

# Mate Sampling Behavior Determines the Density Dependence of Sexual Selection

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Submitted June 7, 2021; Accepted April 19, 2022; Electronically published August 4, 2022

Online enhancements: supplemental PDF.

**ABSTRACT:** Theory predicts that the strength of sexual selection (i.e., how well a trait predicts mating or fertilization success) should increase with population density, yet empirical support remains mixed. We explore how this discrepancy might reflect a disconnect between current theory and our understanding of the strategies individuals use to choose mates. We demonstrate that the density dependence of sexual selection predicted by previous theory arises from the assumption that individuals automatically sample more potential mates at higher densities. We provide an updated theoretical framework for the density dependence of sexual selection by (1) developing models that clarify the mechanisms through which density-dependent mate sampling strategies might be favored by selection and (2) using simulations to determine how sexual selection changes with population density when individuals use those strategies. We find that sexual selection may increase strongly with density if sampling strategies change adaptively in response to density-dependent sampling costs, whereas within-individual plasticity in sampling over time (e.g., due to adaptation to increasing sampling costs as the breeding season progresses) produces weaker density-dependent sexual selection. Our findings suggest that density dependence of sexual selection depends on the ecological context in which mate sampling has evolved.

**Keywords:** population density, sexual selection, mate choice, mate sampling.

## Introduction

Sexual selection, or differences in reproductive success due to heritable variation in the ability to compete for mates or fertilizations, plays an important role in the evolution of elaborate morphological, behavioral, and physiological traits (Andersson 1994) as well as in determining population viability (Kokko and Brooks 2003; Kokko and Mappes 2005).

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The strength of sexual selection (i.e., how well a trait predicts mating or fertilization success) is thought to be fundamentally linked with population density (Emlen and Oring 1977; Eshel 1979; Wade 1995; Shuster and Wade 2003; Kokko and Rankin 2006; Shuster 2009). As population density increases, encounters between individuals become more frequent, presumably providing additional opportunities for individuals with greater mate acquisition ability (e.g., preferred sexual traits or social dominance) to secure mating opportunities at the expense of other individuals of the same sex (Emlen and Oring 1977; Eshel 1979; Wade 1995; Shuster and Wade 2003; Kokko and Rankin 2006; Shuster 2009). Consequently, mating success is expected to become increasingly concentrated among preferred or dominant phenotypes at higher densities, producing stronger sexual selection.

Changes in the strength of sexual selection with population density have important implications for evolutionary and ecological dynamics. Differences in the strength of sexual selection caused by variation in population density over time, for example, can decrease the net effect of selection on trait evolution and maintain genetic variation in sexual traits (Gosden and Svensson 2008; Kasumovic et al. 2008; Rittschof 2010). Consistent spatial differences in population density, on the other hand, can contribute to divergent sexual selection that affects sexual trait diversification and reproductive isolation (Martin and Hosken 2003). Density-dependent changes in the strength of sexual selection can determine whether sexual selection can cause evolutionary suicide (Kokko and Brooks 2003; Kokko and Rankin 2006; Rankin 2007; Candolin and Heuschele 2008; Rankin et al. 2011) and are particularly important for predicting whether sexual selection should facilitate or hinder population growth and persistence (Kokko and Mappes 2005; Kokko and Rankin 2006; Candolin and Heuschele 2008; Sharp and Agrawal 2008; Martínez-Ruiz and Knell 2017). Recently,

density-dependent sexual selection has also been proposed as a potential mechanism promoting coexistence (Kobayashi 2019).

Empirical evidence for stronger sexual selection at higher population densities remains mixed (Head et al. 2008; Pomfret and Knell 2008; Sharp and Agrawal 2008; Aronsen et al. 2013; Wacker et al. 2013; McCullough et al. 2018). Some studies find evidence of stronger sexual selection in denser populations, as predicted by theory (Zeh 1987; Tomkins and Brown 2004; Mobley and Jones 2007; House et al. 2019), whereas others find no effect (Head et al. 2008; Sharp and Agrawal 2008; Wacker et al. 2013) or a negative effect (Conner 1989; McLain 1992; Jirotkul 1999; Pomfret and Knell 2008) of density on the strength of sexual selection. In other studies, the relationship between sexual selection and population density depends on the trait or measure of sexual selection considered (Bertin and Cézilly 2005; Aronsen et al. 2013; McCullough et al. 2018). These varied relationships between density and sexual selection are also reflected in the links between sexual selection and macroevolutionary and macroecological patterns. For example, sexual selection has been associated with increased extinction risk in some systems (Svensson and Waller 2013; Martins et al. 2018) and decreased extinction risk in others (Lumley et al. 2015). This mismatch between theoretical predictions and empirical data suggests a disconnect between current theory and key features of how sexual selection occurs that are necessary to predict changes in sexual selection with population density and, consequently, the associations between sexual selection and higher-level ecological and evolutionary processes.

In the context of premating sexual selection caused by mate choice, or nonrandom mating with respect to potential mates' phenotypes (Halliday 1983), surprisingly few theoretical models have examined the relationship between sexual selection and population density per se (Eshel 1979; Kokko and Rankin 2006). While these highly cited models support the argument that sexual selection should increase with population density, they also greatly simplify the details of how individuals encounter, assess, and choose among potential mates (referred to here as "mate sampling strategies"). Such simplifications are common among models of sexual selection; predicting the evolution of a sexually selected phenotype (e.g., Kirkpatrick 1982; Seger and Trivers 1986), for example, requires knowing how mating success differs among phenotypes but does not necessarily require any assumptions about how those differences emerge. Nevertheless, the differences in mating success that determine the strength of sexual selection are ultimately an emergent outcome of individuals' mate sampling strategies (Seger and Trivers 1986; Wiegmann et al. 1999; Rosenthal 2017), and being explicit about individual's mate sampling strategies can fundamentally alter predicted evolutionary dynamics

(Seger 1985). For example, the evolutionary equilibria predicted by population genetic models of sexual selection may be stable or unstable depending on whether individuals compare potential mates to an absolute standard or to other individuals they have encountered (Seger 1985). Thus, the diversification of sexual traits and preferences might occur primarily by drift along stable lines of evolutionary equilibria (e.g., Kirkpatrick 1982) or through runaway evolution from unstable lines of equilibria (e.g., Seger 1985), depending on how individuals choose their mates.

In the present study, we explore how the density dependence of premating sexual selection caused by mate choice depends on individuals' mate sampling strategies. In the next section, we show that the prediction that sexual selection should generally increase with density follows directly from the mate sampling strategy assumed in previous models—specifically, that each female chooses the most preferred male from a sample that includes every male she encounters and therefore chooses from a larger sample of males at higher densities (Eshel 1979; Kokko and Rankin 2006). In contrast, sampling behaviors predicted by more realistic mate choice decision-making models are not inherently density dependent and do not automatically produce density-dependent sexual selection. In the final section, we provide an updated theoretical framework on the density dependence of sexual selection derived explicitly from the mate sampling strategies expected to be favored by selection in different environments. Specifically, we (1) develop models to clarify how selection might favor features of mate choice decision-making mechanisms that can produce density-dependent mate sampling (as assumed by previous models) and (2) quantify how sexual selection changes with density if individuals use these strategies.

## Sexual Selection Is Not Inherently Density Dependent

### *Mate Sampling Strategies in Previous Models*

Previous theory suggests that sexual selection caused by mate choice depends intrinsically on population density—that is, the density at which mating occurs affects the strength of sexual selection without requiring additional changes to the mate choice process (Eshel 1979; Kokko and Rankin 2006). Here, we demonstrate that this is a property of the particular mate sampling strategy considered in previous models.

The models of Eshel (1979) and Kokko and Rankin (2006) assume that individuals of the choosy sex (hereafter referred to as "females," for brevity) choose the most preferred individuals of the courting sex (hereafter referred to as "males") from however many males they encounter during a breeding season. In other words, females have perfect knowledge of when their breeding opportunity will end

and continue sampling males until that time, at which point they choose a mate. In Eshel's (1979) model, males are either "attractive" or "unattractive," and females will always mate with an attractive male if at least one was encountered—otherwise, they settle for a nonattractive male. In the simulations of Kokko and Rankin (2006), males vary continuously in their phenotype, and females always mate with the male with the largest phenotype value from among all those encountered. Critically, in both cases the number of males each female samples depends only on the number of males she encounters. This is important because both models assume that mate encounters occur in a mass-action-like process, such that females encounter more males at higher population densities. As a result, females choose mates from larger samples at higher densities.

It is well known that mating success becomes increasingly concentrated around preferred sexual trait values if females sample more males (Benton and Evans 1998; Wagner 1998; Rosenthal 2017; Muniz and Machado 2018). In Eshel's (1979) model, for instance, the probability that a female mates with an attractive male is the probability that she encounters at least one attractive male. Given two male phenotypes, the probability of mating with an attractive male is then, according to the binomial probability distribution,  $1 - (1 - p)^{n_{\text{enc}}}$ , where  $p$  is the frequency of attractive males and  $n_{\text{enc}}$  is the number of males encountered. Thus, for  $0 < p < 1$ , the probability that a female mates with an attractive male approaches 1 as the number of males encountered  $n_{\text{enc}}$  increases. For large enough  $n_{\text{enc}}$ , virtually all females mate with an attractive male, and the difference in mating success between attractive and unattractive males (and thus the strength of sexual selection) is maximized.

