



Mate search and mate-finding Allee effect: on modeling mating in sex-structured population models

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Received: 18 May 2017 / Accepted: 17 December 2017 / Published online: 11 January 2018
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Abstract

Many demographic and other factors are sex-specific. To assess their impacts on population dynamics, we need sex-structured models. Such models have been shown to produce results different from those predicted by asexual models, yet need to explicitly consider mating dynamics. Modeling mating is challenging and no generally accepted formulation exists. Mating is often impaired at low densities due to difficulties of individuals in locating mates, a phenomenon termed a mate-finding Allee effect. Widely applied models of this Allee effect assume either that only male density determines the rate at which females mate or that male and female densities are equal. Contrarily, when detailed models of mating dynamics are sometimes developed, the female mating rate is rarely reported, making quantification of the mate-finding Allee effect difficult. Here, we develop an individual-based model of mating dynamics that accounts for spatial search of one sex for another, and quantify the rate at which females mate, depending on male and female densities and under a number of reasonable mating scenarios. We find that this rate increases with male and female densities (hence observing a mate-finding Allee effect), in a decelerating or sigmoid way, that mating can be most efficient at either low or high female densities, and that the mate search rate may undergo density-dependent selection. We also show that mate search trajectories evolve to be as straight as possible when targets are sedentary, yet that when targets move the search can be less straight without seriously affecting the female mating rate. Some recommendations for modeling two-sex population dynamics are also provided.

Keywords Allee effect · Correlated random walk · Density-dependent selection · Evolution · Mating behavior · Two-sex population model

Introduction

By far, the majority of published population models are unstructured with respect to sex, even though their aim is in most cases to study dynamics of sexually reproducing populations. For example, as of 15 December 2016, the Web of Science

database returned 60,341 results for the “population dynamics AND model” query, with only 2095 of them when “sex” was added, 60 if alternatively “two-sex” was added, 116 when “sex-structured” was added, and 109 if “sexually structured” was added. Also, it is virtually impossible to find an account on sex-structured population models in any standard book on mathematical ecology. Exceptions in this respect are the books by Caswell (2001) and Kot (2001), but even there the respective sections on sex-structured models cover only 22 out of 652 and 12 out of 424 pages. Nevertheless, albeit quite technical, a monography on sex-structured modeling exists (Iannelli et al. 2005).

A common yet tacit assumption behind most of the sexually unstructured models aimed to examine dynamics of sexually reproducing populations is that females dominate population dynamics while males do not matter. An underlying rationale here is that there are always enough males or that males and/or females have efficient mate-finding strategies for all females to mate. To avoid complexities

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12080-017-0361-0>) contains supplementary material, which is available to authorized users.

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associated with an explicit consideration of sex, in many other modeling studies males and females share an identical life history so that what actually matters is the total population density. Both these approaches have been questioned repeatedly, pointing to a frequent observation that male densities can be low and limit the female mating rate (Dennis 1989; Boukal and Berec 2002; Berec et al. 2018) or that many demographic and other factors are sex-specific (Møller 2003; Rankin and Kokko 2007; Rankin et al. 2011).

Relevance of any such simplifying assumption is rarely discussed, and its impacts on the obtained results relative to when an explicit sex-structured model is used are virtually unknown. However, sex-structured population models have been shown repeatedly to produce results different from predictions of population models not accounting for sex, quantitatively (Berec and Maxin 2014) but also qualitatively (Boukal et al. 2008). This points to a need to consider males and females explicitly, at least as an initial step in model development, followed, e.g., by an assumption that male and female life histories are identical. Such a two-step procedure of generality and simplification may allow one to reveal any effects sex may have on population dynamics, but also to provide a justified form of any resulting sexually unstructured population model (Berec and Maxin 2013; 2014; Berec et al. 2017b).

The obvious cost of developing sex-structured population models is a need to model mating dynamics and thus reduced analytical tractability of such models. Indeed, the rate at which any particular female mates (or the probability that it mates per a time period), depending on male and female densities, is a core element of any sex-structured population model (Caswell and Weeks 1986; Kot 2001; Iannelli et al. 2005; Bessa-Gomes et al. 2010; Berec and Maxin 2014; Snyder et al. 2017). Since males and females need to find each other to mate, mating is by definition a non-linear process. On the other hand, the encounter process does not differ much from encounters found in other contexts, such as between predators and prey, susceptible and infected individuals in epidemiology or enzyme-substrate encounters in chemical kinetics, an analogy which we also exploit in this article.

Mating functions commonly used to describe the rate at which females mate (i.e. the number of females mated that occur per unit time) are degree-one homogeneous mating functions (Caswell and Weeks 1986; Haderler et al. 1988; Iannelli et al. 2005; Bessa-Gomes et al. 2010). These functions, exemplified, e.g., by the harmonic mean

$$\mathcal{M}(m, f) = 2 \frac{mf}{m + f}, \quad (1)$$

where m and f denote male and female density, respectively, have the defining property that once m and f increase

or decrease by a common factor $\alpha > 0$, the mating rate increases or decreases by the same factor:

$$\mathcal{M}(\alpha m, \alpha f) = \alpha \mathcal{M}(m, f). \quad (2)$$

Since this property implies that

$$\frac{\mathcal{M}(\alpha m, \alpha f)}{\alpha f} = \frac{\mathcal{M}(m, f)}{f}, \quad (3)$$

the female mating rate (i.e., the probability that any particular female mates per unit time) does not change with male and female densities as soon as they are changed by the same factor. This rarely discussed property of the degree-one homogeneous mating functions may be an issue when population densities become low, since finding mates is often more difficult as male density declines (Courchamp et al. 2008; Gascoigne et al. 2009).

Difficulty of females in finding mates at low male densities is commonly referred to as a mate-finding Allee effect (Courchamp et al. 2008; Gascoigne et al. 2009; Kramer et al. 2009; Fauvergue 2013). Allee effects are a density-dependent phenomenon which occurs when the *per capita* population growth rate or a component of fitness increase as population size or density increase. Mating functions accounting for the mate-finding Allee effect, exemplified, e.g., by the hyperbolic function

$$\mathcal{M}(m, f) = \frac{mf}{m + \theta} \quad (4)$$

with a positive parameter θ , are an alternative class of mating functions used in sex-structured population models (Boukal and Berec 2002; Courchamp et al. 2008; Shaw et al. 2018). The characteristic property of this class of functions is that at low densities, increasing male and female densities by the same factor should increase the female mating rate, too:

$$\frac{\mathcal{M}(\alpha m, \alpha f)}{\alpha f} > \frac{\mathcal{M}(m, f)}{f} \quad \text{or} \quad \mathcal{M}(\alpha m, \alpha f) > \alpha \mathcal{M}(m, f), \quad (5)$$

for some small m and f and $\alpha > 1$ (Shaw et al. 2018). No degree-one homogeneous mating function thus represents a mate-finding Allee effect, and vice versa. In addition, the property (5) implies that once we can factorize the mating function as $\mathcal{M}(m, f) = P(m)f$ for some function $P(m)$, the mate-finding Allee effect occurs once $P(m)$ is an increasing function of male density m , at least at low male densities (Boukal and Berec 2002; Courchamp et al. 2008).

Unfortunately, the commonly used Allee-effect-related mating functions such as Eq. 4 do not account for many details of mating dynamics, and assume either that only male density determines a rate at which each female mates or that male and female densities are equal (Dennis 1989; Boukal and Berec 2009; Terry 2015). On the other hand, limited male mating capacity (Wells et al. 1990), refractory time after each mating (Molnár et al. 2008), inter-individual

heterogeneity (Dennis 1989), and many other factors such as protandry (Robinet et al. 2007) and patchiness in individual distribution (Shaw and Kokko 2014) are all drivers of mating dynamics.

