$

In this example, the same phenotypic trait influences juvenile and adult survival and adult reproduction. Phenotypic traits change values as individuals develop, so to make this equation dynamic, it is necessary to incorporate rules for the development of phenotypic traits. When we do this, and when development is influenced by density, then the rates of transition between classes, such as between juveniles and adults, become density dependent. This expands our roster of vital rates through which density-dependent selection can act.

With all of this additional complexity, the demographic details of density-dependent selection become even more important (Charlesworth 1994, Coulson et al. 2022). In a predator-limited population, mean population density is below the level that would be seen were the population food limited. Abundant food means that development rates are unlikely to be density dependent, and organisms can develop to sexual maturity quickly. If predation affects only juvenile survival, such that adults live for a long time, density-dependent selection can select for large, long-lived species. In contrast, if adults and juveniles are vulnerable to predation, density-dependent selection can operate in the opposite direction, selecting for small, fast-lived species. Similar patterns can be observed in food-limited populations when developmental rates are density-dependent.

To this point, our treatment has focused on circumstances in which differences in the mean population size at equilibrium predict the evolutionary outcome. As stated earlier, the assumption beneath the models for these circumstances is that each strategy has the same competitive effect on every other strategy. When strategies differ in their competitive effects on one another, which we denote as an asymmetric competitive environment, we cannot predict the outcome of density-dependent selection from the mean population sizes of each strategy when alone (a so-called pure strategy), and invasion criteria must be used.

Asymmetric competitive environments may be very common. One example of such a situation can occur when selection acts on the ability to compete for a discrete resource like a breeding site or a refuge from predation when the number of such sites is limited and unaffected by the number of individuals competing for them (Wallace 1975, Bell et al. 2021). Another example is sexual selection when males compete for mates, but the number of males does not limit the fecundity of females in the population (Whitlock 2000). In these cases, selection determines which strategy is most fit through its ability to outcompete the others but does not determine how many individuals contribute to the next generation.

Sexual selection is particularly interesting in this regard because sexual conflict can introduce considerably more complexity to an asymmetrically competitive situation. When traits that enhance male mating success have deleterious effects on female vital rates, the strategy that is most fit in males can reduce female fitness (Holland & Rice 1999), which can, in turn, drive changes in population numbers (Kokko & Brooks 2003). Examples of such sexual conflict include the graspers of water striders (Arnqvist 1989), forced insemination attempts in mosquitofish (Horth & Travis 2002), and the seminal proteins of *Drosophila* males (Wigby & Chapman 2005). Given that increased densities may elevate the intensity of sexual selection (see Section 3.2.3), sexual conflict of this type forces a linkage between density-dependent selection and density-dependent population dynamics that would have been absent otherwise.

This is an underexplored area in density-dependent selection theory. As with models of natural selection, models of this process must integrate across the entire life history, with evolution minimizing the value of model terms where density dependence operates most strongly and maximizing the value of density-independent terms. These models are more complex because they must incorporate the demography of both sexes (Schindler et al. 2015).

The complexity increases further if we consider natural and sexual selection simultaneously. If adult female fertility is strongly density dependent through natural selection, evolution selects for female strategies that can persist at the highest population densities, and these are often strategies with low reproductive rates. As such strategies increase in frequency, there is likely to be even greater competition between males for reproductive opportunities. This, in turn, leads to an increase in the correlated, deleterious effects on females. How often this conflict occurs is an open empirical question; the theory for its consequences is an open theoretical one.

Where does all this leave the state of density-dependent selection? While the details clearly matter, we can recite some general principles:

- Density-dependent selection in symmetric competitive environments acts to maximize mean population size at equilibrium.
- Selection for increased mean population size results in a reduction in the per capita demographic rates most strongly influenced by density.
- To counter selection for a reduced density-dependent per capita demographic rate, density-dependent selection also selects for an increase in the number of individuals and the proportion of the population in the demographic class most strongly influenced by density dependence.
- The outcome of density-dependent selection depends not only upon details of where in the life history density dependence operates but also on the ecological source of the density dependence

In the next sections, we review empirical data with an eye toward assessing two issues. First, how well do those data fulfill the predictions of theory? In particular, because theory indicates that details matter for the predictions themselves, we review what the data say about which details appear to matter and why. Second, we assess the prevalence of density-dependent selection, from its baseline prerequisites (Section 3.1) to its demonstrations in laboratory and field studies of natural and sexual selection (Section 3.2).

3. THE EVIDENCE FOR DENSITY-DEPENDENT SELECTION

3.1. Genetic Variation in Norms of Reaction to Density

For density-dependent selection to drive evolutionary change, there must be genetic variation in the norms of reaction of fitness-related traits in response to shifts in density. There is a considerable empirical body of work that has tested for such genetic variation (**Table 1**). Additional studies report genetic variation in reaction norms by using relevant proxies for density like resource availability or resource quality (Via 1991, Semlitsch 1993, Blanckenhorn 1998, Lewis et al. 2012).