A similar effect occurs in Kokko and Rankin's (2006) model, in which females prefer males with the largest values of a continuously varying sexual trait, which we denote  $x$ . Because each female chooses the male with the largest trait from among all those she encounters, the expected trait value of the chosen male  $E(x_{n_{\text{enc}}}^*)$  is the largest  $x$  expected in a sample of  $n_{\text{enc}}$  males (i.e., the expected value of the  $n_{\text{enc}}$ th order statistic),

$$E(x_{n_{\text{enc}}}^*) = n_{\text{enc}} \int_0^{\infty} x f(x) F(x)^{n_{\text{enc}}-1} dx, \quad (1)$$

where  $f(x)$  is the distribution of sexual trait values among males in the population (i.e., the probability density function) and  $F(x)$  is the proportion of males with sexual trait values less than or equal to a given value (i.e., the cumulative distribution function; Janetos 1980; Real 1990). For a variety of possible distributions of sexual trait values  $f(x)$ ,  $E(x_{n_{\text{enc}}}^*)$  is an increasing function of  $n_{\text{enc}}$  (Janetos 1980; Real 1990). Consequently, as  $n_{\text{enc}}$  increases, the average phenotype of chosen males increases, producing stronger sexual selection. Thus, an increase in sexual selection with popu-

lation density follows directly from the assumption that mate sampling is determined entirely by the number of males encountered and therefore increases with density.

#### *Fitness-Maximizing Mate Sampling Strategies*

A female with no other constraints on her sampling behavior should indeed sample every male she can before choosing the best from among them (Janetos 1980). However, it may be unrealistic to assume that mate sampling is constrained only by the number of males encountered, particularly because sampling likely incurs costs in many, if not most, cases. Potential costs include energetic demands (Gibson and Bachman 1992; Milinski and Bakker 1992; Wong and Jennions 2003; Byers et al. 2005; Dunn and Whittingham 2007; Booksmythe et al. 2008), predation or parasitism (Gibson and Bachman 1992; Godin and Briggs 1996; Grafe 1997; Karino et al. 2000; DeRivera et al. 2003; Su and Li 2006; Booksmythe et al. 2008; Martin and Wagner 2010), and failing to mate or mating too late in the season (Crowley et al. 1991; de Jong and Sabelis 1991; Backwell and Passmore 1996; Kokko and Mappes 2005; Bleu et al. 2012; Henshaw 2018). Selection is therefore unlikely to favor mate sampling strategies in which females continue sampling males as long as new males are encountered. Instead, selection should favor strategies that maximize fitness by balancing the benefits of mating with males with preferred sexual traits against the costs of finding them (Janetos 1980; Real 1990; Reynolds and Gross 1990; Wagner 1998).

Theory on the strategies females might use to balance the costs and benefits of mate sampling has mostly focused on identifying possible rules for when to accept a male and stop sampling (Janetos 1980; Real 1990; Gibson and Langen 1996; Priklopil et al. 2015; Rosenthal 2017). Females might, for example, accept the most preferred male from a sample of a certain size (i.e., a best-of- $n$  sampling strategy) or accept the first male that meets some internal standard (i.e., a threshold sampling strategy; Janetos 1980; Real 1990; Gibson and Langen 1996; Priklopil et al. 2015; Rosenthal 2017). This approach has provided insights into how ecological conditions affect selection on the parameters of sampling strategies (e.g., the value of  $n$  or the threshold; Bleu et al. 2012; Priklopil et al. 2015) and the relative performance of different strategy types (Janetos 1980; Real 1990; Luttbeg 2002). However, these simple rules often fail to capture the complexity of mate choice decisions in empirical systems (Hovi and Rätti 1994; Dale and Slagsvold 1996; Luttbeg 1996; Reaney 2009; Beckers and Wagner 2011; Castellano et al. 2012; Kensinger and Luttbeg 2014; Uy et al. 2015).

Recent attempts to provide a comprehensive theory of mate sampling behavior have shifted focus to the cognitive

processes underlying mate choice decisions (Bateson and Healy 2005; Phelps et al. 2006; Castellano 2009, 2010, 2015; Castellano and Cermelli 2011; Castellano et al. 2012). This framework posits that mate choice is the result of a cognitive process in which females integrate imperfect information about males over time until the evidence in favor of accepting a particular male reaches some threshold. Mate sampling behavior therefore emerges from the interaction between stochastic “decision variables,” or dynamic internal representations of the evidence in support of different mating options, and a “decision rule” that specifies how evidence is interpreted to commit to a decision to mate or continue sampling (Castellano 2009, 2010, 2015; Castellano and Cermelli 2011; Castellano et al. 2012). These types of decision-making models differ from previous theory by (i) specifying the rules used to commit to a decision in terms of a female’s certainty about her options and (ii) explicitly considering how evidence accumulates as new information is perceived and integrated with prior experience (Castellano 2009). This shifts the focus from the specific criterion for accepting a male (e.g., being the most preferred in a sample of  $n$  males) to the general process by which females must use imperfect information to form evidence of males’ acceptability and translate this evidence into a decision (Castellano 2009). Classic models of mate sampling behavior can be seen as special cases within this conceptually broader class of decision-making models (Castellano and Cermelli 2011) while also allowing for features of mate choice that troubled earlier theory, including repeated sampling of individual males (Luttbeg 1996), sensory biases (Castellano 2015), and irrational mate choice (Roe et al. 2001). Despite this additional complexity, these types of decision-making models make the unifying prediction that females balance the costs and benefits of mate sampling by choosing a mate after they accumulate sufficient evidence of his acceptability, even if they could encounter more males or acquire additional information about their quality.

#### *Mate Sampling Determines the Density Dependence of Sexual Selection*

To demonstrate that the density dependence of sexual selection depends on how females sample mates, we develop an individual-based simulation similar to that of Kokko and Rankin (2006) and compare the change in sexual selection with population density if females (1) continue sampling until the end of the breeding season and choose the most preferred male from among all those encountered (referred to here as a “best-of-all” strategy), as in Eshel (1979) and Kokko and Rankin (2006), or (2) choose a mate after accumulating sufficient evidence that a given male is acceptable, as predicted by the cognitive framework of mate choice

decision-making. Note that we find qualitatively similar results for other sampling strategies, such as those in which females obtain perfect information about each male and compare him to an internal standard (e.g., a fixed-threshold sampling strategy) or to other males she has encountered (e.g., a best-of- $n$  sampling strategy; see the supplemental PDF).

*Simulation Methods.* Each simulation consists of a single breeding season of length  $T$  in a population of  $N_{\text{total}}$  individuals with sex ratio  $r$  (females/males). This choice of temporal scale reflects our goal of understanding the relationship between population density and the strength of premating sexual selection caused by mate choice as it might be measured in a typical empirical study. However, it is important to note that this is only one component of the total sexual selection that may be acting on a trait in a natural system. As such, it is more precise to say that our model demonstrates how the contribution of premating sexual selection caused by mate choice to total sexual selection changes with population density.

The population occupies a two-dimensional area  $A$  such that the population density  $d = N_{\text{total}}/A$ . For each of the  $[r/(1+r)] \times N_{\text{total}}$  females in the population, we draw the number of encounters with males during the breeding season from a Poisson distribution with a rate parameter equal to the expected number of encounters with males by a female, which depends on population density as follows. Assuming individuals move linearly at a constant speed  $v$ , the mean speed of other individuals from the perspective of a focal individual (e.g., a sampling female) is  $4v/\pi$  (Hutchinson and Waser 2007). A female encounters a male and may sample him if they pass within a detection distance  $D$  of each other. Thus, the total “detection area” covered by each male per time step due to their motion relative to a focal female is  $2D \times 4v/\pi = 8Dv/\pi$  (Hutchinson and Waser 2007). There are  $[1/(1+r)] \times N_{\text{total}}$  males in the population, so the total area covered per time step by all males relative to a focal female is  $[1/(1+r)] \times N_{\text{total}} \times 8Dv/\pi$ . In an area  $A$ , the expected number of males that covered an area including the focal female and are therefore encountered by her is  $\lambda = \{[1/(1+r)] \times N_{\text{total}} \times 8Dv/\pi\}/A$  (Hutchinson and Waser 2007). The expected total number of encounters with males by a female over the breeding season is then  $\lambda \times T$ . For more complicated movement patterns, the relationship between density and encounter rate must often be derived using simulations, although the resulting relationships are in many cases qualitatively similar to the analytically tractable case we consider (Hutchinson and Waser 2007).

The males encountered by each female are selected randomly with replacement from the  $[1/(1+r)] \times N_{\text{total}}$  males in the population. This implies that (i) males’ traits do not



affect their encounter rate, (ii) individual males may be encountered multiple times, and (iii) females do not compete for males. This latter point implies that the distribution of the male sexual trait does not change over the breeding season because of mating. As in Kokko and Rankin (2006), the sexual trait  $x$  is normally distributed among males with mean  $\bar{x}$  and variance  $\sigma_x$  (i.e.,  $f(x) = N(\bar{x}, \sigma_x)$ ), and females prefer males with the largest  $x$  values. However, we consider two different sampling strategies females might use to choose a mate with large  $x$ . In the first case, females continue sampling until the end of the season and choose the male with the largest  $x$  among those encountered (the best-of-all strategy), as in Kokko and Rankin (2006). In the second case, females continue sampling until they accumulate sufficient evidence that an encountered male meets their standard for acceptance. We outline the details of this second scenario below.