In this article, we use an individual-based simulation model, as well as an analytic approach, to study how various characteristics of the mate-finding process (rate and directionality of movement, limitations of male mating potential, length of refractory period after mating, learning, inter-individual heterogeneity, and evolution of rate and directionality of movement) may affect the probability of females mating within a mating season, depending on male and female densities. These explorations are motivated by the need to represent mating rates or probabilities correctly in sex-structured population models, and in particular, the need to account for mate-finding Allee effects. Many of the underlying determinants of mating success mentioned above have been studied in various publications, but to our knowledge, there is no study that merges and rigorously compares the respective influence of each of these. Seeing the effects of these different drivers of mating dynamics side-by-side and contrasted could help unravel commonalities and differences between mating systems, and how these characteristics affect vulnerability of a species to mate-finding Allee effects. In particular, some explicit recommendations are provided for researchers who want to model two-sex (or even one-sex) population dynamics without including the level of detail required by an individual-based model.

Model description

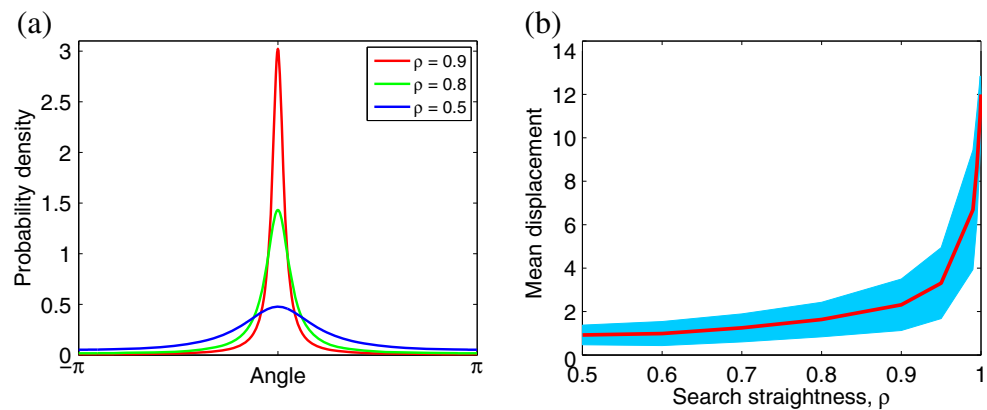
Here, we develop a spatially explicit, individual-based model of seasonal mating dynamics. The population is structured by sex, with males and females initially randomly distributed over a square habitat of area H^2 (we set $H = 20$ in simulations). For simplicity, in our main simulations, we consider one sex to be the searching (and hence moving) sex (the searcher) while the other to be sedentary (the target), yet we also test for robustness of our results by assuming that the targets may also move. Each searcher has a random initial movement direction and is characterized by a mate search rate q and a mate detection distance δ within which it detects a target. The mating season has length ϕ . When at any moment during a searcher's movement step (see below) a target occurs in the searcher's detection neighborhood, those two individuals mate. We assume periodic boundary conditions such that individuals stepping off the habitat on one side appear on the other side. To test for robustness of our results, we also consider a kind of reflecting boundary conditions such that when an individual would step off the habitat, it does not move and randomly reassigns its movement direction. While females are assumed to mate at

most once, males can mate up to several times; see below for more details. When the targets move, too, they are characterized by a movement rate q_t and move before the searchers do. We note that movement and mate search have the same meaning in this article if movement is related to the searchers. Targets may move but do not search in the sense that they do not have the mate detection neighborhood. No mortality is assumed to occur during the mating season.

The core element of our model is how the searchers (and moving targets) actually move. A commonly used approximation of animal movement is a connected series of straight lines that define individual movement steps (Hutchinson and Waser 2007). This allows movement to be characterized by just two variables: lengths of movement steps (or move lengths) and turning angles between successive movement steps. We let movement be continuous in both space and time which means that all locations during the movement step are visited, and choose a correlated random walk (CRW) as our model of individual movement (Kareiva and Shigesada 1983; Bartumeus et al. 2005, 2008). The CRW model combines a distribution of move lengths with a non-uniform angular distribution of turning angles. We assume a fixed time interval Δt (Hutchinson and Waser 2007) which when multiplied by an individual's mate search rate q (or target movement rate q_t) determines a move length of that individual (we set $\Delta t = 0.01$ in simulations). The angular distribution of turning angles (i.e., relative angles between two successive movement directions) is usually symmetric and peaked around zero, which introduces a directional persistence or degree of correlation in the random walk. We choose a wrapped Cauchy distribution (WCD) of turning angles, in which directional persistence is controlled by a shape parameter ρ (Bartumeus et al. 2005). Whereas $\rho = 0$ gives a uniform distribution with no correlation between successive movement directions, $\rho = 1$ represents full correlation and straight search (Bartumeus et al. 2005). Several examples of the WCD are provided in Fig. 1a. Clearly, the mean displacement of an individual during the mating season of length ϕ increases with increasing the parameter ρ which we refer to as the search straightness from here on (Fig. 1b).

Specific mating scenarios that we consider in this article are summarized in Table 1. Naturally, we start with the scenario most commonly used in the literature: all individuals of each sex are the same and males have an unlimited mating potential, meaning that the density of males available to mating does not change during the mating season. The other scenarios then in one way or another deviate from this baseline scenario. The particular deviations we adopt appear to represent the most simple and likely also quite common mating-related characteristics that one may think of, and this is exactly why we select them here. Two scenarios consider limitations in the male

Fig. 1 **a** A wrapped Cauchy distribution for different values of ρ . For $\rho = 1$, corresponding to straight search, the distribution has a singular peak at zero angle. **b** The mean displacement during the mating season for different values of ρ ; mean \pm one standard deviation over 160 searchers are given. All searchers move at the rate $q = 3$ for the mating season of length $\phi = 4$



mating potential. We first define the male mating potential directly as the maximum number of matings n_m a male can accomplish within the mating season. Alternatively, the male mating potential may be limited indirectly by a need of males to enter a refractory period T upon mating. For example, following copulation, males of the gypsy moth *Lymantria dispar* typically rest for an entire day prior to mating again (Blackwood et al. 2012). In principle, the refractory period may represent time a male spends coupled with a female when mating, caring for the mated female or their offspring (mate guarding, paternal care) or time a male needs to recover and replenish resources (e.g., nuptial gift or simply energy) to be ready for another mating. In this way, the refractory time is somewhat akin to the time predators need to handle its prey (Jeschke et al. 2002). We then assume that the searchers may learn to mate more effectively as a result of previous encounters with their targets, a scenario that we are not aware of from the literature. Since no two individuals are exactly the same, in the final scenario we allow for heterogeneity among searchers in the two constituent quantities of each movement step: the mate search rate q and the search straightness ρ .

Clearly, there are many other drivers of mating dynamics, including protandry (Robinet et al. 2007) and patchiness in individual distribution (Shaw and Kokko 2014), and actually any combination of those and the ones we consider can be imagined. We reiterate that we select here some of the scenarios that likely represent the most simple and widespread mating-related deviations from the commonly considered, yet idealized baseline scenario. For each mating

scenario, we examine the probability that a female mates within the mating season, depending on male and female densities, since this relationship helps reveal any possible mate-finding Allee effect in mating dynamics (Dennis 1989; Boukal and Berec 2002; Shaw et al. 2018). In line with our definition of the mate-finding Allee effect this means that at low densities, increasing male and female densities by the same factor should lead to an increase in the female mating probability. To assess variability in the proportion of females that succeed to mate, we replicate each scenario 100 times. When consideration of either males or females as the searching sex gives the same results, results only for the case of male searchers are presented.