It is important to distinguish two patterns of genetic variation in reaction norms. First, increasing density could result in the crossing over of reaction norms, which causes some genotypes to have higher fitness at low density, while others have enhanced fitness at the higher densities. These crossing reaction norms are the fuel for generating alternative combinations of mean trait values at different densities. Second, changes in density can cause changes in variance among

Table 1 Studies that tested for genetic variation in response to manipulations of density or a proxy for density

Taxa	Species	Traits	Treatment	G×E	Comparison	Citation
Invertebrate	*Drosophila melanogaster*	Life history	Density	yes	Within species	Lewontin 1955
Invertebrate	*Scathophaga stercoraria*	Life history	Resources	yes	Within species	Blanckenhorn 1998
Invertebrate	*Panorpa cognata*	Reproductive	Resources	yes	Within species	Engqvist 2008
Invertebrate	*Tenagogerris euphrosyne*	Behavior	Density	yes	Within species	Han & Brooks 2015
Invertebrate	*Drosophila melanogaster*	Life history	Density	yes	Within species	Horvath & Kalinka 2016
Fish	*Poecilia reticulata*	Sexual selection	Resources	yes	Within species	Hughes et al. 2005
Invertebrate	*Tribolium castaneum*	Life history	Resources	yes	Within species	Via 1991
Invertebrate	*Tribolium castaneum*	Life history, sexual selection	Resources	yes	Within species	Lewis et al. 2012
Plant	*Solanum carolinense*	Life history	Density	yes	Within species	McNutt et al. 2012
Invertebrate	*Tetrahymena thermophila*	Life history	Density	yes	Within species	Pennekamp et al. 2014
Plant	*Abutilon theophrasti*	Life history	Density, resources	yes	Within species	Sugiyama & Bazzaz 1997
Plant	*Polygonum pensylvanicum*	Life history	Density	yes	Within species	Thomas & Bazzaz 1993
Amphibian	*Hyla gratiosa*	Life history	Density	no	Within species	Travis 1983
Plant	*Acanthoscelides obtectus* Say	Life history	Density	yes	Within species	Tucic et al. 1991
Invertebrate	*Drosophila melanogaster*	Life history	Density	yes	Within species	Clark & Feldman 1981
Plant	*Arabidopsis thaliana*	Life history	Density	yes	Within species	Palacio-Lopez et al. 2020
Plant	*Salvia lyrata*	Life history	Density	yes	Within species	Shaw 1986
Plant	*Raphanus sativus*	Life history	Density	yes	Within species	Mazer & Schick 1991
Plant	*Erigeron annuus*	Life history	Density	yes	Within species	Bennington & Stratton 1998
Amphibian	*Rana lessonae*	Life history	Resources	yes	Between species	Semlitsch 1993
Invertebrate	*Aedes aegypti*	Life history	Density, resources	yes	Between sexes	Bedhomme et al. 2003
Plant	*Impatiens capensis*	Life history, morphology	Density	yes	Population divergence	Donohue & Schmitt 1999, Donohue et al. 2000
Plant	*Arabidopsis thaliana*	Life history, morphology	Density	yes	Population divergence	Donohue et al. 2005
Fish	*Heterandria formosa*	Life history	Density	no	Population divergence	Leips et al. 2009
Fish	*Heterandria formosa*	Life history	Density	yes	Population divergence	Leips et al. 2000

(*Continued*)

Table 1 ***(Continued)***

Taxa	Species	Traits	Treatment	G×E	Comparison	Citation
Plant	*Bouteloua rigidiseta*	Life history	Density	yes	Population divergence	Miller & Fowler 1993
Plant	*Ranunculus reptans*	Life history	Density	yes	Population divergence	Prati & Schmid 2000
Plant	*Ranunculus reptans*	Life history	Density	yes	Population divergence	Van Kleunen & Fischer 2001
Invertebrate	*Achroia grisella*	Sexual selection	Density	yes	Population divergence	Zhou et al. 2008
Fish	*Rivulus hartii*	Life history	Resources	yes	Population divergence	Walsh & Reznick 2008
Invertebrate	*Drosophila melanogaster*	Life history	Density	yes	Lab selection	Perez & Garcia 2002
Invertebrate	*Drosophila melanogaster*	Life history	Density	no	Lab selection	Shenoi et al. 2016
Invertebrate	*Drosophila melanogaster*	Life history	Density	yes	Lab selection	Bierbaum et al. 1989
Invertebrate	*Nicrophorus vespilloides*	Life history	Density	yes	Lab selection	Schrader et al. 2017

Abbreviation: G×E, gene-by-environment interaction.

genotypes without any crossing over of reaction norms, thereby minimizing the opportunity for density-dependent selection.

While the two patterns are not mutually exclusive, the published literature primarily reports evidence for crossing reaction norms (**Table 1**). The most striking examples demonstrate dramatic rank order changes in the fitness of genotypes as a function of density (Lewis et al. 2012, Horvath & Kalinka 2016). Other studies have revealed changes in variance in addition to crossing reaction norms (McNutt et al. 2012).

Density-dependent selection can contribute to sexual dimorphisms at some densities when the sexes differ in reaction norms. Dimorphic norms can also reflect differences between the sexes in how individual traits contribute to fitness. For example, in male *Aedes aegypti*, longevity and body mass decreased with increased density, while development time was unchanged; females displayed the opposite pattern in these traits (Bedhomme et al. 2003). Development time is a crucial component for fitness in males, more so than longevity or body mass; conversely, for females, development time is much less important than body size.

In some cases, increased density or proxies for density can lead to shifts in reaction norms that persist beyond the parental generation (Bashey 2006, Bitume et al. 2014). For example, in the two-spotted spider mite, individuals disperse further when experiencing higher densities. However, offspring exposed to the same density disperse further when born to parents that experienced higher density (Bitume et al. 2014). This effect extends backward to the grandparental generation, although not if grandoffspring are exposed to lower densities.

Genetic variation in reaction norms among populations within a species or among species can reveal how different reaction norms have evolved in response to different density regimes (Donohue & Schmitt 1999, Donohue et al. 2000, Leips et al. 2000, Prati & Schmid 2000, Van Kleunen & Fischer 2001, Walsh & Reznick 2008). For example, Leips et al. (2000) found that populations of the least killifish (*Heterandria formosa*) that naturally experienced high population density responded to high density with larger declines in offspring size but smaller declines in brood size than those from a population typically found at lower densities. Van Kleunen & Fischer (2001) showed that response to herbivory by the stoloniferous plant (*Ranunculus reptans*) is stronger in genotypes that originated from high competition (high density) environments compared with genotypes from low competition sites.