We assume that a female considers a male acceptable if his trait value  $x$  meets some minimum standard,  $x_{\text{crit}}$ . However, as a result of noisiness inherent in signal transmission and perception, she cannot assess  $x$  perfectly and instead perceives a trait value  $x_p$  with probability  $g(x_p|x) = N(x, \sigma_{\text{error}})$ , where  $x$  is the male's actual trait and  $\sigma_{\text{error}}$  quantifies the error due to signal transmission and perception. She cannot, therefore, be sure of a male's acceptability; she must estimate the probability that the male is acceptable given the perceived trait,  $x_p$ , and any available prior evidence. We denote this probability  $\Pr(x \geq x_{\text{crit}}|x_p)$ . According to Bayes' theorem,

$$\Pr(x \geq x_{\text{crit}}|x_p) = \left[ \frac{\Pr(x_p|x \geq x_{\text{crit}})}{\Pr(x_p)} \right] Q(x \geq x_{\text{crit}}), \quad (2)$$

where  $\Pr(x_p|x \geq x_{\text{crit}}) = \int_{x_{\text{crit}}}^{\infty} g(x_p|x)f(x) dx / \int_{x_{\text{crit}}}^{\infty} f(x) dx$  is the probability of perceiving trait  $x_p$  given the male is acceptable,  $\Pr(x_p) = \int_{-\infty}^{\infty} g(x_p|x)f(x) dx$  is the probability of perceiving trait  $x_p$  regardless of the male's acceptability, and  $Q(x \geq x_{\text{crit}})$  is the prior probability of the male's acceptability. The prior probability  $Q(x \geq x_{\text{crit}})$  describes a female's previous information about a male—we assume that the first time a male is encountered,  $Q(x \geq x_{\text{crit}})$  is the proportion of acceptable males in the population,  $1 - F(x_{\text{crit}})$ . On subsequent encounters,  $Q(x \geq x_{\text{crit}})$  equals the value of  $\Pr(x \geq x_{\text{crit}}|x_p)$  from the previous encounter with that male. Thus, the posterior probability of a male's acceptability changes during encounters using Bayesian updating (Castellano and Cermelli 2011; Castellano et al. 2012; Castellano 2015). We refer to this scenario as the “Bayesian sampling strategy.”

For each encounter, the trait perceived by a female,  $x_p$ , is drawn from the distribution  $g(x_p|x)$ , where  $x$  is the trait of the encountered male. We then cycle over the female's encounters in random order, calculating for each the pos-

terior probability of acceptability  $\Pr(x \geq x_{\text{crit}}|x_p)$  (eq. [2]). The first encounter in which  $\Pr(x \geq x_{\text{crit}}|x_p)$  exceeds a threshold  $p_{\text{crit}}$  produces a decision to mate with that male. Thus,  $\Pr(x \geq x_{\text{crit}}|x_p)$  is the decision variable quantifying the evidence of a male's acceptability, and the decision to mate if  $\Pr(x \geq x_{\text{crit}}|x_p) \geq p_{\text{crit}}$  is the decision rule. While this is one of many possible sets of decision variables and decision rules, we expect our qualitative conclusions to be robust to these details—regardless of the standards for male acceptability or the evidence needed to commit to mating, females decide by gathering evidence until some stopping-point criterion is reached (Castellano 2009).

If none of a female's encounters produces a posterior probability of acceptability that satisfies her decision rule, she remains unmated. Thus, a female's sampling behavior and, consequently, her choice of mate depends only on the interaction between the stochastic decision variable (the posterior probability of acceptability) and the decision rule (to mate if the posterior probability exceeds a threshold). We note that female mating failures may be rare in at least some empirical systems, although they do occur (see Rhainds 2010, 2013, 2019). However, there is no mechanism inherent to the mate choice decision-making process that automatically matches individuals' decisions to their risk of remaining unmated. Avoiding mating failures requires the evolution of additional adaptations, such as the ability to detect deteriorating breeding conditions and respond by choosing a mate at random. In some cases, adaptations to avoid remaining unmated can produce changes in the average mate sampling behavior and, thus, sexual selection with density (see “Assumptions and Biological Relevance” below). Nevertheless, these adaptations are not emergent properties of the decision-making process, although they can arise from the evolution of the mate choice decision-making process in particular ecological contexts. Here, we do not assume that any such adaptations have evolved and, in doing so, isolate the effects of the decision-making process per se on the density dependence of sexual selection. We discuss the importance of adaptations to avoid failing to mate in greater detail below (see “Assumptions and Biological Relevance”) and model the effects of such adaptations explicitly (see “The Evolution of Density-Dependent Mate Sampling”).

In each simulation, we record the number of times each male is chosen as mate. We quantify the strength of sexual selection by calculating the selection gradient  $\beta$  for the sexual trait  $x$  (i.e., the slope of a regression of males' relative fitnesses on their  $z$ -transformed sexual trait values; Lande and Arnold 1983). We also quantify sexual selection in terms of the opportunity for sexual selection,  $I_{\text{mates}}$  (i.e., the mean-standardized variance in male reproductive success; Wade 1979), as this measure is widely used in empirical studies (Krakauer et al. 2011). The choice

of the selection metric does not qualitatively affect our conclusions (see the supplemental PDF); we present our results in terms of the selection gradient  $\beta$  because we are primarily interested in how population density affects the realized strength of sexual selection rather than the capacity for sexual selection to operate (Krakauer et al. 2011).

To determine how sexual selection changes with population density for each sampling strategy, we conduct 100 replicate simulations at densities  $d = [0.05, 0.1, 0.2, 0.4, 0.6, 0.8, 1, 1.2, 1.4, 1.6, 1.8, 2, 3, 4, 5]$  individuals/area. To control for differences in the total number of individuals, we set  $N_{\text{total}} = 500$  across all simulations and vary the total area,  $A = [10,000, 5,000, 2,500, 1,250, 833, 625, 500, 416, 357, 313, 278, 250, 167, 125, 100]$ . We visualize the change in the sexual selection gradient  $\beta$  with density by plotting the mean  $\pm$  SD of  $\beta$  calculated across the 100 replicates as a function of simulated population density  $d$ . To provide a quantitative measure of the density dependence of sexual selection, we calculate the coefficient of variation (CV) in the mean selection gradient  $\beta$  across densities.

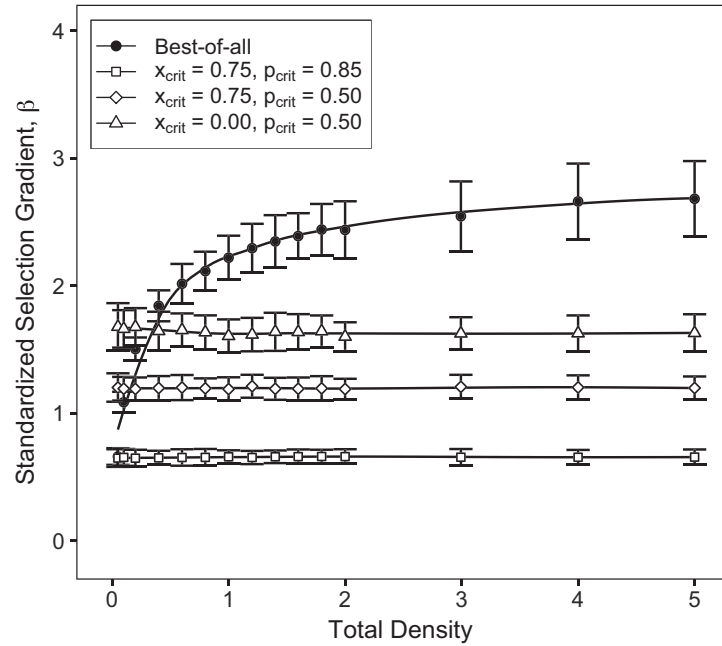
*Simulation Results.* If females use a best-of-all sampling strategy, the strength of sexual selection (measured as the sexual selection gradient,  $\beta$ ; Lande and Arnold 1983) increases with density, at least for low to intermediate densities (filled symbols, fig. 1), as predicted by previous theory. At very high densities, sexual selection changes less with density because the selection gradient approaches a maximum determined by the distribution of sexual traits in males. In other words, once the most attractive males secure almost all mating opportunities, there is little potential to further intensify sexual selection. For our default parameter values (see fig. 1), the change in strength of sexual selection with density produces an overall CV in the mean sexual selection gradient  $CV(\beta) = 0.29$ .

In contrast, if females use a Bayesian strategy, the strength of sexual selection depends on the value of the criterion for mate acceptability ( $x_{\text{crit}}$ , in this case) and the evidence needed to induce a decision,  $p_{\text{crit}}$ , but does not increase in response to population density per se (open symbols, fig. 1). The CV in the sexual selection gradient across densities  $CV(\beta)$  is  $\leq 0.01$  for all  $x_{\text{crit}}$  and  $p_{\text{crit}}$  considered. The consistency in sexual selection across densities in this case reflects the fact that sampling behavior is determined by the dynamics of the decision-making mechanism (i.e., the decision variable and decision rule), not by the availability of males in the environment. At high density, a female may encounter many males over the season, but she still samples only as many as it takes to be sufficiently certain that one meets her standards. Conversely, at low densities more females may still be sampling males at the end of the breeding season, but those females that

mate have chosen males using the same criteria as females at high densities. Thus, the expected phenotype of successful males—and therefore the sexual selection gradient—does not change with density.