Also, we consider some evolutionary scenarios, following a constant population composed of M males and F females over n_g generations. This may represent a situation where the offspring production is always large enough and the excess offspring die due to density dependence, a common assumption in eco-genetic models (Howard and Lively 2003; Pound et al. 2004). At the end of each generation, all adults die yet the search strategies of the successfully mated searchers are stored. The new generation of searchers is then created such that each searcher is assigned a search strategy (the mate search rate q or the search straightness ρ) equally from those successfully mated searchers. Mutations in the search strategies are allowed such that small deviations from the assigned values of q or ρ occur with a low probability p_m , following a normal distribution with zero mean and given variance σ_m^2 . If the search rate or search straightness are to become negative, they are set to 0. If ρ is to become

Table 1 Mating scenarios we consider in this paper

Number	Label	Short description
1	Baseline	Unlimited male polygyny, most common in theory
2	Limited	Finite male mating potential
3	Refractory	Refractory period of males after each mating
4	Learning	Searchers learn to mate more efficiently
5	Heterogeneity	Individual heterogeneity in movement steps

larger than 1 it is set to 1. We track mean and variance of the distribution of q or ρ over the searchers that succeed to mate, and replicate each evolutionary scenario 10 times.

Faster search requires more resources that could otherwise be used elsewhere. Therefore, in some evolutionary scenarios, the mate search rate q is traded off with another life history trait. There are several well-documented examples of such trade-offs. For example, faster searchers may have reduced reproductive capacity (Zera and Denno 1997). Here we assume that faster searchers have reduced endurance (Levitan 2000). In particular, as the mating season proceeds the mate search rate q deteriorates. We consider a sigmoid drop in the mate search rate with time t , using the formula

$$q(t) = q_0 \frac{a^k}{a^k + t^k}, \quad k > 1. \tag{6}$$

Here, q_0 is the mate search rate at the beginning of the mating season, a is time at which the mate search rate drops to half its initial value, and $k > 1$ is the degree of sigmoidity. If a is a searcher’s characteristic that is negatively related to its initial mate search rate q_0 (i.e., if the mate search rate deteriorates faster in initially faster searchers) then initially faster searchers may turn out to be less mobile in a later part of the mating season. We assume an inversely proportional relationship $a = \phi\mu_q/q_0$ for a population mean of q equal to μ_q . This implies that individuals with the initial mate search rate $q_0 = \mu_q$ have $q = q_0/2$ at $t = \phi$, that is, at the end of the mating season. When k is low the decrease in q is relatively steady. On the other hand, for large enough k , q stays close to q_0 for some time, but quickly falls to almost zero around time $t = a$. Hence, large values of k may also model a situation when individuals die during the mating season such that those with larger q_0 die sooner.

Results

Mating dynamics

Scenario 1: Baseline Let all individuals of each sex be identical and males have an unlimited mating potential, so that no mating removes males from the pool of available mates. Let there be F sedentary females and M searching males such that by time t each male accomplishes searching an area $A(t)$. If females are randomly positioned over the habitat of area H^2 , then the probability that a female mates by time t is

$$P(t; M) = 1 - \left(1 - \frac{A(t)}{H^2}\right)^M = 1 - \left(1 - \frac{A(t)}{H^2}\right)^{mH^2} \approx 1 - \exp(-A(t)m) =: P(t; m), \tag{7}$$

where $m = M/H^2$ is male density and the approximation holds for H^2 large enough relative to $A(t)$.

Disregarding for a moment female removal due to successful mating, the mean number of encounters a female makes with males in a time interval since t to $t + dt$ is $[A(t + dt) - A(t)]m$. Hence, the female’s encounter rate with males is

$$\lim_{dt \rightarrow 0} \frac{[A(t + dt) - A(t)]m}{dt} = A'(t)m, \tag{8}$$

where $A'(t)$ denotes derivative of $A(t)$. Most published encounter models assume that $A(t) = \beta t$ for a positive constant β , meaning that the searchers scan a new area β each time unit (Hutchinson and Waser 2007). The female’s encounter rate then equals βm . As a consequence, the rate at which females mate equals $\beta m f$ and follows the mass action law. In addition, $P(t; m) = 1 - \exp(-\beta m t)$ and the encounter process is a homogeneous Poisson process. A straightforward example here is a situation where the searchers are moving independently at a constant rate q along straight trajectories ($\rho = 1$) (Hutchinson and Waser 2007; Snyder et al. 2017). For this situation, we have $\beta = 2\delta q$ and the probability that a female mates (i.e., meets at least one male) during the mating season of length ϕ is

$$P(\phi; m) = 1 - \exp(-2\delta q m \phi). \tag{9}$$

The female mating probability (9) is independent of female density and increases with male density m . Therefore, this scenario implies a mate-finding Allee effect. Equation 9 also appears as a solution of an analytical model of seasonal mating dynamics. With $\beta m f$ as the rate at which females mate, the appropriate analytical model of seasonal mating dynamics is (see also Appendix A)

$$\begin{aligned} \frac{dm}{dt} &= 0, \\ \frac{df}{dt} &= -\beta m f. \end{aligned} \tag{10}$$

Since due to the unlimited male mating potential the male density m stays constant, the density of unmated females declines exponentially as $f(t) = f_0 \exp(-\beta m t)$ for an initial female density f_0 . The proportion of females mated at the end of the mating season of length ϕ thus is

$$P(\phi; m) = 1 - \exp(-\beta m \phi). \tag{11}$$

Assuming straight search ($\rho = 1$), our individual-based simulations confirm that the female mating probability is independent of female density and follows the theoretical prediction (9) (Fig. 2a). The female densities 0.02, 0.08, and 0.19 selected for this and all the other scenarios that follow correspond to the respective female mating probabilities 0.2, 0.6, and 0.9 under the baseline scenario.

While individuals searching at a constant rate q always scan a constant area $2\delta q$ per unit time, when search trajectories are not straight the areas searched in any two subsequent time steps overlap. Moreover, this overlap