While we have focused on the many studies showing genetic variation in reaction norms, in some cases only a subset of traits displayed genotype-by-environment interactions (Hughes et al. 2005, Lewis et al. 2012, Han & Brooks 2015). In fact, some investigators found no evidence for genetic variation in reaction norms of key traits in response to density (Travis 1983, Leips et al. 2009, Shenoi et al. 2016). Nevertheless, the literature offers substantial evidence that natural populations harbor the raw material necessary for adaptive evolution of responses to density.

3.2. Demonstrations of Density-Dependent Selection

3.2.1. Laboratory studies. The popularity of the theory of *r*- and *K*-selection inspired laboratory experiments designed to test the predicted trade-off between adaptation to low densities and adaptation to high densities. In each of these studies, populations were maintained in the laboratory at low or high densities for many generations, after which the experimenters measured population growth rate, equilibrium density, competitive ability, organism size, and in some cases, demographic variables.

These experiments produced mixed results. Mueller's (1997) early work with *Drosophila melanogaster* found a trade-off; when compared with populations maintained in uncrowded conditions, populations maintained in crowded conditions had higher growth rates when measured at higher densities, lower growth rates when measured at lower densities, higher equilibrium densities, and greater competitive ability. In contrast, Luckinbill (1978, 1984) found a positive correlation between population growth rates and saturation densities in *Escherichia coli*.

While there were methodological questions about some of this work (Mueller 1997, Mueller et al. 2005), on the whole, these mixed results suggested that predictions based only on population parameters were inadequate (see Section 2.2). A more expansive approach was to recognize that with density dependence, the details matter. Mueller (1988) built a mathematical model of density-dependent selection in *Drosophila* based on studies of how larval crowding affected somatic growth rates, development time, and body size, along with the connections between those individual traits and larval survival and adult fecundity. This model's predictions were contingent on how individual traits responded to density. Guided by this model, subsequent laboratory studies of *Drosophila* found ample evidence of density-dependent selection and adaptation. Fly populations maintained at high larval densities typically evolved greater larval survival, higher pupation height, increased tolerance to urea and ammonia, longer development times, and larger body sizes (Mueller et al. 2005). However, as Mueller (1988) predicted, details mattered. In experiments that used different per capita food levels, a different suite of outcomes emerged, with flies evolving higher feeding rates, shorter development times, larger egg sizes, and no increased tolerance to urea and ammonia (Venkitachalam et al. 2022).

Laboratory natural selection experiments on other organisms were similarly successful; burying beetles (Schrader et al. 2017) and medaka fish (Bouffet-Halle et al. 2021) evolved larger body sizes, and medaka also evolved longer development times in response to high density.

A striking result of some studies was density-dependent evolution of the reaction norms of individual traits. Bierbaum et al. (1989) found that larval development time displayed less plasticity to density in populations of *D. melanogaster* that had evolved at high density, compared with those from low-density treatments. Perez & Garcia (2002) reported a similar result for biomass, with reduced plasticity to density having evolved in high-density populations. The opposite pattern was reported by Shenoi et al. (2016): Body mass in high-density populations became more sensitive to density. Why this was so—which details mattered—remains unclear.

Evolution of reaction norms has not proven universal. Shenoi et al. (2016) found no evidence for the evolution of the reaction norm of adult longevity to density, even though longevity had increased in the high-density populations. A similar result was reported by Schrader et al. (2017) in their study of burying beetles; although mean larval mass evolved upward as larval density increased, the norm of reaction did not change. Why norms did not evolve in these cases when they did in others remains to be explored.

One of the most consistent results from nearly all laboratory studies of density-dependent selection in *Drosophila* was the evolution of increased competitive ability at high densities (Mueller et al. 2005, Venkitachalam et al. 2022). Luckinbill (1978) found the same result in his work with *Escherichia coli* but not in his studies of *Paramecium* species (Luckinbill 1979). Laboratory evolution of competitive ability has a parallel in studies of natural populations. Bradshaw & Holzapfel (1989) found that individual pitcher plant mosquitos from high-density populations had greater competitive ability than those from low-density populations. Guppies from high-density populations proved to be better intraspecific (Potter et al. 2019) and interspecific (Anaya-Rojas et al. 2021) competitors than guppies from low-density populations.

3.2.2. Field studies of natural selection.

The evidence for density-dependent selection and evolution in nature stems from three types of studies: (*a*) long-term demographic studies, (*b*) density manipulations, and (*c*) comparisons between populations that differ in density.

3.2.2.1. Long-term field studies.

Several long-term studies that tracked variation in population density in conjunction with phenotypic traits have demonstrated density-dependent selection. For example, 24 years of monitoring a wild Soay sheep population showed that the intensity of selection on several morphological traits covaried positively with density (Hayward et al. 2018). A 13-year study of red deer found interactions in calf survival between population density and genotype (Coulson et al. 1998). Density-dependent selection maintains a color polymorphism in barn owls (*Tyto alba*); red individuals are favored at low densities, while white individuals are favored at high densities (Kvalnes et al. 2022). Similarly, Sinervo et al. (2000) showed that side-blotched lizards (*Uta stansburiana*) with orange throats, which produce many eggs, are favored at low densities, while yellow-throated individuals, which produce large eggs, are favored at high densities. Saether et al. (2016) found that low population densities favor larger clutch sizes in great tits, while higher population densities favor smaller clutch sizes. Kentie et al. (2020) reported that larger size and longer generation time are favored at low population densities in Soay sheep, but short generation time and small body size are favored at high densities. In experimentally transplanted guppy populations, males evolved delayed maturity only after the populations attained high densities (Reznick et al. 2019). In great tits, low density favored faster explorers, but high density favored less exploratory behavior (Nicolaus et al. 2016).