*Assumptions and Biological Relevance.* It is important to note that we do not claim that females in nature necessarily use the specific strategy assumed above. Features of mate sampling strategies (e.g., decision rules) vary among and within taxa (Kensinger and Luttbegg 2014), and sensory systems may only approximate Bayesian computations (Collins et al. 2006; Lange and Dukas 2009). Nevertheless, our simulations provide two primary insights. First, females' sampling strategies qualitatively affect how sexual selection is expected to change with the population density at which mating occurs. Second, more realistic models of mate sampling than those considered by previous theory, including a Bayesian strategy based on a cognitive framework of mate choice decision-making, are not intrinsically density dependent and, consequently, do not automatically produce density-dependent sexual selection (figs. 1, S1, S4). This suggests that density-dependent sexual selection does not emerge from the core cognitive mechanisms thought to underlie mate choice decision-making and must instead arise from the adaptation of the decision-making machinery to specific ecological conditions.

The lack of density dependence in our simulations occurs because a female that fails to encounter a male whose perceived trait satisfies her decision rule remains unmated. As mentioned above, female mating failures may be rare in at least some empirical systems. Some authors have suggested that this should be expected because of strong selection for traits that mitigate this risk (Kokko and Mappes 2005; Rhainds 2010). Adaptations to avoid mating failure might include sampling fewer males when they are encountered infrequently (e.g., at low densities; Crowley et al. 1991; de Jong and Sabelis 1991; Kokko and Mappes 2005; Bleu et al. 2012; Henshaw 2018) or as conditions become less suitable for reproduction (Backwell and Passmore 1996; Borg et al. 2006; Beckers and Wagner 2011; Atwell and Wagner 2014; Passos et al. 2014; Wacker et al. 2016). One might even imagine a scenario in which females avoid failing to mate altogether by detecting when conditions are becoming unsuitable for reproduction and returning to a previously sampled male to mate (Janetos 1980; Real 1990; Gibson and Langen 1996; Rosenthal 2017). These behavioral adaptations could produce weaker sexual selection at lower densities. If, for example, unmated females returned to previously sampled males, sexual selection would be weaker at low densities because under those conditions females encounter fewer males on average and would therefore more often “settle” for a nonpreferred male as opportunities to reproduce come to an end.



**Figure 1:** Changes in the strength of sexual selection (measured as the standardized selection gradient,  $\beta$ ) with total population density for different mate sampling strategies that females use to choose their mates. Points and error bars represent means and standard deviations calculated across 100 replicate simulations at each density. We use loess regressions to visualize trends. In a best-of-all strategy, females choose the male with the largest sexual trait from among all those encountered, as assumed by previous models. In the remaining strategies, females choose males on the basis of accumulated evidence of their acceptability, as predicted by models of the cognitive mechanisms of mate choice decision-making. The value of  $x_{\text{crit}}$  denotes the minimum acceptable male sexual trait, and  $p_{\text{crit}}$  represents the critical value of the posterior probability that a male is acceptable,  $\Pr(x \geq x_{\text{crit}} | x_p)$ , required for a female to commit to mating. Results are shown for a male trait distribution  $f(x) = N(0, 1)$ ,  $\text{var}_{\text{error}} = 0.5$ , breeding season length  $T = 100$ , sex ratio  $r = 1$ , and total area covered per male per time step  $8Dv/\pi = 1$ .

We should be careful, however, not to assume a priori the existence of behaviors that produce density-dependent mate sampling simply because they provide a more optimistic perspective of individuals' abilities to avoid remaining unmated. Indeed, a growing literature suggests that female mating failures are more widespread than typically thought, and in some cases a large percentage of females may remain unmated (Rhainds 2010, 2013, 2019). Considering the evolution of such behaviors explicitly, rather than taking them for granted, might provide a clearer path toward disentangling the varied relationships between density and sexual selection. For example, the scenario described above in which females avoid failing to mate by returning to previously sampled males requires that females can (i) obtain accurate information about when it is their final chance to mate and (ii) remember and relocate individual males. While these conditions may apply to some systems, they are unlikely to be universal. Thus, a valuable yet overlooked first step in predicting when sexual selection should change with population density is to consider how density-dependent mate sampling might be favored by selection and how sexual se-

lection should change with density if females have evolved to use these strategies. In the following section, we focus on what are likely the most general adaptations for reducing the risk of failing to mate and how they may lead, directly or indirectly, to density-dependent sexual selection.

### The Evolution of Density-Dependent Mate Sampling

We explore two general mechanisms through which selection might produce density-dependent mate sampling and provide some preliminary insights into how sexual selection should change with density if females use these sampling strategies. We use mathematical models that explicitly link (1) the evolution of mate sampling behavior in response to the costs and benefits of sampling and (2) sexual selection on male sexual traits caused by females' mating decisions.

We consider density-dependent mate sampling behavior that might evolve (i) as a result of selection for different mate sampling behaviors at different densities per se or (ii) as a by-product of selection for changes in sampling behavior over a breeding season. To determine the changes

in mate sampling behavior that might be favored by selection under each mechanism, we develop a model that predicts the sampling behavior that maximizes females' expected fitness given the benefits and costs of sampling. We then use the sampling behavior predicted by our model to simulate mating interactions with males across a range of population densities and quantify the resulting density dependence of the sexual selection on the male sexual trait. These results provide a starting place for predicting how sexual selection should change with population density if selection has led, directly or indirectly, to the evolution of density-dependent mate sampling behaviors.

#### *Adaptive Responses to Density-Dependent Costs and Benefits of Sampling*

Selection may favor density-dependent mate sampling if density per se affects the fitness benefits of mating with males with preferred sexual traits, the fitness costs of sampling males, or both (Crowley et al. 1991; de Jong and Sabelis 1991; Kokko and Mappes 2005; Kokko and Rankin 2006; Bleu et al. 2012; Henshaw 2018). There are numerous ways in which the fitness benefits or costs of mate sampling might change with population density, many of which likely depend on the study system in question (Kokko and Rankin 2006). For generality, we focus here on a cost that is likely a fundamental (and perhaps unavoidable) aspect of mate sampling and that may often be tightly linked to population density: the risk of failing to mate.

Given that there is some time period within which reproduction must occur (e.g., a female's lifetime), sampling more males increases the risk that a female will fail to find a mate before this period ends (i.e., the wallflower effect sensu de Jong and Sabelis 1991). Moreover, the risk of failing to mate likely decreases in denser populations because potential mates are encountered more frequently (Crowley et al. 1991; de Jong and Sabelis 1991; Kokko and Mappes 2005; Bleu et al. 2012; Henshaw 2018). Thus, the risk of failing to mate may produce density-dependent sampling costs that favor density-dependent mate sampling—specifically, selection should be expected to favor increased mate sampling in denser populations (Crowley et al. 1991; de Jong and Sabelis 1991; Kokko and Mappes 2005; Bleu et al. 2012; Henshaw 2018). The risk of failing to mate may therefore be a pervasive cost that can favor the evolution of density-dependent mate sampling and, consequently, produce stronger sexual selection at high density.

#### *Adaptive Temporal Plasticity in Mate Sampling*

Density-dependent mate sampling might also evolve as a by-product of selection for temporal plasticity in sampling

behavior over the breeding season (Kokko and Mappes 2005). In this case, density-dependent sampling does not evolve in response to effects of population density per se—rather, it emerges from an interaction between the density at which sampling occurs and temporal plasticity in mate sampling strategies that has evolved in response to other factors, such as changing sampling costs or benefits over the breeding season (Kokko and Mappes 2005). Thus, temporal plasticity in mate sampling can lead to density-dependent mate sampling without requiring an evolutionary history of exposure to the different densities individuals currently experience (Kokko and Mappes 2005). This mechanism of the evolution of density-dependent mate sampling might be particularly relevant given that contemporary variation in population density for many study systems may be driven to a large extent by recent and rapid environmental change. Moreover, temporal plasticity in mate sampling is well documented among empirical systems (Backwell and Passmore 1996; Borg et al. 2006; Beckers and Wagner 2011; Atwell and Wagner 2014; Passos et al. 2014; Wacker et al. 2016).

To illustrate, consider a hypothetical female whose breeding season ends when the environment becomes unsuitable for reproduction (e.g., due to drought or frost). Since environmental conditions vary from year to year, the length of the breeding season is uncertain, and she therefore faces some risk that the breeding season will end before she finishes sampling and chooses a mate. However, for many systems, such as those that rely on seasonally abundant prey (Noordwijk et al. 1995; Visser et al. 1998; Shave et al. 2019) or ephemeral abiotic conditions (James and Shine 1985; Backwell and Passmore 1996; Chou et al. 2019), the probability that environmental conditions will become unsuitable for reproduction increases over the breeding season. This produces time-dependent costs of sampling because the probability of the breeding season ending and the female remaining unmated increases with time. In situations like this, the optimal sampling criteria (e.g.,  $x_{\text{crit}}$ ) depends on the time  $t$  in the breeding season ( $x_{\text{crit}}(t)$ ). At the beginning of the breeding season the chance of remaining unmated is extremely small, and hence her fitness would be maximized if she accepts only the most preferred males ( $x_{\text{crit}}(t)$  is large). As time progresses the chance of remaining unmated increases, and as a result the optimal  $x_{\text{crit}}(t)$  decreases. The exact number of males a given female samples emerges from the interaction between  $x_{\text{crit}}(t)$  and the rate at which she encounters males. If males are encountered very frequently, then females will rarely need to continue sampling late into the season, and most mating decisions will be made using sampling strategies that are optimal early in the season (and vice versa; Kokko and Mappes 2005). Population density can therefore affect mate sampling indirectly through an effect on male encounter rate,



provided female sampling behavior changes over the breeding season.