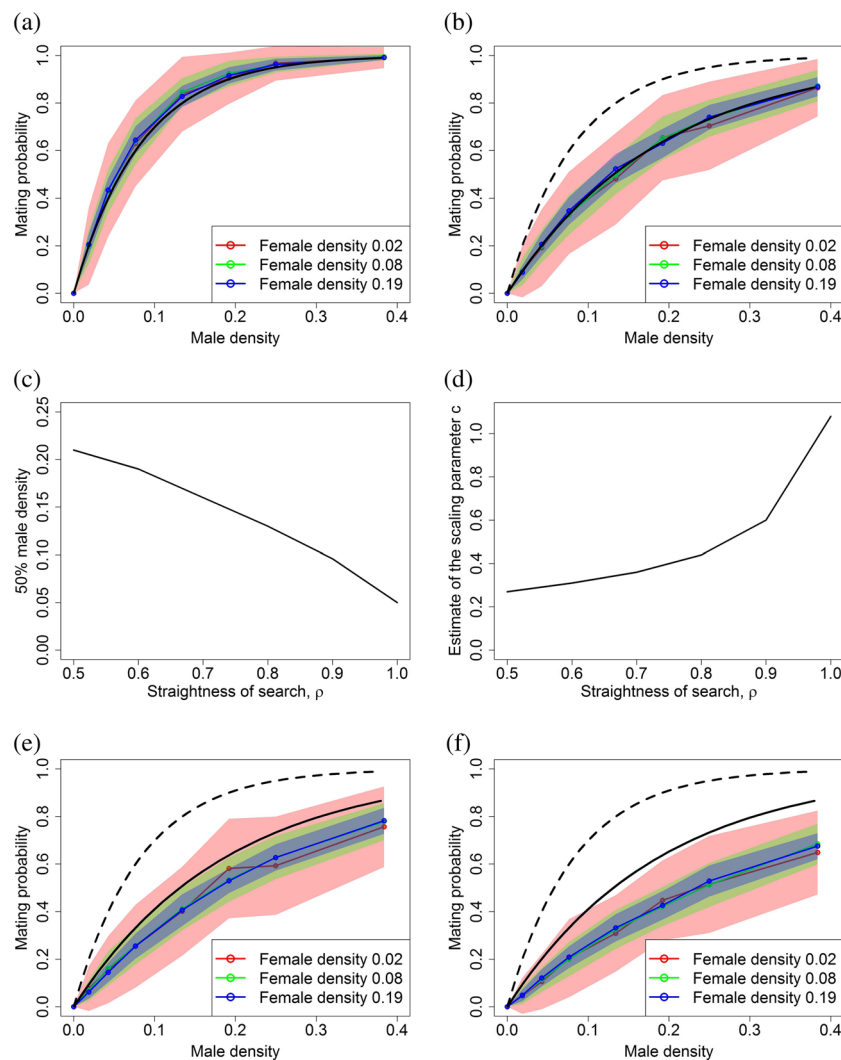


Fig. 2 The baseline scenario, with males as the searching sex. **a** Female mating probability with straight search ($\rho = 1$), **b** female mating probability for search with $\rho = 0.8$, **c** male density at which 50% females mate as a function of the search straightness ρ , **d** estimate of the factor c scaling the area searched per unit time as a function of the search straightness ρ . Common parameters: mate detection distance $\delta = 0.5$, mate search rate $q = 3$, mating season length $\phi = 4$. **e–f** Effect of changing ϕ and q such that their product stays the same ($=12$) as in panel **b**, with $\rho = 0.8$ and $\delta = 0.5$; **e** $\phi = 6$, $q = 2$; **f**

$\phi = 12$, $q = 1$. The solid black lines in panels **a**, **b**, **e**, **f** are plots of the form $1 - \exp(-2\delta q m \phi c)$, where m is male density and $c = 1$ in panel **(a)** and $c = 0.44$ in panels **(b, e, f)**. The dashed black lines in panels **a**, **e**, **f** are identical to the solid line in panel **a**, to indicate deviations from when search is straight ($\rho = 1$). The shaded regions in panels **(a, b, e, f)** and in all figures that follow correspond to \pm one standard deviation of the female mating probability, calculated from simulating 100 mating seasons. When females are the searchers and males are sedentary and randomly positioned over the habitat the results are the same

depends on an angle between two successive movement directions, with the angle following the WCD and hence determined by the search straightness $\rho < 1$. As a consequence, the new area searched per movement step is lower than $2\delta q \Delta t$ (and moreover varies from one time step to another). As a result (which actually holds for any other scenario that follows), for any male density m the female mating probability declines with decreasing the search straightness ρ (Fig. 2b–c).

It is unclear whether any of the female mating probability curves for $\rho < 1$ can be approximated by the formula (9), or rather by its straightforward modification $1 -$

$\exp(-2\delta q m \phi c)$, with a scaling factor $0 < c < 1$ that may depend on all of the search-area-affecting quantities: search straightness ρ , mate detection distance δ , mate search rate q , and mating season length ϕ . Fitting this function to data combining the results obtained for all three examined female densities (like all data in panels a or b of Fig. 2) demonstrates that the scaling factor c declines with decreasing ρ , and declines in a non-linear way (Fig. 2d). Moreover, exploring an effect of varying the parameters q and ϕ such that their product is fixed, lower female mating probabilities are observed for lower mate search rates or longer mating seasons (Fig. 2e–f). All this suggests

that although the formula $P(\phi; m) = 1 - \exp(-\beta m\phi)$ apparently provides a reasonable and easy fit of the observed simulation results under the baseline scenario, the parameter $\beta = 2\delta q c$ is not any simple function of $\rho, \delta, q,$ and ϕ .

We now explore how the female mating probability changes when some of the assumptions behind the baseline scenario are not met. Assuming that the female’s encounter rate with males equals βm for a positive constant β , we also derive for each scenario an analytical model of seasonal mating dynamics that allows tracking densities of mated females over time (Appendix A).

Scenario 2: Limited Males often have a seriously limited mating potential. Therefore, we examine an effect of limited male polygyny, assuming that males can mate once or twice; note that mating once corresponds to male monogamy. When males have a limited mating potential, the female mating probability depends on the female density, too. In particular, the mating probability declines as the female density grows, since females compete for males that are the limiting resource (Fig. 3). This dependence is strongest when males are monogamous ($n_m = 1$) and the search

is straight ($\rho = 1$; Fig. 3a), but quickly weakens as male mating potential increases (Fig. 3b) or the search straightness ρ declines (Fig. 3c).

Since the female mating probability is an increasing function of male and female densities kept at a constant ratio (Fig. 3d), a mate-finding Allee effect occurs also here. In Appendix A, we develop an analytical model of seasonal mating dynamics when males have a limited mating potential and the male-female encounters follow the mass action law. For the case of male monogamy ($n_m = 1$) that model can be solved analytically and is a good approximation of our individual-based simulations when the search is straight ($\rho = 1$; Fig. 3d).

Scenario 3: Refractory Upon mating, males often need some time before resuming mate search. We assume there is a refractory period T such that upon mating, males are for this period temporarily unavailable to females and stop moving. Any finite value of T actually limits the number of matings each male may have within the mating season. Hence, higher refractory periods imply lower female mating probabilities (Fig. 4). Actually, as T goes from zero to the