3.2.2.2. Density manipulation experiments.

Density-dependent natural selection has been found through short-term manipulations (Farkas & Montejo-Kovacevich 2014, Le Galliard et al. 2015) as well as multi-year perturbations (Svensson & Sinervo 2000, Calsbeek & Smith 2007). For example, Calsbeek & Smith (2007) altered the density of brown anoles (*Anolis sagrei*) across seven islands and three consecutive years and found that increasing density consistently favored a larger body size.

3.2.2.3. Population comparisons.

Organisms that reside in environments with different density regimes provide strong evidence for density-dependent selection and adaptive evolution in trait values and trait plasticity (Donohue et al. 2000, Leips et al. 2000, Van Kleunen & Fischer 2001). In elegant studies of *Impatiens capensis* from sunny (high density) versus shady (low density) sites, Donohue et al. (2000) showed that the sunny population exhibits greater plasticity in internode length and flowering date than the woodland population. In the shady site, those trait combinations are maladaptive (Dudley & Schmitt 1996, Donohue et al. 2001).

It is important to note that not all investigators observed shifts in trait values or trait plasticity between populations that differed in density. Experimental variation in population densities had no impact on life history traits or on equilibrium densities in pitcher plant mosquitos (*Wyeomyia smithii*) from populations that experienced characteristically different levels of density (Bradshaw & Holzapfel 1989). In the fish *Heterandria formosa*, increased density promoted a plastic increase in offspring size, but that plasticity was similar in two populations with very different historical regimes of density (Leips et al. 2009).

3.2.3. Sexual selection. Variation in population density is often associated with variation in male traits in ways that suggest the signature of density-dependent sexual selection. For example, higher population densities have been associated with larger sperm counts and testis sizes (Kustra et al. 2019), presumably reflecting the association of high density with increased sperm competition (Lupold et al. 2020). Gage (1995) found that male moths raised at low density invested more in structures associated with finding mates (increased head and thorax size) and less in features associated with intense sperm competition (testis size) than males raised at high density.

The signature of density-dependent sexual selection might also be in associations between variation in density and variation in male mating behaviors, either in the rates at which males exercise particular behaviors or in the particular behavioral tactics males deploy (Sato et al. 2014, Holwell et al. 2016). For example, in some species, males increase mate guarding at higher densities (Sato et al. 2014, Lipkowski et al. 2019). In a case in which mate guarding behavior decreased at a higher density, males instead ensured paternity by increasing copulation rates at the higher density (Hoi et al. 2011).

While there is consensus on the importance of population density for the evolution of mating systems and male behaviors, the empirical evidence for the role of density in sexual selection is inconsistent. Many studies have found the intensity of sexual selection to change with population density—in one or other direction—but without any change in the direction of selection on individual traits (Conner 1989, Shuster 1989, McLain 1992, Rittschof 2010, Aronsen et al. 2013, Buzatto et al. 2015, Fowler-Finn et al. 2017). There are other studies that failed to demonstrate any effect of population density on the intensity or direction of sexual selection (Wacker et al. 2013, Morales-Mata et al. 2022). In a laboratory study with *Drosophila melanogaster*, Sharp & Agrawal (2008) found that the intensity of sexual selection on individual genes increased with density for some genes but decreased with density for others.

Nonetheless, there are compelling examples of density-dependent sexual selection. Levitan (2002) contrasted selection on sperm characters among three species of sea urchins exhibiting large differences in population density. High population densities favored faster sperm, while low densities favored slower sperm with greater longevity. Radwan (1993) and Tomkins & Brown (2004) demonstrated in mites and earwigs, respectively, that selection favored either fighters or nonfighters at different densities; however, in mites, fighters had higher reproductive success at low density, whereas in earwigs, fighters were favored at high densities. McCullough et al. (2018) experimentally manipulated density in dung beetles to reveal that the correlation between mating success and fertilization success decreased as density increased. This change suggested that postmating processes of sexual selection played a more important role at higher density. In line with this suggestion, there was negative directional selection on testis mass at lower density but positive directional selection at higher density. The positive directional selection on testis mass at high density was opposed by negative directional selection on horn length, further supporting the hypothesis that as population density increases, selection shifts from favoring mating success to instead enhancing fertilization success.

4. SYNTHESIS

Density-dependent selection is not rare. In natural populations, it occurs in a variety of contexts through diverse agents. From sperm traits in sea urchins (Levitan 2002) to the shade-elongation response in *Impatiens* (Donohue et al. 2000), nature offers many examples of contrasting patterns of trait variation at different regimes of population density. Laboratory natural selection experiments reinforce this conclusion, from larger body masses in burying beetles (Schrader et al. 2017) to higher pupation heights in *D. melanogaster* (Mueller 1988).

These examples are united by a simple principle derived from theory: Density-dependent selection acts to counter the negative effects of density on those vital rates most closely connected to fitness. When the connections between trait values and vital rates change with changes in population density, selection promotes contrasting trait values at different densities. This principle may be clearer in some studies than others. It is nicely illustrated in the cycles of density and life history in lizards (Sinervo et al. 2000). It may be less obvious in cases of sexual selection. For one reason, sexual selection is usually assumed to be soft because every offspring must have one paternal and one maternal parent. How often this is true, meaning how often sexual conflict affects the absolute fitness of females, is an open question. For another reason, empirical work on sexual selection is divorced from density-dependent sexual selection theory. New work ought to connect these areas more directly.

While our review of the literature suggests that density-dependent selection is not rare, our review also suggests that it is not well understood. As evidence, we point to the mixed results of laboratory studies testing predictions about the relationship between r and K and the inconsistent results on how sexual selection varies with population density. We support our contention further by pointing to soft selection. While the idea has a long history, there are few compelling demonstrations of its legacy in natural populations beyond the elegant work of Bradshaw & Holzapfel (1989). A compelling demonstration would combine population dynamics, demography, and studies of selection on life histories and competitive ability, whether for resources or mates. This is not to assert that sexual selection is never soft but to argue that we remain largely uninformed about how often density-dependent selection is divorced from density-dependent population dynamics. The emerging evidence on sexual conflict suggests that this separation may not be as common as is often supposed.