### *Predicting the Density Dependence of Mate Sampling*

*The Stochastic Dynamic Programming Model.* To determine the changes in female sampling behavior with population density that might be favored by selection through the mechanisms described above, we expand on the model presented above (see “Mate Sampling Determines the Density Dependence of Sexual Selection”) to allow females to use sampling strategies that depend on population density and time in the breeding season. We develop a stochastic dynamic programming (SDP) model to determine the mate sampling behaviors that maximize a female’s expected fitness in a given breeding season given density- or time-dependent sampling costs. SDP models are discrete time models that incorporate information about states, such as the time in the mating season; the options available to individuals, such as accepting a mate or keep sampling; and the fitness consequences (e.g., changes in offspring production or survival) of those options (Clark and Mangel 2000) to predict strategies that maximize expected fitness. We present here an SDP model for females that choose their mates using a Bayesian sampling strategy, although our results are similar for other plausible sampling strategies (e.g., threshold and best-of- $n$  strategies; see the supplemental PDF). Our model predicts the optimal combination of  $x_{\text{crit}}^*$ , the minimum acceptable male trait, and  $p_{\text{crit}}^*$ , the critical level of evidence necessary to mate, both of which may vary with time  $t$  in the breeding season.

We assume that it takes some time to assess the sexual trait of an encountered male, although this handling time may be very short. We set the length of each time step  $t$  equal to the time required to assess a male; females that encounter more than one male per  $t$  can sample only one of them. For a female still sampling at time step  $t$ , the expected fitness accrued between time  $t$  and the end of the breeding season is  $W[t]$ .

A male is encountered at time  $t$  with probability  $1 - \exp(-\lambda)$ . As before,  $\lambda = \{[1/(1+r)] \times N_{\text{total}} \times 8Dv/\pi\}/A$  per time step, where  $d = N_{\text{total}}/A$  is the population density. If no male is encountered, the female has no choice but to continue sampling. If a male is encountered, she perceives a trait value  $x_p$  with probability  $g(x_p|x)$ , which depends on the male’s actual trait  $x$  and the assessment error  $\sigma_{\text{error}}$ . If the posterior probability that he is acceptable given  $x_p$ ,  $\Pr(x \geq x_{\text{crit}}|x_p)$ , is at least  $p_{\text{crit}}$ , she mates with him and stops sampling. The minimum value of the perceived trait that causes her to mate,  $x_{p_{\text{crit}}}$ , is the smallest value of  $x_p$  for which  $\Pr(x \geq x_{\text{crit}}|x_p) = [\Pr(x_p|x \geq x_{\text{crit}})/\Pr(x_p)]Q(x \geq x_{\text{crit}}) \geq p_{\text{crit}}$ . For the large populations we consider ( $N_{\text{total}} = 500$ ), repeat encounters with individ-

ual males are very rare. Thus,  $Q(x \geq x_{\text{crit}}) \approx 1 - F(x_{\text{crit}})$ . This would also apply to situations in which females cannot remember individual males. For situations in which females sample small numbers of males repeatedly (e.g., leks), the model can be expanded to track information about individual males, although this becomes computationally intractable for any more than a couple of males (Luttbegg 1996). The probability that a randomly encountered male is chosen is then  $1 - G(x_{p_{\text{crit}}})$ , where  $G(x_{p_{\text{crit}}}) = \int_{-\infty}^{x_{p_{\text{crit}}}} \int_{-\infty}^{\infty} g(x_p|x)f(x) dx dx_p$  is the cumulative distribution of perceived male traits evaluated at  $x_{p_{\text{crit}}}$ .

A mating female’s fitness depends on the chosen male’s trait  $x$  according to a function  $B(x)$ . This implies that the male trait is an honest signal of female fitness, either through direct or indirect fitness benefits (or costs). The male trait  $x$  varies among males as described in our initial simulations (i.e.,  $f(x) = N(\bar{x}, \sigma_x)$ ). We assume that females choose mates to increase their fitness, such that preferred males provide the largest  $B(x)$ . We thus present results for a linearly increasing  $B(x)$ , given the preference for males with  $x \geq x_{\text{crit}}$ . The precise shape of  $B(x)$  and the corresponding criterion for male acceptability does not affect our qualitative model predictions (see the supplemental PDF). The expected phenotype of accepted males is the average  $x$  for values of  $x_p \geq x_{p_{\text{crit}}}$ :

$$E(x_{x_{p_{\text{crit}}}}) = \frac{1}{\int_{x_{p_{\text{crit}}}}^{\infty} \int_{-\infty}^{\infty} g(x_p|x)f(x) dx dx_p} \times \int_{x_{p_{\text{crit}}}}^{\infty} \int_{-\infty}^{\infty} x \times g(x_p|x)f(x) dx dx_p. \quad (4)$$

The fitness payoff to a female that encounters an acceptable male is then  $B[E(x_{x_{p_{\text{crit}}}})]$ . This payoff does not depend on time  $t$ , as we assume that the distribution of male sexual traits does not vary over time and that any direct costs of time spent sampling (e.g., predation, energy loss) are negligible.

If instead the female continues sampling mates, no fitness is obtained in the current time step, but she may assess an additional male in the next time step  $t + 1$ . However, the female’s breeding season ends within the next time step with probability  $\mu(t)$ , which may change with  $t$ . Thus, the breeding season length  $T$  is not certain, and a sampling female always faces some risk of failing to mate. We assume that females have only one breeding opportunity in their lifetime, such that females that fail to mate have zero fitness. Mate sampling therefore comes at a fitness cost due to the risk of failing to mate. Note that our model would also describe the behavior of females with multiple breeding opportunities, provided they sample males before choosing a mate in each opportunity. Our model could be further extended to consider females that

recall males from previous breeding opportunities or that change their sampling over subsequent seasons (e.g., due to senescence), although we do not explore these scenarios here.

With probability  $1 - \mu(t)$ , the female's breeding season continues (i.e.,  $t$  increases by 1), and she has expected future fitness  $W[t + 1]$ . The female's expected fitness at time  $t$  is given by the dynamic programming equation

$$W[t] = \max_{x_{\text{crit}}, p_{\text{crit}}} \left\{ [1 - \exp(-\lambda)] \times [1 - G(x_{p_{\text{crit}}})] \times B \left[ E \left( x_{x_{p_{\text{crit}}}} \right) \right] + \left( 1 - \left\{ [1 - \exp(-\lambda)] \times [1 - G(x_{p_{\text{crit}}})] \right\} \right) \times [1 - \mu(t)] \times W[t + 1] \right\}, \quad (5)$$

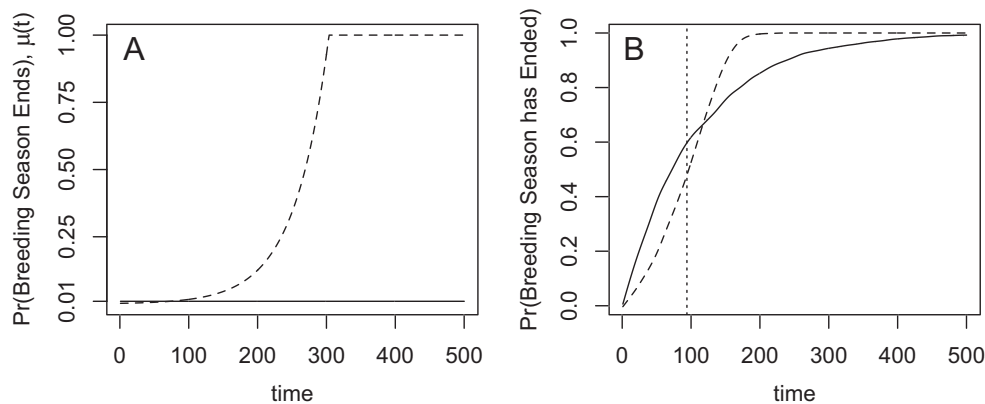
where the expected fitness  $W[t]$  is maximized over the minimum acceptable male trait,  $x_{\text{crit}}$ , and the amount of evidence needed to mate,  $p_{\text{crit}}$ .

We solve the SDP model using backward iteration (Clark and Mangel 2000). Specifically, we work backward from a final point in time  $\hat{T}$ , where  $\hat{T}$  is chosen such that >99% of females finish sampling before  $\hat{T}$  time steps given our choice of  $\mu(t)$  (i.e.,  $\hat{T}$  vastly exceeds the expected breeding season length). Our choice of  $\hat{T}$  has a negligible effect on the fitness payoffs (and thus optimal sampling) because the probability that a female is still sampling at  $t = \hat{T}$  is very small. A hypothetical female sampling at time  $\hat{T}$  has

a future fitness expectation of zero (i.e.,  $W[\hat{T} + 1] = 0$ ) because females have only one breeding season. We calculate at time  $\hat{T}$  the combination of  $x_{\text{crit}}$  and  $p_{\text{crit}}$  that maximizes expected fitness, which we denote  $x_{\text{crit}}^*(\hat{T})$  and  $p_{\text{crit}}^*(\hat{T})$ , and record the associated fitness payoff  $W[\hat{T}]$ . We then step back to time  $\hat{T} - 1$  and again determine the optimal decision using the expected future fitness payoff  $W[\hat{T}]$  calculated in the previous step. This procedure is repeated to determine the optimal behavior for each time step  $t$ .