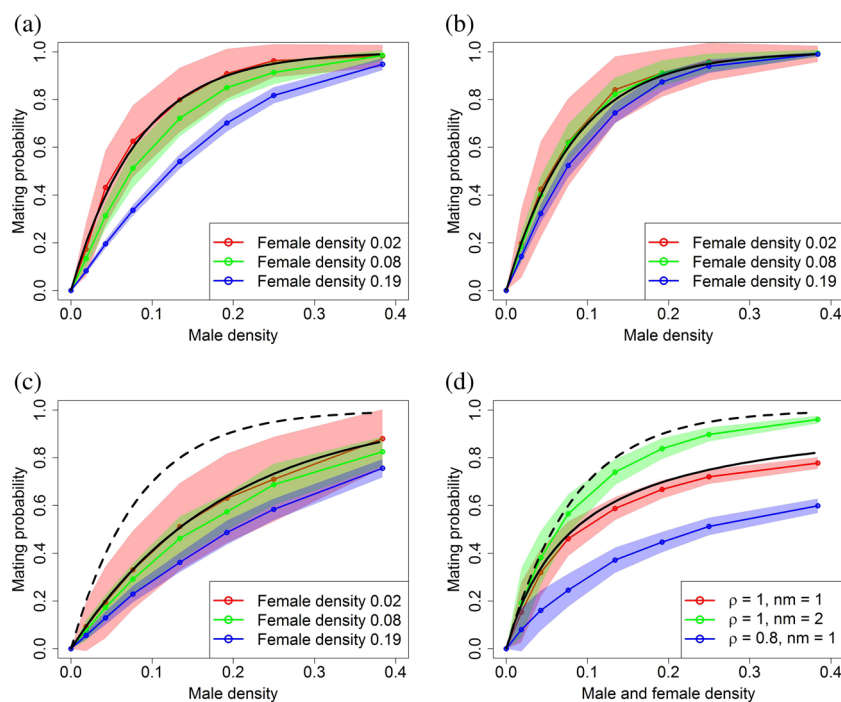
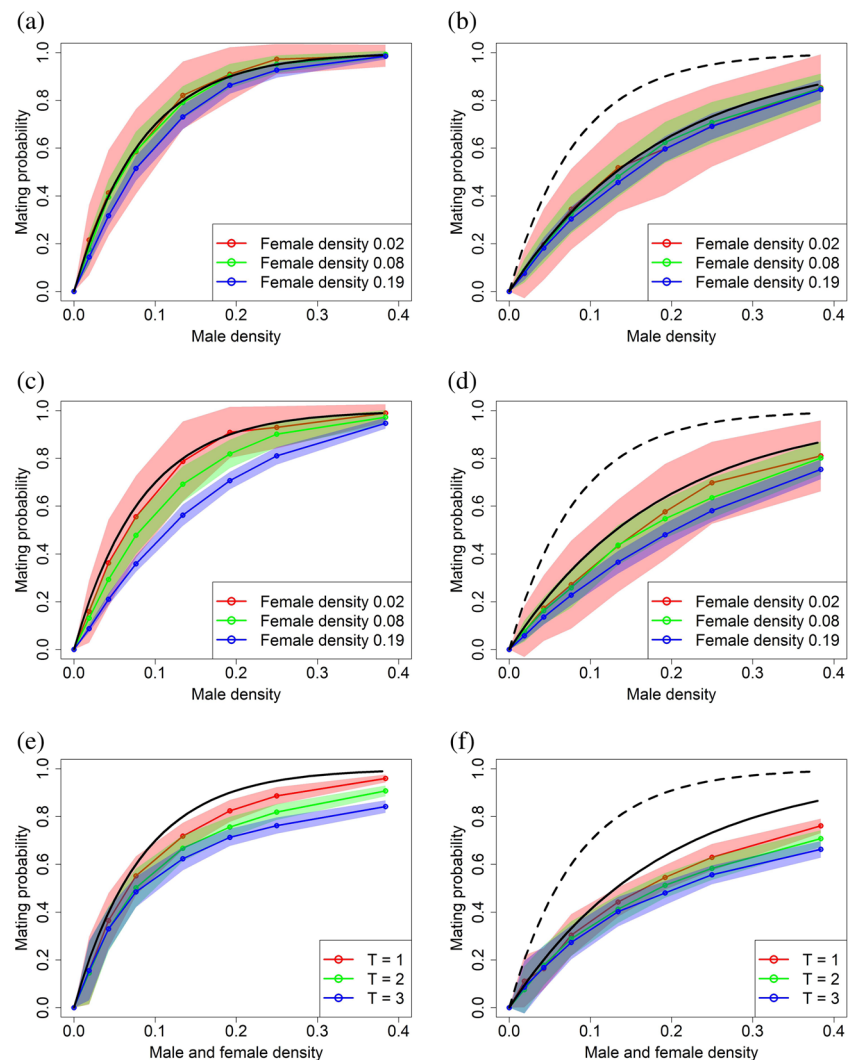


Fig. 3 The limited scenario, with males as the searching sex. **a** Female mating probability with straight search ($\rho = 1$) and up to one mating allowed for each male ($n_m = 1$), **b** female mating probability with straight search ($\rho = 1$) and up to two matings allowed for each male ($n_m = 2$), **c** less straight search with $\rho = 0.8$ and $n_m = 1$, **d** initial male and female densities are varying and equal, and the female mating probability as depending on the search straightness (ρ) and number of matings allowed for each male (n_m) is plotted. Other parameters and legend are as in Fig. 2. The solid black lines are plots of the form

$1 - \exp(-2\delta q m\phi c)$, where m is male density and $c = 1$ in panels (a, b) and $c = 0.44$ in panel (c). The dashed black line in panel c is identical to the solid lines in panels a, b, to indicate deviations from when search is straight ($\rho = 1$). Panel d the solid black line is the theoretical prediction of the form $2\delta q m\phi / (1 + 2\delta q m\phi)$, where m is male (= female) density (see model (15) in Appendix A); the dashed black line is a plot of the form $1 - \exp(-2\delta q m\phi)$, where m is male (= female) density. When females are the searchers and males are sedentary and randomly positioned over the habitat the results are the same

Fig. 4 The refractory scenario, with males as the searching sex. Left column: $\rho = 1$. Right column: $\rho = 0.8$. Top row: refractory period $T = 1$. Middle row: refractory period $T = 3$. Other parameters and legend are as in Fig. 2. The solid black lines are plots of the form $1 - \exp(-2\delta q m \phi c)$, where m is male density and $c = 1$ ($c = 0.44$) in the left (right) column. The dashed black lines in panels (b, d, f) are identical to the solid lines in panels (a, c, e), to indicate deviations from when search is straight ($\rho = 1$). When females are the searchers and males are sedentary and randomly positioned over the habitat the results are the same



mating season length ϕ we effectively have a transition from unlimited male polygyny (scenario 1) to male monogamy ($n_m = 1$ in scenario 2). As a consequence, as T approaches ϕ , the female mating probability becomes more and more female-density-dependent (Fig. 4). The actual difference between the refractory and limited scenarios lies in that here the number of matings each male may have is limited from above by ϕ/T , but the actual number can be lower. This is confirmed in Appendix A where the analytical model of seasonal mating dynamics corresponding to the refractory scenario with $T = 2$ gives female mating probabilities slightly but consistently lower than the model for the limited scenario with $n_m = 2$. Again, since the female mating probability is an increasing function of male and female densities kept at a constant ratio (Fig. 4e–f), a mate-finding Allee effect occurs also here.

Scenario 4: Learning A feature common to all of the above scenarios is that the female mating probability increases

with the male and female densities in a decelerating way. In predator-prey systems, a commonly found Holling type II functional response quantifying the rate at which a predator consumes prey as a function of prey density has an analogous form (Jeschke et al. 2002). Likewise, the Michaelis-Menten kinetics producing a decelerating shape of the reaction rate as a function of substrate concentration is one of the fundamental models of enzyme kinetics (Klipp et al. 2005). However, a sigmoid response function is also known from these fields. In particular, a sigmoid Holling type III functional response is known to emerge from the assumption that predators learn to catch prey more effectively from their previous attempts (Real 1977). Similarly, in cooperative enzyme kinetics, binding of a substrate to an enzyme may increase binding affinity of another substrate to the same enzyme which produces a sigmoid reaction rate as a function of substrate concentration (Klipp et al. 2005). However, we know neither of any data that would support a sigmoid form of the female

mating probability, nor of any model of mating dynamics that would produce such a form.

By analogy with the latter functional forms and their underlying mechanisms, we assume that males are able of some learning from their previous mating attempts. In particular, males are initially inexperienced and become experienced only after they encounter n_t females. Moreover, inexperienced males mate with a female upon encounter with a probability p_0 , while experienced males mate with an enhanced probability $p_1 > p_0$ (more generally, we may think of the probability of mating upon encounter as a non-decreasing function of the number of females already encountered). To see whether a sigmoid form occurs at all and to allow for comparison with the other scenarios we consider, we examine the most extreme case with $p_0 = 0$ and $p_1 = 1$.