Our discussion of theory suggests why our understanding is lagging: Density-dependent selection can produce a range of outcomes, depending upon the details of how it acts. Deriving a correct prediction from theory requires knowing which ecological or social agent acts through population density, how density affects vital rates, at which stage of the life cycle density exerts its selective effect, which phenotypic traits influence the important vital rates at that critical stage, what are the functional forms of the density response of those phenotypes for different genotypes, and how the stage at which density acts selectively contributes to population dynamics. Few studies have been able to address all of these requirements, directly or indirectly.

While we compiled a number of examples of density-dependent selection, the prevalence of density-dependent processes in nature suggests that examples of density-dependent selection should be abundant. Why aren't they? An obvious answer is that it is difficult to build a compelling case. We suggest more subtle answers. Density-dependent selection theory was embraced almost immediately by ecologists studying life-history diversity in various groups of organisms. This was because density-dependent selection in age- or stage-structured populations made explicit predictions about the evolution of life histories based on vital rates that ecologists could readily measure. In addition, some of the predictions from density-dependent life-history theory were qualitatively different from those derived from theory that did not incorporate density dependence (Charlesworth 1994). This embrace may have hidden the broader potential importance of density-dependent selection from biologists interested in traits like coloration, morphology, or behavior.

We also suggest that the oversimplification of density-dependent selection theory and the failure to verify predictions of that oversimplified theory acted as a deterrent to many biologists. The classic oversimplification is that genotypes that promoted higher population growth rates at very low densities would exhibit lower population growth rates at very high densities. As we show in the theory section, this trade-off is expected only under certain conditions. A similar oversimplification leads to the prediction that density-dependent selection always leads to an increase in the equilibrium population size. In this light, Luckinbill's (1978, 1979, 1984) mixed results on both counts should have inspired more work than they did.

To conclude, we suggest that the enthusiasm of ecologists for density-dependent selection led many to consider it as a process operating only through intraspecific competition. This was the implicit reasoning behind *r*- and *K*-selection (MacArthur & Wilson 1967). The elaborations and alternatives that followed (Pianka 1970, Grime 1977) reinforced this view. We argue that density-dependent selection can act through any ecological agent. The critical issue is that regardless of what ecological agent is causing death or reproductive failure, whenever the strength of that ecological agent depends on population density, natural selection always favors a strategy that counters the effects of that agent at the densities at which it does the most damage. Taking this principle to heart can lead to a broader view of density-dependent selection and a fuller appreciation of its centrality in both ecology and evolutionary biology.

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LITERATURE CITED

Anaya-Rojas JM, Bassar RD, Potter T, Blanchette A, Callahan S, et al. 2021. The evolution of size-dependent competitive interactions promotes species coexistence. *J. Anim. Ecol.* 90:2704–17

Anderson WW. 1971. Genetic equilibrium and population growth under density-regulated selection. *Am. Nat.* 105:489–98

Antonovics J, Levin DA. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annu. Rev. Ecol. Syst.* 11:411–52

Arnqvist G. 1989. Sexual selection in a water strider: the function, mechanism of selection and heritability of a male grasping apparatus. *Oikos* 56:344–50

Aronsen T, Berglund A, Mobley KB, Ratikainen II, Rosenqvist G. 2013. Sex ratio and density affect sexual selection in a sex-role reversed fish. *Evolution* 67:3243–57

Bashey F. 2006. Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* 60:348–61

Bedhomme S, Agnew P, Sidobre C, Michalakis Y. 2003. Sex-specific reaction norms to intraspecific larval competition in the mosquito *Aedes aegypti*. *J. Evol. Biol.* 16:721–30

Bell DA, Kovach RP, Robinson ZL, Whiteley AR, Reed TE. 2021. The ecological causes and consequences of hard and soft selection. *Ecol. Lett.* 24:1505–21

Bennington CC, Stratton DA. 1998. Field tests of density- and frequency-dependent selection in *Erigeron annuus* (Compositae). *Am. J. Bot.* 85:540–45

Bierbaum TJ, Mueller LD, Ayala FJ. 1989. Density-dependent evolution of life-history traits in *Drosophila melanogaster*. *Evolution* 43:382–92

Bitume EV, Bonte D, Ronce O, Olivieri I, Nieberding CM. 2014. Dispersal distance is influenced by parental and grand-parental density. *Proc. R. Soc. B* 281:20141061

Blanckenhorn WU. 1998. Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. *Evolution* 52:1394–407

Bonenfant C, Gaillard JM, Coulson T, Festa-Bianchet M, Loison A, et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Adv. Ecol. Res.* 41:313–57

Bouffet-Halle A, Meriguet J, Carmignac D, Agostini S, Millot A, et al. 2021. Density-dependent natural selection mediates harvest-induced trait changes. *Ecol. Lett.* 24:648–57

Boyce MS. 1984. Restitution of *r*-selection and *K*-selection as a model of density-dependent natural selection *Annu. Rev. Ecol. Syst.* 15:427–47

Bradshaw WE, Holzapfel CM. 1989. Life-historical consequences of density-dependent selection in the pitcher-plant mosquito, *Wyeomyia smithii*. *Am. Nat.* 133:869–87

Bulmer MG. 1974. Density-dependent selection and character displacement. *Am. Nat.* 108:45–58

Buzatto BA, Roberts JD, Simmons LW. 2015. Sperm competition and the evolution of precopulatory weapons: Increasing male density promotes sperm competition and reduces selection on arm strength in a chorusing frog. *Evolution* 69:2613–24

Calsbeek R, Smith TB. 2007. Probing the adaptive landscape using experimental islands: density-dependent natural selection on lizard body size. *Evolution* 61:1052–61

Charlesworth B. 1994. *Evolution in Age-Structured Populations*. New York: Cambridge Univ. Press. 2nd ed.