*Scenarios Modeled.* The risk of failing to mate generates a density-dependent sampling cost. This occurs because population density affects the encounter rate with males. At low densities, females take longer to mate because of decreased encounter rates with males and thus face greater risk that the season ends before they have mated. To determine how mate sampling should change with density in response to this density-dependent sampling cost, we solve the SDP model for each of the 15 different population densities considered in our initial simulations (see "Mate Sampling Determines the Density Dependence of Sexual Selection"). To isolate the effect of density-dependent sampling costs on the optimal behavior, we keep  $\mu(t)$  constant over the breeding season.

To determine the optimal temporal pattern of sampling under time-dependent costs, we then let  $\mu(t)$  increase over the breeding season, as is likely the case for many organisms (e.g., because of ephemeral breeding conditions; fig. 2). We model the increase in  $\mu(t)$  as an exponential function, representing seasonal environments where breeding conditions are suitable and relatively stable for some time



**Figure 2:** Possible temporal patterns of the probability  $\mu(t)$  that the breeding season ends at time  $t$  (A) and the corresponding expected probability that the season will have ended by time  $t$  (B). Solid lines represent a case in which the probability that the season ends is constant over time ( $\mu(t) = 0.01$ ). Long-dashed lines represent a case in which the probability that the season ends increases over time; at some  $t$ , successful reproduction becomes impossible ( $\mu(t) = \min(0.0001 + 0.0023e^{0.02t}, 1)$ ). Lines in B are generated by Monte Carlo simulations of the scenarios depicted in A and are smoothed using a smoothing parameter of 0.5. The expected (i.e., mean) length of the reproductive opportunity is approximately equivalent in either case (~94 time steps), as denoted by the vertical short-dashed line.

before deteriorating and becoming wholly unsuitable. Specifically,  $\mu(t) = \min[a + b \times \exp(c \times t), 1]$ . We truncate the value of  $\mu(t)$  at 1 because the probability can never exceed unity (fig. 2A). The  $a$  term allows us to flexibly set the minimum  $\mu(t)$ —here, we choose  $a$ ,  $b$ , and  $c$  such that the mean length of the reproductive opportunity in our simulations is approximately equal to the case in which  $\mu(t)$  is constant ( $\sim 94$  time steps; vertical short-dashed line in fig. 2B). Note that in this case the SDP model predicts how sampling should change with time. The density dependence in mate sampling that emerges from this temporal plasticity can be observed only when individuals use the predicted strategy at different population densities.

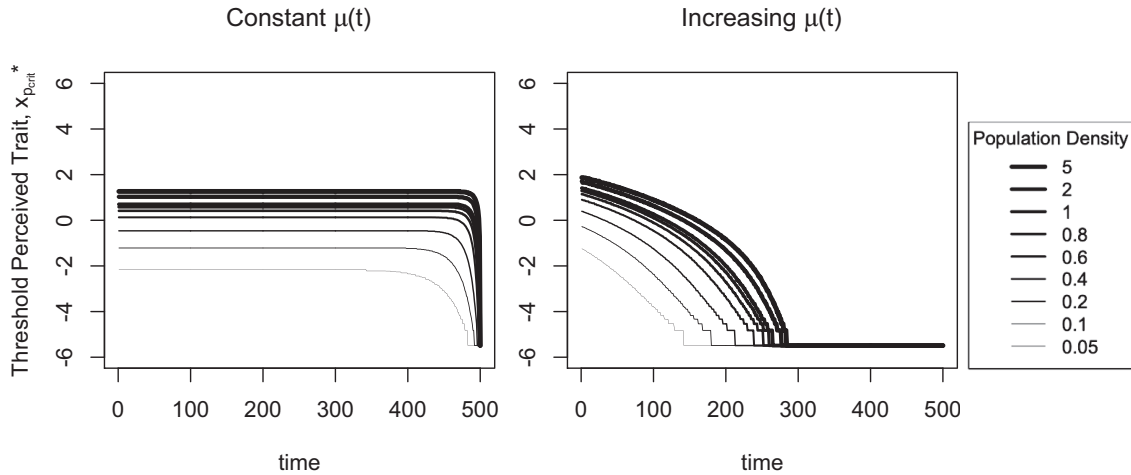
**Sampling Behavior Predicted by the SDP Model.** As expected, females maximize their fitness by increasing the minimum acceptable perceived trait  $x_{p,crit}^*$  at higher population densities (fig. 3A, 3B). The increase in  $x_{p,crit}^*$  is non-linear because at very high densities females encounter males almost as quickly as they can be assessed. If the probability the breeding season ends  $\mu(t)$  is constant,  $x_{p,crit}^*$  does not change with time over the length of reproductive opportunity that most females experience (i.e.,  $t \leq 400$ ; fig. 3A). The decrease in  $x_{p,crit}^*$  near the final time  $\hat{T}$  (fig. 3A) is an artifact of the finite time interval used to solve the SDP model; these sampling behaviors are almost never expressed because the vast majority of females' breeding opportunities end long before  $\hat{T}$  (fig. 2B). In contrast, if  $\mu(t)$  increases with time,  $x_{p,crit}^*$  decreases rapidly over the time

available to reproduce (fig. 3B). Note that  $n^*(t)$  begins at higher values in this case—this occurs because we chose  $\mu(t)$  such that the expected breeding season length was similar to the scenario in which  $\mu(t)$  is constant, and this requires beginning the season with a lower  $\mu(t)$ . We find qualitatively similar results for other plausible sampling strategies and relationships between female fitness and male traits given by  $B(x)$  (see the supplemental PDF).

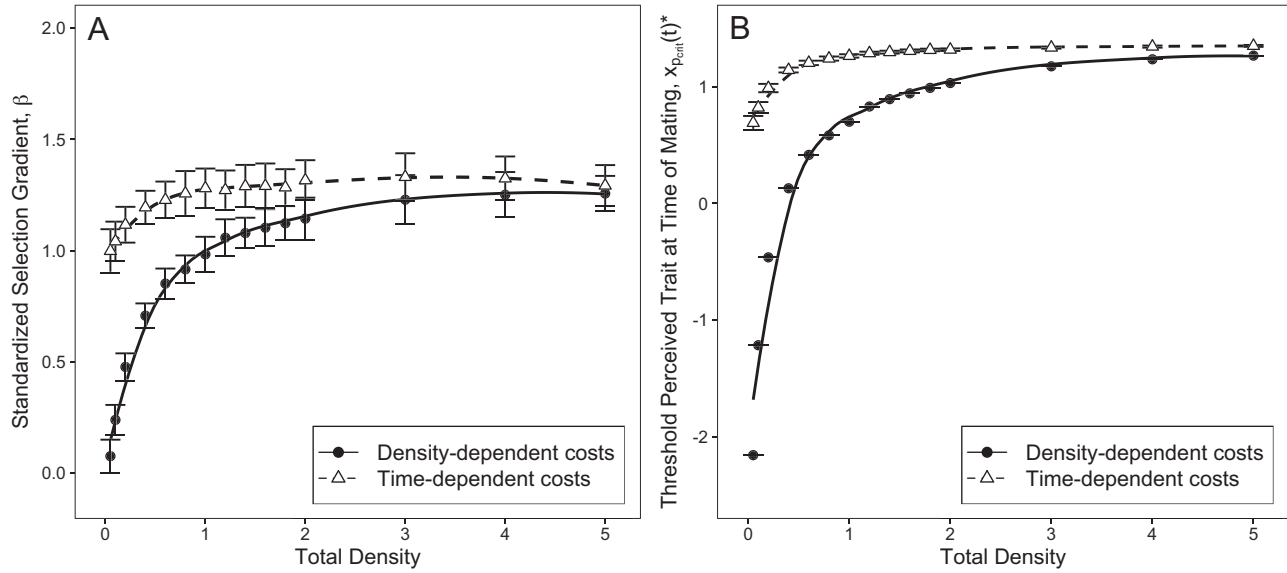
### Simulating Mating Interactions and Quantifying Sexual Selection

**Simulation Methods.** We repeat the simulations described above to predict the density dependence of sexual selection on the male trait. However, we now assume that females follow the optimal mate sampling strategies identified by the SDP models. In other words, the SDP model results are used as a lookup table specifying what a female should do given the time in her breeding season and her sampling history with males.

In each time step, we cycle over females who have not yet mated and whose breeding season has not yet ended. For each such female, we draw a random number between 0 and 1; if this number falls below the probability of encountering a male at the current density,  $1 - \exp(-\lambda)$ , she encounters a male. If she does, we draw the sexual trait perceived by the female,  $x_p$ , from the distribution  $g(x_p|x)$ , where  $x$  is the encountered male's actual trait, and calculate the posterior probability of his acceptability,  $\Pr(x \geq x_{p,crit} | x_p)$



**Figure 3:** Results of the optimization model predicting female sampling for two scenarios of temporal change in the probability  $\mu(t)$  that the reproductive opportunity ends: a constant  $\mu(t)$  (A) or an exponentially increasing  $\mu(t)$  (B). Lines represent the minimum sexual trait value perceived by a female that will produce a commitment to a mating decision,  $x_{p,crit}^*$ , at different times in the breeding season  $t$ . Line widths represent different population densities to which the populations are adapted. The stochastic dynamic programming model predictions for population densities of 1.2, 1.4, 1.6, 1.8, 3, and 4 are not shown to reduce clutter, as  $x_{p,crit}^*$  varies little among the highest densities.