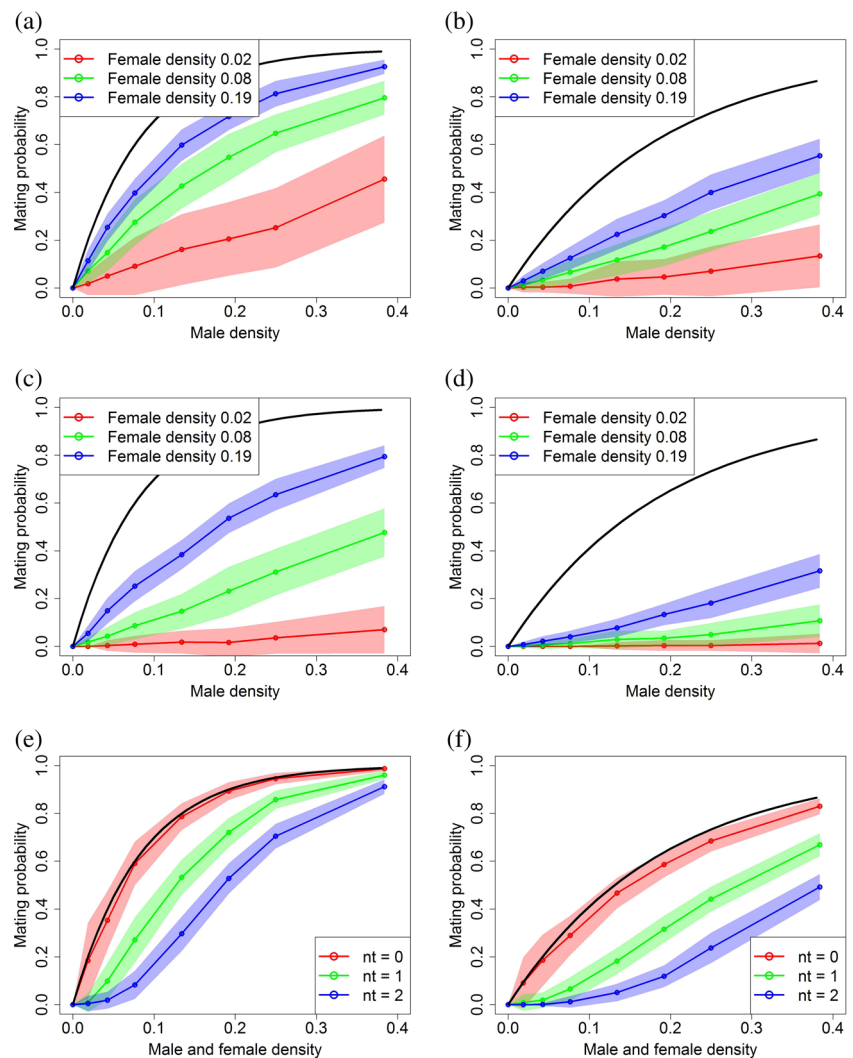
An analytical model (18) we develop in Appendix A for this scenario suggests that a sigmoid female mating probability relationship to male and female densities may

indeed occur (Fig. 12 in Appendix A), and our individual-based simulations confirm that. While no clear relationship results when female density is kept constant and only male density varies (Fig. 5a–d), a sigmoid relationship appears when the ratio of male and female densities stays constant (Fig. 5e–f). Here, the relationship is the more sigmoid the more encounters with females are needed for males to become experienced (Fig. 5e–f) and also the larger is difference between the probabilities p_0 and p_1 (results not shown).

In predator-prey systems, a sigmoid Holling type III functional response can also arise if prey can utilize refuge sites with lessened risk of predation or predators forage optimally on several prey types (Křivan 2013). We leave for “Discussion” the question of whether a similar analogy can be imagined also for mating systems.

Scenario 5: Heterogeneity Real searchers are certainly heterogeneous in many ways. Here, we return to the baseline

Fig. 5 The learning scenario, with males as the searching sex. Males have unlimited mating potential. Left column: $\rho = 1$. Right column: $\rho = 0.8$. Top row: one encounter with a female is needed for a male to become experienced ($n_t = 1$). Middle row: two encounters with females are needed for a male to become experienced ($n_t = 2$). Common parameters: $p_0 = 0$ (inexperienced males do not mate), $p_1 = 1$ (experienced males mate with certainty). Other parameters and legend are as in Fig. 2. The solid black lines are plots of the form $1 - \exp(-2\delta q m \phi c)$, where m is male density and $c = 1$ ($c = 0.44$) in the left (right) column. When females are the searchers and males are sedentary and randomly positioned over the habitat the results are the same



scenario and assume there is inter-individual variability in the movement step characteristics: the mate search rate q or the search straightness ρ . We initially assume q to be Gamma-distributed, with mean μ_q and variance $\text{var } q$. Surprisingly, variance in the female mating probability does not appear to respond to changes in variance in the mate search rate, at least within the inspected range (Fig. 6). On the other hand, the mean female mating probability differs for when males or females are the searching sex and is higher when males are the searchers (Fig. 6). Moreover, this difference increases with increasing variance $\text{var } q$ in the mate search rate q (Fig. 6). We discuss on why this happens in the “Discussion” section.

Alternatively, we assume that the mate search rate q is constant but allow the search straightness ρ to vary among the individual searchers, using a Beta distribution to describe variability in ρ (Fig. 7a). As variability in the search straightness grows there is a tendency for a higher proportion of individuals to have ρ closer to 1 (Fig. 7a).

The associated simulation results are then in line with this: the female mating probability increases with increasing variance in ρ (Fig. 7b–d).

Evolution

Regardless of the mating and evolutionary scenario (males or females searching, mate search rate q evolving or not, mate search costs present or not, any male mating potential), evolution takes the search straightness ρ sooner or later to the value of 1, i.e., search eventually becomes straight (Fig. 8a). In reality, even when information about targets is poor or lacking, search is rarely straight, with the turning angle distribution determined by fine-grained spatial inhomogeneities or perceived risk of predation (Bartumeus et al. 2008). Nevertheless, given an upper bound on the search straightness ρ , evolution in our model takes all individuals to this upper bound (with some small variation around it due to mutations and stochasticity). As we already

Fig. 6 The heterogeneity scenario. Males are polygynous. **a–b** Gamma distributions of the mate search rate q with $\mu_q = 3$ and **a** $\text{var } q = 2$, and **b** $\text{var } q = 5$. **c–d** Males are the searching sex. **e–f** Females are the searching sex. **c, e** $\text{var } q = 2$. **d, f** $\text{var } q = 5$. Solid black lines in panels (**c–d**) and dashed black lines in panels (**e–f**) are male approximations (22). Solid black lines in panels (**e–f**) and dashed black lines in panels (**c–d**) are female approximations (23). Other parameters and legend are as in Fig. 2; $\rho = 0.9$