Charlesworth B, Giesel JT. 1972. Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. *Am. Nat.* 106:388–401

Childs DZ, Rees M, Rose KE, Grubb PJ, Ellner SP. 2004. Evolution of size-dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model. *Proc. R. Soc. B* 271:425–34

Chitty D. 1967. The natural selection of self-regulatory behavior in animal populations. *Proc. Ecol. Soc. Aust.* 2:51–78

Clark AG, Feldman MW. 1981. Density-dependent fertility selection in experimental populations of *Drosophila melanogaster*. *Genetics* 98:849–69

Clarke B. 1973. Mutation and population size. *Heredity* 31:367–79

Conner J. 1989. Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. *Evolution* 43:1378–86

Coulson T, Catchpole EA, Albon SD, Morgan BJT, Pemberton JM, et al. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–31

Coulson T, Felmy A, Potter T, Passione G, Montgomery RA, et al. 2022. Density-dependent environments can select for extremes of body size. *Peer Commun. Evol. Biol.* 2:e49

Coulson T, Tuljapurkar S, Childs DZ. 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *J. Anim. Ecol.* 79:1226–40

Coulson TN, Albon SD, Pemberton JM, Slate J, Guinness FE, Clutton-Brock TH. 1998. Genotype by environment interactions in winter survival in red deer. *J. Anim. Ecol.* 67:434–45

de Roos AM. 2021. Dynamic population stage structure due to juvenile–adult asymmetry stabilizes complex ecological communities. *PNAS* 118:e2023709118

Donohue K, Messiqua D, Pyle EH, Heschel MS, Schmitt J. 2000. Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in *Impatiens capensis*. *Evolution* 54:1956–68

Donohue K, Polisetty CR, Wender NJ. 2005. Genetic basis and consequences of niche construction: plasticity-induced genetic constraints on the evolution of seed dispersal in *Arabidopsis thaliana*. *Am. Nat.* 165:537–50

Donohue K, Pyle EH, Messiqua D, Heschel MS, Schmitt J. 2001. Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. *Evolution* 55:692–702

Donohue K, Schmitt J. 1999. The genetic architecture of plasticity to density in *Impatiens capensis*. *Evolution* 53:1377–86

Dudley SA, Schmitt J. 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *Am. Nat.* 147:445–65

Einum S, Robertsen G, Fleming IA. 2008. Adaptive landscapes and density-dependent selection in declining salmonid populations: going beyond numerical responses to human disturbance. *Evol. Appl.* 1:239–51

Engen S, Wright J, Araya-Ajoy YG, Saether BE. 2020. Phenotypic evolution in stochastic environments: the contribution of frequency- and density-dependent selection. *Evolution* 74:1923–41

Engqvist L. 2008. Genetic variance and genotype reaction norms in response to larval food manipulation for a trait important in scorpionfly sperm competition. *Funct. Ecol.* 22:127–33

Farkas TE, Montejo-Kovacevich G. 2014. Density-dependent selection closes an eco-evolutionary feedback loop in the stick insect *Timema cristinae*. *Biol. Lett.* 10:20140896

Fowler-Finn KD, Cruz DC, Rodriguez RL. 2017. Local population density and group composition influence the signal-preference relationship in *Enchenopa* treehoppers (Hemiptera: Membracidae). *J. Evol. Biol.* 30:13–25

Gage MJG. 1995. Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. *Proc. R. Soc. B* 261:25–30

Grime JP. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111:1169–94

Han CS, Brooks RC. 2015. The interaction between genotype and juvenile and adult density environment in shaping multidimensional reaction norms of behaviour. *Funct. Ecol.* 29:78–87

Harrison JG, Shapiro AM, Espeset AE, Nice CC, Jahner JP, Forister ML. 2015. Species with more volatile population dynamics are differentially impacted by weather. *Biol. Lett.* 11:20140792

Hayward AD, Pemberton JM, Berenos C, Wilson AJ, Pilkington JG, Kruuk LEB. 2018. Evidence for selection-by-environment but not genotype-by-environment interactions for fitness-related traits in a wild mammal population. *Genetics* 208:349–64

Hoi H, Tost H, Griggio M. 2011. The effect of breeding density and male quality on paternity-assurance behaviours in the house sparrow, *Passer domesticus*. *J. Ethol.* 29:31–38

Holland B, Rice WR. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *PNAS* 96:5083–88

Holt RD, Bonsall MB. 2017. Apparent competition. *Annu. Rev. Ecol. Evol. Syst.* 48:447–71

Holwell GI, Allen PJD, Goudie F, Duckett PE, Painting CJ. 2016. Male density influences mate searching speed and copulation duration in millipedes (Polydesmida: *Gigantowales chisholmi*). *Behav. Ecol. Sociobiol.* 70:1381–88

Horth L, Travis J. 2002. Frequency-dependent numerical dynamics in mosquitofish. *Proc. R. Soc. B* 269:2239–47

Horvath B, Kalinka AT. 2016. Effects of larval crowding on quantitative variation for development time and viability in *Drosophila melanogaster*. *Ecol. Evol.* 6:8460–73

Hughes KA, Rodd FH, Reznick DN. 2005. Genetic and environmental effects on secondary sex traits in guppies (*Poecilia reticulata*). *J. Evol. Biol.* 18:35–45

Kentie R, Clegg SM, Tuljapurkar S, Gaillard JM, Coulson T. 2020. Life-history strategy varies with the strength of competition in a food-limited ungulate population. *Ecol. Lett.* 23:811–20

Kokko H, Brooks R. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fenn.* 40:207–19

Kokko H, Rankin DJ. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos. Trans. R. Soc. B* 361:319–34