**Figure 4:** Changes in the sexual selection gradient  $\beta$  (A) and the threshold perceived sexual trait  $x_{p_{\text{crit}}}$  for each female at the time of mating (B), with population density for a Bayesian sampling strategy. Filled symbols correspond to simulations in which sampling changes adaptively with density in response to density-dependent sampling costs (i.e., the risk of failing to mate), as predicted by the stochastic dynamic programming (SDP) model (fig. 3A). Open symbols denote simulations in which sampling does not change adaptively in response to density-dependent sampling costs but does change with density as a by-product of temporal plasticity in sampling predicted by the SDP model in response to time-dependent sampling costs (i.e., an increasing probability that the breeding season ends; fig. 3B). In the latter case, results are shown for simulations in which females use the temporal pattern of sampling that is optimal in a population of total density  $d = 1$ .

(eq. [2]). She mates with this male if  $\Pr(x \geq x_{\text{crit}}^*(t) | x_p) \geq p_{\text{crit}}^*(t)$  (or, equivalently, if  $x_p \geq x_{p_{\text{crit}}}^*$ ), where  $x_{\text{crit}}^*(t)$  and  $p_{\text{crit}}^*(t)$  are the optimal values of the minimum acceptable male trait  $x_{\text{crit}}$  and evidence necessary to commit to a decision  $p_{\text{crit}}$  predicted by the SDP model at time  $t$ . If she does not encounter a male or does not choose the male she encounters, she continues searching, and we draw a random number between 0 and 1 to determine whether the female's breeding season ends within the next time step. If it ends, she remains unmated. Otherwise, she is again available to encounter a male in the next time step  $t + 1$ . We track the number of times each male is chosen and, at the end of the season, calculate the standardized selection gradient  $\beta$ . Results are also presented in terms of the opportunity for sexual selection  $I_{\text{mates}}$  in the supplemental PDF. We also record the value of  $x_{p_{\text{crit}}}^*$  at the time of mating for each female.

To determine how sexual selection changes with population density when density-dependent mate sampling has evolved in response to density-dependent sampling costs (here, the risk of failing to mate), we conducted 100 replicate simulations at each density in which females use the optimal strategy predicted by the SDP model for the density at which mating occurs. To isolate the effect of changes in mate sampling that evolve in response to density-dependent sampling costs per se, we use the strat-

egies that are optimal if  $\mu(t)$  remains constant over the breeding season.

We then determine how the strength of sexual selection changes with population density if mate sampling changes with density as a by-product of the evolution of temporal plasticity in mate sampling. We again conduct 100 replicate simulations at each density, but females now use sampling behaviors that are optimal if the costs of mate sampling (i.e., the probability that the breeding season ends  $\mu(t)$ ) increase over time. To isolate the effect of temporal plasticity in sampling on the density dependence of sexual selection, we assume that females use the optimal temporal pattern for a single historical density to which they are adapted across all population densities at which mating interactions are simulated (i.e., females are not locally adapted or adaptively plastic with respect to density-dependent costs per se).

For each set of simulations described above, we plot the mean  $\pm$  SD of the selection gradient  $\beta$  as a function of population density. To quantify the overall density dependence of sexual selection for each mechanism of the evolution of density-dependent mate sampling, we calculate the CV in the mean selection gradient  $\beta$  across densities for each set of simulations. To relate the density dependence of sexual selection to the changes in sampling with density that emerge, directly or indirectly, from the predictions of our



SDP model, we also plot the mean  $\pm$  SD of the number of males sampled across population densities. In the supplemental PDF, we also present these results for simulations in which females use the sampling behaviors predicted by the SDP model in response to both density- and time-dependent sampling costs (i.e., fig. 3B). These results are qualitatively identical to the case in which females use the strategies that are optimal given density-dependent sampling costs alone.

*Simulation Results.* Our simulations demonstrate that the sexual selection gradient  $\beta$  increases strongly with population density if mate sampling changes with density because of adaptation to density-dependent sampling costs (filled symbols, fig. 4A). The increase in  $\beta$  with density is nonlinear, reflecting the nonlinear increase in the minimum acceptable perceived trait,  $x_{\text{crit}}$ , with density (filled symbols, fig. 4B). The CV in the mean  $\beta$  across densities suggests that the strength of sexual selection varies by nearly half of its average value across densities ( $CV(\beta) = 0.41$ ). We obtain similar results for other sampling strategies considered by earlier theory (see the supplemental PDF).

The sexual selection gradient  $\beta$  also increases nonlinearly with population density if mate sampling varies with density as a by-product of changes in females' sampling over time in response to time-dependent sampling costs (i.e., the probability  $\mu(t)$  that the reproductive opportunity ends increases over time; open symbols, fig. 4A, 4B). Notably, the density-dependent change in  $\beta$  is weaker than if mate sampling changes in response to density-dependent sampling costs ( $CV(\beta) = 0.08$  vs.  $CV(\beta) = 0.41$ , respectively), and  $\beta$  is larger across all densities (compare filled and open symbols, fig. 4A). This occurs despite a much wider range in the number of males sampled and likely reflects the fact that females already sample more males on average at lower densities when they are adapted to time-dependent sampling costs (open symbols, fig. 4B). This produces a larger minimum value of  $\beta$ . Again, qualitatively similar results hold for other fitness functions and sampling strategies (see the supplemental PDF).

### Discussion

We show that mate sampling strategies qualitatively affect the expected density dependence of sexual selection caused by mate choice. The classic prediction that sexual selection should be stronger at higher densities follows immediately from the simplifying assumption that mate sampling is limited only by mate availability. Theory on the evolution of mate sampling strategies suggests that the number of males sampled should instead be determined by the costs and benefits of sampling, and we demonstrate

that sexual selection does not depend intrinsically on population density if females use strategies that balance this trade-off. Finally, we develop theoretical models of optimal mate sampling to explore how density-dependent sampling might evolve, and we explicitly link the predicted behaviors to the expected density dependence of sexual selection. We find that the effect of density on the risk of failing to mate may generally select for density-dependent mate sampling, and if females use the strategies that are optimal for the densities they experience, sexual selection may indeed increase strongly with population density. While density-dependent mate sampling may also emerge as a by-product of temporal plasticity in mate sampling, this generally produces a weaker change in sexual selection with density than if sampling changes with density as a result of density-dependent costs per se.

The finding that density-dependent sexual selection is not an intrinsic property of mate choice but rather requires the evolution of density-dependent mate sampling strongly suggests that the density dependence of sexual selection in natural systems depends on the ecological context in which mate sampling has evolved. The optimal sampling behavior may generally change with density because of the change in the risk of failing to mate, for example, but this does not imply that females will express the optimal sampling strategy for the densities they experience. For female sampling behavior to change adaptively with density, females must be locally adapted to among-population differences in density or have evolved the ability to detect and respond adaptively to the densities they experience (i.e., adaptive plasticity). This may be more likely in systems that have an evolutionary history of exposure to different densities. Nevertheless, the evolution of such adaptive responses may be limited by factors such as gene flow, correlations between sampling behaviors and other traits, and/or rapid or unpredictable changes in population density (Moran 1992; Padilla and Adolph 1996; DeWitt et al. 1998; Crespi 2000; Tufto 2000; Murren et al. 2015; Brady et al. 2019a, 2019b). Some of these limiting factors may themselves be correlated with density (e.g., gene flow and genetic drift; Lenormand 2002; Brady et al. 2019a, 2019b). Changes in sexual selection with population density ranging from the flat lines in figure 1 to the slope in figure 4A might all be reasonable, depending on the degree to which mate sampling behavior changes adaptively with density per se. Given that contemporary variation in population density for many study systems may be largely due to recent and rapid changes in harvesting regimes, land use, or climatic conditions, researchers should consider whether populations are likely to have evolved locally adapted or plastic responses to contemporary differences in population density. Future studies that explore the conditions under which the evolution of density-dependent

sampling through local adaptation or behavioral plasticity can keep pace with contemporary changes in population density will be helpful in refining our intuition about when to expect mate sampling behavior—and thus sexual selection—to vary with population density.

Sexual selection may also increase with population density if mate sampling changes with density as a by-product of temporal plasticity that evolves because of time-dependent sampling costs. While our study is not the first to demonstrate that temporal plasticity in sampling can interact with population density to produce density-dependent sampling behavior (Kokko and Mappes 2005), our optimization model demonstrates that time-dependent sampling costs (and the risk of failing to mate in particular) may be a general mechanism favoring such plasticity. Previous models focus on plasticity that can evolve if females mate multiply and produce offspring at a rate proportional to overall quality of the males with whom she mates (Kokko and Mappes 2005). Females can then balance the risk of failing to mate against the benefits of high-quality mates by choosing a first mate relatively indiscriminately and then sampling more extensively in subsequent matings to increase offspring quality (Kokko and Mappes 2005). We show that temporal plasticity in mate sampling may also be favored by selection for singly mating females, provided the costs of sampling change over time.

In many study systems, the costs of sampling likely increase over time, if for no other reason than environmental conditions are only transiently suitable for successful reproduction. Many species rely on seasonally abundant prey to provision their offspring and suffer reduced fitness if reproduction occurs after prey abundance peaks (Noordwijk et al. 1995; Visser et al. 1998; Shave et al. 2019). In others, the time frame for successful reproduction may be limited by predation risk (Naef-Daenzer et al. 2001; Chou et al. 2019), temperature (Chou et al. 2019), precipitation (James and Shine 1985), or tidal conditions (Backwell and Passmore 1996). Nevertheless, there may be species for which the conditions needed for successful reproduction are relatively constant over time, such as those that inhabit more stable (e.g., tropical or deep water) habitats (James and Shine 1985; Bernard and Cumming 1997; Sulikowski et al. 2007; Teichroeb and Sicotte 2008; Harry et al. 2010). Of course, the costs of sampling may change over time for other reasons. If, for example, males are unavailable for remating for some time, mate choice may itself produce increasing sampling costs as preferred males become scarce.