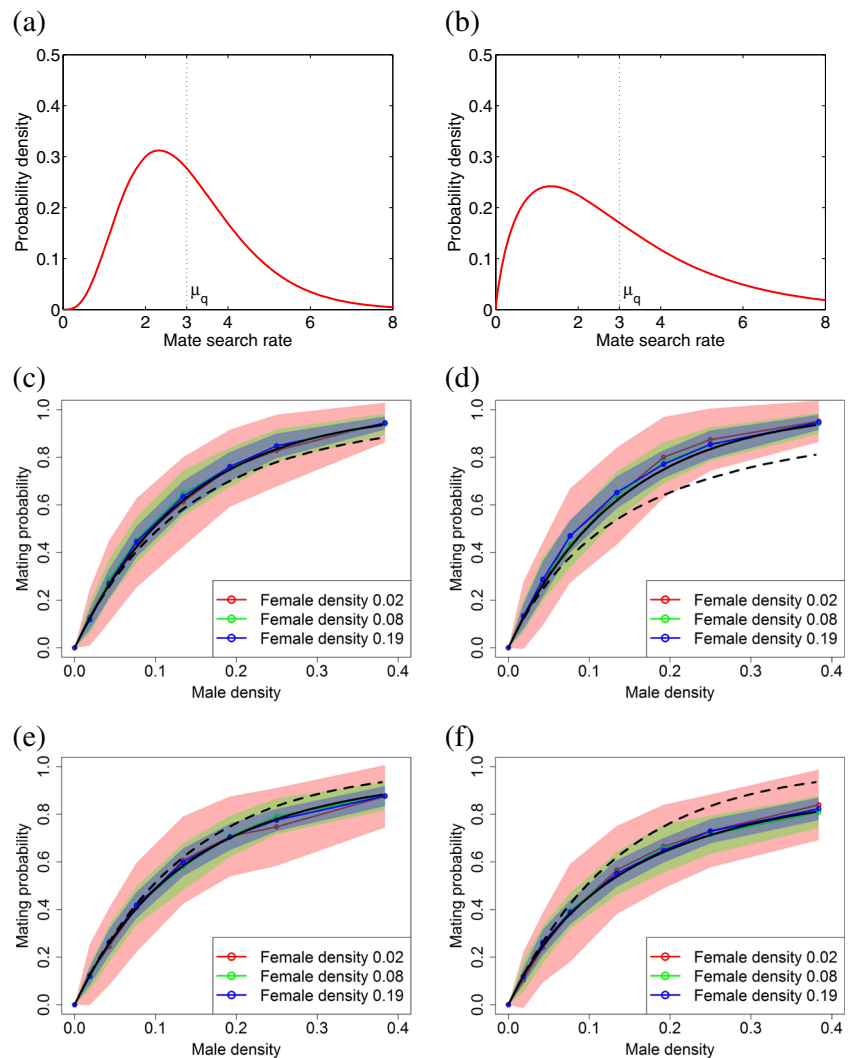
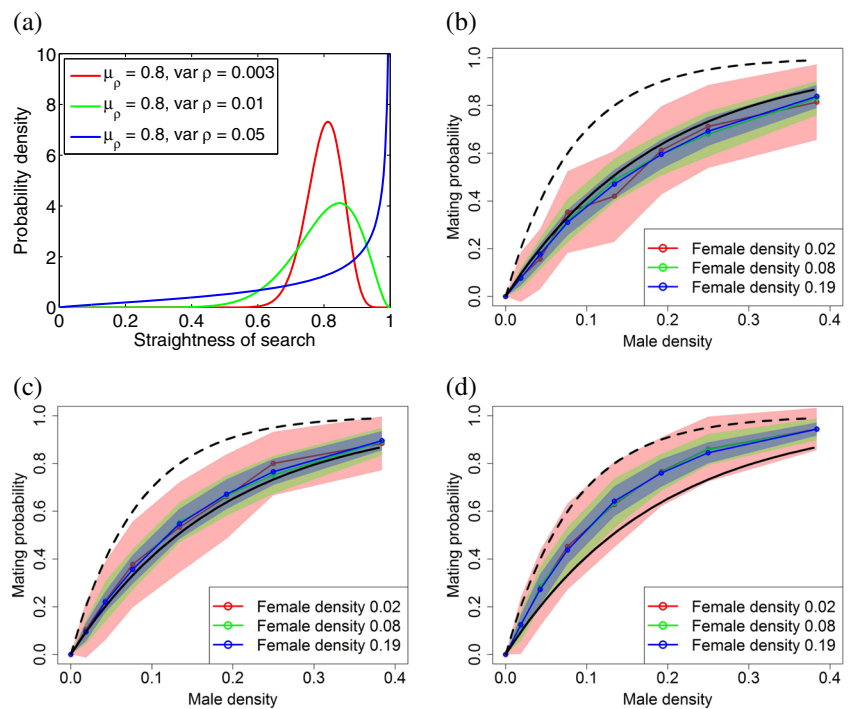


Fig. 7 Effect of individual heterogeneity in the straightness of search ρ , with males as the searching sex. Males are polygynous. Panel **a** shows how the Beta distribution used to generate individual values of ρ looks like for the selected parameter values. **b–d** Female mating probability under $\mu_\rho = 0.8$ and **a** $\text{var } \rho = 0.003$, **b** $\text{var } \rho = 0.01$, and **c** $\text{var } \rho = 0.05$. Other parameters and legend are as in Fig. 2. The solid and dashed lines correspond to the baseline model with $\rho = 0.8$ (i.e. $c = 0.44$) and $\rho = 1$ (i.e. $c = 1$), respectively. When females are the searching sex an increase in the female mating probability with increasing ρ is slower (results not shown)



know, all else being equal, lower values of ρ generally result in lower female mating probabilities, because of smaller new areas searched through per time step, and this is most likely the reason for evolution to reach as highest value of ρ as possible. In the following, we therefore focus just on evolution of the mate search rate q , for males or females searching, for population densities $m = f = 0.1$ or $m = f = 0.2$, for two levels of mate search costs ($k = 4$ and $k = 20$ in the formula (6)), and for the search straightness $\rho = 0.9$ (as we emphasize earlier, search in nature is rarely straight, but other values of ρ produced analogous results).

When no costs are imposed on mate search then the mate search rate q evolves to ever higher values in runaway

selection which in turn means ever higher female mating probability (Fig. 9). Interestingly, while there is no effect of density when females search, the mate search rate evolves faster at higher density when males are the searching sex (Fig. 9). The presence of the mate search costs, in the form of the initially higher mate search rates deteriorating faster as mating season proceeds, prevents runaway selection to ever higher values of q (Figs. 10 and 11). Density appears to play a role when any sex is searching: larger values of q evolve in denser populations (Figs. 10 and 11). Moreover, the difference in q between populations of higher and lower densities is larger when males are the searching sex and when the mate search costs are larger (Figs. 10 and 11).

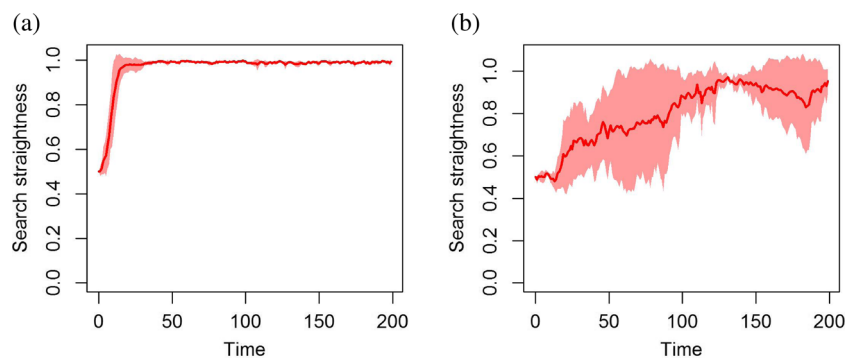
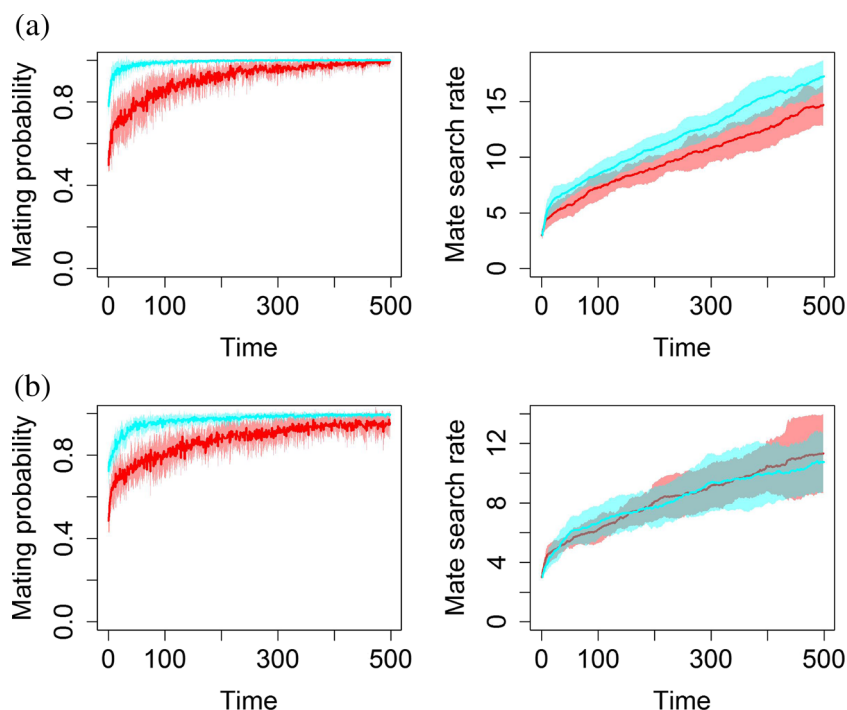