Kustra MC, Kahrl AF, Reedy AM, Warner DA, Cox RM. 2019. Sperm morphology and count vary with fine-scale changes in local density in a wild lizard population. *Oecologia* 191:555–64

Kvalnes T, Saether BE, Engen S, Roulin A. 2022. Density-dependent selection and the maintenance of colour polymorphism in barn owls. *Proc. R. Soc. B* 289:20220296

Lande R, Engen S, Saether BE. 2009. An evolutionary maximum principle for density-dependent population dynamics in a fluctuating environment. *Philos. Trans. R. Soc. B* 364:1511–18

Le Galliard JF, Paquet M, Mugabo M. 2015. An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *J. Evol. Biol.* 28:1144–55

Leips J, Richardson JML, Rodd FH, Travis J. 2009. Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, *Heterandria formosa*. *Evolution* 63:1341–47

Leips J, Travis J, Rodd FH. 2000. Genetic influences on experimental population dynamics of the least killifish. *Ecol. Monogr.* 70:289–309

Levitan DR. 2002. Density-dependent selection on gamete traits in three congeneric sea urchins. *Ecology* 83:464–79

Lewis SM, Tigreros N, Fedina T, Ming QL. 2012. Genetic and nutritional effects on male traits and reproductive performance in *Tribolium* flour beetles. *J. Evol. Biol.* 25:438–51

Lewontin RC. 1955. The effects of population density and composition on viability in *Drosophila melanogaster*. *Evolution* 9:27–41

Lipkowski K, Plath M, Klaus S, Sommer-Trembo C. 2019. Population density affects male mate choosiness and morphology in the mate-guarding amphipod *Gammarus roeselii* (Crustacea: Amphipoda). *Biol. J. Linn. Soc.* 126:899–911

Luckinbill LS. 1978. r and K selection in experimental populations of *Escherichia coli*. *Science* 202:1201–3

Luckinbill LS. 1979. Selection and the *r/K* continuum in experimental populations of protozoa. *Am. Nat.* 113:427–37

Luckinbill LS. 1984. An experimental analysis of a life history theory. *Ecology* 65:1170–84

Lupold S, de Boer RA, Evans JP, Tomkins JL, Fitzpatrick JL. 2020. How sperm competition shapes the evolution of testes and sperm: a meta-analysis. *Philos. Trans. R. Soc. B* 375:20200064

MacArthur R. 1970. Species packing and competitive equilibrium for many species. *Theor. Popul. Biol.* 1:1–11

MacArthur RH. 1962. Some generalized theorems of natural selection. *PNAS* 48:1893–97

MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton Univ. Press

Mallet J. 2012. The struggle for existence: how the notion of carrying capacity, *K*, obscures the links between demography, Darwinian evolution, and speciation. *Evol. Ecol. Res.* 14:627–65

Malthus TR. 1798 (1986). An essay on the principle of population. In *The Works of Thomas Robert Malthus*, ed. EA Wrigley, D Souden, pp. 1–139. London: Pickering & Chatto

Matthysen E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28:403–16

Mazer SJ, Schick CT. 1991. Constancy of population parameters for life-history and floral traits in *Raphanus sativus* L.1. Norms of reaction and the nature of genotype by environment interactions. *Heredity* 67:143–56

McCullough EL, Buzatto BA, Simmons LW. 2018. Population density mediates the interaction between pre- and postmating sexual selection. *Evolution* 72:893–905

McLain DK. 1992. Population density and the intensity of sexual selection on body length in spatially or temporally restricted natural populations of a seed bug. *Behav. Ecol. Sociobiol.* 30:347–56

McNutt DW, Halpern SL, Barrows K, Underwood N. 2012. Intraspecific competition facilitates the evolution of tolerance to insect damage in the perennial plant *Solanum carolinense*. *Oecologia* 170:1033–44

Metz JAJ, Geritz SAH, Meszena G, Jacobs FJA, van Heerwaarden JS. 1995. *Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction*. Laxenburg, Austria: Int. Inst. Appl. Syst. Anal.

Miller RE, Fowler NL. 1993. Variation in reaction norms among populations of the grass *Bouteloua rigidiseta*. *Evolution* 47:1446–55

Morales-Mata JI, Potti J, Camacho C, Martinez-Padilla J, Canal D. 2022. Phenotypic selection on an ornamental trait is not modulated by breeding density in a pied flycatcher population. *J. Evol. Biol.* 35:610–20

Mueller LD. 1988. Density-dependent population growth and natural selection in food-limited environments: the *Drosophila* model. *Am. Nat.* 132:786–809

Mueller LD. 1997. Theoretical and empirical examination of density-dependent selection. *Annu. Rev. Ecol. Syst.* 28:269–88

Mueller LD, Rauser CL, Rose MR. 2005. Population dynamics, life history, and demography: lessons from *Drosophila*. *Adv. Ecol. Res.* 37:77–99

Nicolaus M, Tinbergen JM, Ubels R, Both C, Dingemanse NJ. 2016. Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecol. Lett.* 19:478–86

Palacio-Lopez K, King CM, Bloomberg J, Hovick SM. 2020. Natural selection on traits and trait plasticity in *Arabidopsis thaliana* varies across competitive environments. *Sci. Rep.* 10:21632

Pennekamp F, Mitchell KA, Chaine A, Schtickzelle N. 2014. Dispersal propensity in *Tetrahymena thermophila* ciliates—a reaction norm perspective. *Evolution* 68:2319–30

Perez A, Garcia C. 2002. Evolutionary responses of *Drosophila melanogaster* to selection at different larval densities: changes in genetic variation, specialization and phenotypic plasticity. *J. Evol. Biol.* 15:524–36