The probable ubiquity of time-dependent sampling costs suggests that temporal plasticity may be a general feature of mate sampling strategies. Indeed, there are many empirical examples of temporal plasticity in mate sampling

behavior (Backwell and Passmore 1996; Borg et al. 2006; Beckers and Wagner 2011; Atwell and Wagner 2014; Passos et al. 2014; Wacker et al. 2016). Moreover, the resulting density dependence of mate sampling behavior does not require an evolutionary history of exposure to the different population densities females now experience—instead, it emerges from an interaction between density and temporal plasticity in mate sampling strategies that has evolved for other reasons (Kokko and Mappes 2005). It may therefore be reasonable to expect that density-dependent mate sampling arises more frequently as a by-product of temporal plasticity in sampling than as an adaptation to different densities per se, particularly for taxa in which differences in density are the result of recent environmental changes. However, our results suggest that even optimal temporal plasticity in mate sampling generally produces weaker density dependence in the strength of sexual selection than adaptive responses to effects of population density per se on the costs of sampling. Taken with recent meta-analytical evidence suggesting that temporal changes in mate choice behavior are on average weak (Dougherty 2021), it seems possible that the most likely route to the evolution of density-dependent sampling may tend to produce relatively weak changes in sexual selection.

#### *Biological Relevance and Future Directions*

We focus on relatively simple mating behaviors and ecological contexts in which they evolve to provide an accessible, general foundation for the importance of mate sampling behavior in the density dependence of sexual selection. There are many plausible biological scenarios other than those considered above that deserve further attention. Below, we discuss some common scenarios to which our model may be readily extended, as well as some in which the expected outcomes are less clear but provide promising avenues for future study.

*Multiply Mating Females.* Females in our model mate and reproduce once in their lifetimes, but in many species females accept multiple males per reproductive event, reproduce multiple times, or both. The implications of mating with multiple males in each reproductive event for density-dependent sexual selection are discussed in detail elsewhere (Kokko and Mappes 2005). Below, we describe the application of our framework to females that reproduce multiple times in their lives (i.e., experience multiple breeding seasons).

If females experience multiple breeding seasons, the expected future fitness at the end of a season  $W[\hat{T} + 1]$  is not zero (as in our model) but is the expected fitness of a female at the beginning of the next season  $W[t = 1]$

weighted by the probability of surviving between seasons. If between-season survival is constant over individuals' lives, then the optimal sampling behavior would be the same from one season to the next, much as it is the same from one time step to the next during the breeding season if the probability that the season ends is constant (fig. 3A). The expected mate sampling dynamics and, thus, the density dependence of sexual selection would be identical to the single-mating model.

If surviving to the next season becomes less likely over time (e.g., because of senescence), then females might benefit from sampling fewer males later in life as future reproductive opportunities dwindle. This occurs for the same reason that females benefit from sampling fewer males later in the season when the costs of sampling increase over time (fig. 3B), although in this case the shift in behavior happens among, rather than within, seasons. Like within-season plasticity, among-season plasticity might interact with density to produce density-dependent mate sampling. In this case, density-dependent sampling would arise from shifts in the age distribution of females that mate during the season rather than the time in the season at which they mate. For example, if the population experienced a sudden decrease in density, more young females (which sample many males) would remain unmated than older females (which sample few males). This would decrease the strength of sexual selection compared with the same population at high density. Senescence of females over multiple reproductive opportunities may therefore be another general mechanism for the (indirect) evolution of density-dependent mate sampling that deserves further study.

These dynamics may be complicated considerably if females store sperm. Future fitness expectations then also depend on the female's fertilization state at the season's end, potentially producing among-season trade-offs in mate sampling behavior. A female might, for example, benefit from mating randomly in her first season and using the stored sperm to guard against mating failure while sampling large numbers of males in subsequent seasons. This "trading-up" strategy may be particularly pronounced if a female's fitness also depends on sperm quality and there is last-male sperm precedence (Kokko and Mappes 2005). The resulting among-season plasticity in sampling could produce density-dependent sexual selection, although interestingly the underlying shift in the age distribution of mating females would be opposite that expected if females senesce (i.e., older/mated females, which sample more males, would more often remain unmated at low population densities). It is unclear which effect, if either, would dominate in cases where sperm storage and senescence co-occur. Studies focusing on how sperm storage/precedence interacts with patterns of senescence to shape selection on among-season changes in sampling behavior are

needed to better understand how sexual selection changes with density for systems in which females reproduce multiple times.

*Small Populations and Repeated Encounters.* Our model considers a large, freely mixing population such that repeated encounters with individual males are very rare. Natural populations, on the other hand, can be relatively small, and nonrandom movement is likely the norm. We might expect a nontrivial proportion of encounters to occur between the same males and females.

The cognitive framework of mate choice decision-making describes how repeated samples are integrated to update females' estimates of a male's acceptability (Castellano 2009). What is less clear is how selection might act on decisions to revisit males instead of attempting to encounter new ones. Luttbegg (1996) demonstrated that females that can recall and relocate males might benefit from restricting their sampling to only a few males with the greatest evidence in favor of their acceptability. These types of sampling strategies may have implications for the density dependence of sexual selection (e.g., if resampling males allows females to accurately choose the most preferred males) and thus exert strong sexual selection even when the total number of males encountered is low (e.g., at low population density). The effects of repeat encounters and, more generally, interactions between population size and population density for optimal mate sampling behavior and the density dependence of sexual selection deserve further study.

*Relationships between Female Fitness and Male Traits.* For the different forms of the relationship between female fitness and male traits we consider, females benefit from sampling more males at higher densities and, if sampling costs increase over time, earlier in the breeding season (see the supplemental PDF). This suggests that the changes in mate sampling and sexual selection with population density that emerge when females have evolved to use these strategies do not depend qualitatively on how female fitness varies with the trait of her mate. Nevertheless, the relationship between female fitness and the male trait may affect the magnitude of the change in sexual selection with density. If, for example, female fitness is saturating over the distribution of male traits in the population, then high-quality males are common and females benefit from sampling few males even at high densities and early in the season (fig. S10A, S10B). The magnitude of the change in sexual selection with density may therefore be somewhat weaker than if female fitness is an accelerating function of traits in the population, in which case high-quality males are rare and females benefit from sampling many of them if conditions are favorable (fig. S10C, S10D).

The relationship between female fitness and the male traits in the population may change over generations if the male trait distribution evolves in response to sexual selection caused by female mate choice. Take, for example, the case described above in which females benefit from sampling many males because their fitness is an accelerating function of the male traits in the population. An evolutionary response of the male trait distribution to sexual selection caused by females' sampling behavior would move the distribution toward the female fitness peak and diminish the benefit to females of sampling. Female fitness may eventually become a saturating or stabilizing function of the male traits available in the population. In this sense, the relationships between female fitness and male fitness we consider can be viewed as extremes along a continuum of scenarios that might arise at different stages of the evolution of male traits through premating sexual selection caused by mate choice. The observed magnitude of density dependence of sexual selection in a given system may therefore depend on the factors shaping the coevolution of the male trait distribution and female sampling behavior.

*Direction of Density Dependence.* Our model captures some, but not all, of the empirically observed variation in the relationship between density and sexual selection. We find that increases in sexual selection with density can be negligible or substantial depending on the degree of adaptation to density- or time-dependent sampling costs, but we do not find any cases in which the strength of sexual selection decreases with density. Many of the empirical cases of negative density-dependent sexual selection can be explained by processes other than those considered here, such as density-mediated switches between alternative reproductive tactics by males (Jirotkul 1999; Pomfret and Knell 2008). That said, our understanding of how mate sampling affects density-dependent sexual selection is nascent, and future studies may find plausible ecological conditions in which adaptive sampling behaviors can also produce negative density dependence.

### Conclusion

Our study demonstrates that the density dependence of sexual selection caused by female mate choice depends critically on the details of how females sample mates. Changes in sexual selection with density are not intrinsic to the process of sampling and choosing mates but can occur if individuals adjust their sampling behavior with density as a direct result of density-dependent sampling costs or as a by-product of temporal plasticity in sampling behavior. Future studies aimed at further resolving the conditions in which these and other features of sampling strategies evolve will be

instrumental in understanding how population density shapes variation in sexual selection within and among taxa.

### Acknowledgments

John DeLong, Daizaburo Shizuka, and Andrew Tyre contributed many hours of helpful discussion about these ideas. The members of the Ecology, Evolution, and Behavior program at the University of Nebraska–Lincoln, particularly the Animal Behavior Reading Group, provided valuable feedback on this project at various stages. We are greatly indebted to the Blackmon lab at Texas A&M University for sharing its computational resources. J.C.W. was supported by a Presidential Fellowship provided by the University of Nebraska–Lincoln.

### Statement of Authorship

J.C.W. conceptualized the study, developed the model and simulation code, conducted the model analysis, and led the manuscript preparation. E.A.H. and B.T. supervised the development of the concept and analytical approach and extensively reviewed and edited the manuscript throughout its many stages.

### Data and Code Availability

The source code underlying this article has been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.1c59zw3xd>; Watts et al. 2022).

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Associate Editor: Julia B. Saltz  
Editor: Daniel I. Bolnick