Pianka ER. 1970. On *r*- and *K*-selection. *Am. Nat.* 104:592–97

Potter T, King L, Travis J, Bassar RD. 2019. Competitive asymmetry and local adaptation in Trinidadian guppies. *J. Anim. Ecol.* 88:330–42

Prati D, Schmid B. 2000. Genetic differentiation of life-history traits within populations of the clonal plant *Ranunculus reptans*. *Oikos* 90:442–56

Radwan J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. *Behav. Ecol. Sociobiol.* 33:201–8

Reznick DN, Bassar RD, Handelsman CA, Ghalambor CK, Arendt J, et al. 2019. Eco-evolutionary feedbacks predict the time course of rapid life-history evolution. *Am. Nat.* 194:671–92

Rittschof CC. 2010. Male density affects large-male advantage in the golden silk spider, *Nephila clavipes*. *Behav. Chem. Ecol.* 21:979–85

Roughgarden J. 1971. Density-dependent natural selection *Ecology* 52:453–68

Saether BE, Visser ME, Grotan V, Engen S. 2016. Evidence for *r*- and *K*-selection in a wild bird population: a reciprocal link between ecology and evolution. *Proc. R. Soc. B* 283:20152411

Sato Y, Sabelis MW, Egas M. 2014. Alternative male mating behaviour in the two-spotted spider mite: dependence on age and density. *Anim. Behav.* 92:125–31

Schindler S, Gaillard JM, Gruning A, Neuhaus P, Traill LW, et al. 2015. Sex-specific demography and generalization of the Trivers–Willard theory. *Nature* 526:249–52

Schrader M, Jarrett BJM, Rebar D, Kilner RM. 2017. Adaptation to a novel family environment involves both apparent and cryptic phenotypic changes. *Proc. R. Soc. B* 284:20171295

Semlitsch RD. 1993. Adaptive genetic variation in growth and development of tadpoles of the hybridogenetic *Rana esculenta* complex. *Evolution* 47:1805–18

Sharp NP, Agrawal AF. 2008. Mating density and the strength of sexual selection against deleterious alleles in *Drosophila melanogaster*. *Evolution* 62:857–67

Shaw RG. 1986. Response to density in a wild population of the perennial herb *Salvia lyrata*: variation among families. *Evolution* 40:492–505

Shenoi VN, Ali SZ, Prasad NG. 2016. Evolution of increased adult longevity in *Drosophila melanogaster* populations selected for adaptation to larval crowding. *J. Evol. Biol.* 29:407–17

Shuster SM. 1989. Male alternative reproductive strategies in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among α-males, β-males and γ-males. *Evolution* 43:1683–98

Sinervo B, Svensson E, Comendant T. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406:985–88

Soderquist L, Broberg A, Rosenberg V, Sletvold N. 2020. Predicting heterosis and inbreeding depression from population size and density to inform management efforts. *J. Appl. Ecol.* 57:1459–68

Sugiyama S, Bazzaz FA. 1997. Plasticity of seed output in response to soil nutrients and density in *Abutilon theophrasti*: implications for maintenance of genetic variation. *Oecologia* 112:35–41

Svensson E, Sinervo B. 2000. Experimental excursions on adaptive landscapes: density-dependent selection on egg size. *Evolution* 54:1396–403

Thomas SC, Bazzaz FA. 1993. The genetic component in plant size hierarchies: norms of reaction to density in a *Polygonum* species. *Ecol. Monogr.* 63:231–49

Tilman D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton Univ. Press

Tomkins JL, Brown GS. 2004. Population density drives the local evolution of a threshold dimorphism. *Nature* 431:1099–103

Travis J. 1983. Variation in development patterns of larval anurans in temporary ponds. I. Persistent variation within a *Hyla gratiosa* population. *Evolution* 37:496–512

Tucic N, Milosevic M, Gliksman I, Milanovic D, Aleksic I. 1991. The effects of larval density on genetic variation and covariation among life-history traits in the bean weevil (*Acanthoscelides obtectus* Say). *Funct. Ecol.* 5:525–34

Tuljapurkar S. 1990. *Population Dynamics in Variable Environments*. Berlin: Springer Verlag

Tuljapurkar SD, Orzack SH. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor. Popul. Biol.* 18:314–42

Turchin P. 2003. *Complex Population Dynamics*. Princeton, NJ: Princeton Univ. Press

Van Kleunen M, Fischer M. 2001. Adaptive evolution of plastic foraging responses in a clonal plant. *Ecology* 82:3309–19

Venkitachalam S, Das S, Deep A, Joshi A. 2022. Density-dependent selection in *Drosophila*: evolution of egg size and hatching time. *J. Genet.* 101:13

Verhulst P-F. 1838. Notice sur la loi que la population poursuit dans son accroissement. *Corresp. Math. Phys.* 10:113–21

Via S. 1991. Variation between strains of the flour beetle *Tribolium castaneum* in relative performance on five flours. *Entomol. Exp. Appl.* 60:173–82

Wacker S, Mobley K, Forsgren E, Myhre LC, de Jong K, Amundsen T. 2013. Operational sex ratio but not density affects sexual selection in a fish. *Evolution* 67:1937–49

Wallace B. 1975. Hard and soft selection revisited. *Evolution* 29:465–73

Walsh MR, Reznick DN. 2008. Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. *PNAS* 105:594–99

Webber QMR, Vander Wal E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. *J. Anim. Ecol.* 87:113–27

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7:510–23

Whitlock MC. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* 54:1855–61

Wigby S, Chapman T. 2005. Sex peptide causes mating costs in female *Drosophila melanogaster*. *Curr. Biol.* 15:316–21

Zhou YH, Kuster HK, Pettis JS, Danka RG, Gleason JM, Greenfield MD. 2008. Reaction norm variants for male calling song in populations of *Achroia grisella* (Lepidoptera: Pyralidae): toward a resolution of the lek paradox. *Evolution* 62:1317–34