Fig. 8 Evolution of the search straightness ρ . Males are the searching sex and have an unlimited mating potential. **a** Sedentary females. **b** Females moving at rate $q_t = 6$ and having the movement straightness

$\rho_t = 0.9$. Males and females are kept at densities $m = f = 0.2$ (blue; $M = F = 80$). Parameters: $q = 3$, $\delta = 0.5$, $\phi = 4$, $\text{var } \rho = 0.01$, mutation probability $p_m = 0.05$, mutation variance $\sigma_m^2 = 0.2$

Fig. 9 Evolution of the mate search rate q when there are no costs on mate search. **a** Males are the searching sex. **b** Females are the searching sex. Males are polygynous. Males and females are kept at densities $m = f = 0.1$ (red; $M = F = 40$) or $m = f = 0.2$ (blue; $M = F = 80$). Parameters: $\delta = 0.5$, $\phi = 4$, $\rho = 0.9$, $\text{var } q = 1$, mutation probability $p_m = 0.05$, mutation variance $\sigma_m^2 = 0.5$



Robustness of simulation results

We have tested for robustness of our simulation results in three different ways. First, throughout the “Results” section, we have compared our simulation results to those produced by the analytical models developed in Appendix A and found qualitative and also reasonable quantitative agreement, provided the appropriate factors were used

to scale non-straight search scenarios. Here, we discuss the effects of reflecting rather than periodic boundary conditions and of moving rather than sedentary targets.

Results with reflecting boundary conditions stay qualitatively the same compared with those due to periodic boundary conditions and there is also close quantitative agreement. In particular, the female mating probabilities under the reflecting boundary conditions are consistently

Fig. 10 Evolution of the mate search rate q when costs on mate search are relatively low. **a** Males are the searching sex. **b** Females are the searching sex. Males are polygynous. Males and females are kept at densities $m = f = 0.1$ (red; $M = F = 40$) or $m = f = 0.2$ (blue; $M = F = 80$). Parameters: $\delta = 0.5$, $\phi = 4$, $\rho = 0.9$, $\text{var } q = 1$, $a = \phi \mu_q / q_0$, $k = 4$, mutation probability $p_m = 0.05$, mutation variance $\sigma_m^2 = 0.5$

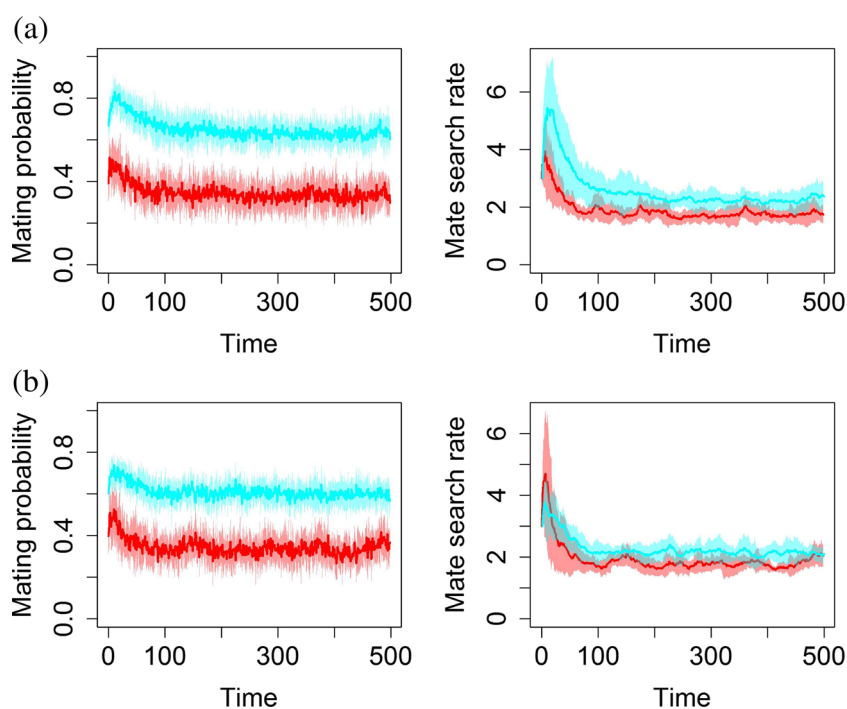
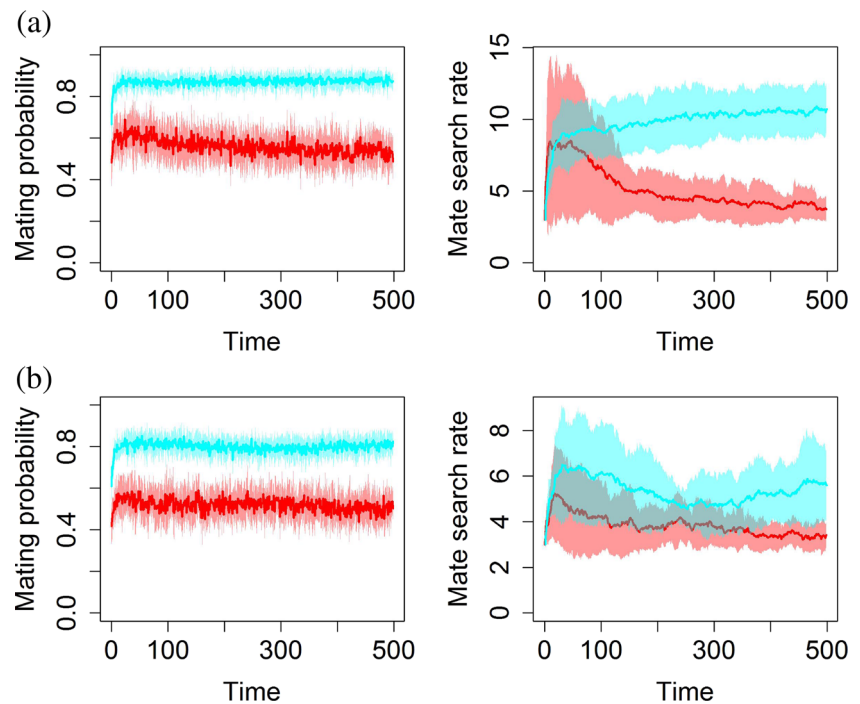


Fig. 11 Evolution of the mate search rate q when costs on mate search are relatively high. **a** Males are the searching sex. **b** Females are the searching sex. Males are polygynous. Males and females are kept at densities $m = f = 0.1$ (red; $M = F = 40$) or $m = f = 0.2$ (blue; $M = F = 80$). Parameters: $\delta = 0.5$, $\phi = 4$, $\rho = 0.9$, $\text{var } q = 1$, $a = \phi\mu_q/q_0$, $k = 20$, mutation probability $p_m = 0.05$, mutation variance $\sigma_m^2 = 0.5$



slightly lower than under the periodic ones (Figs. S1 and S2 in Appendix S1 in Electronic Supplementary Material). This is apparently because in the former case it takes some time to individuals getting close to the boundary to rebound back into the habitat.

In non-evolutionary scenarios, moving targets increase the chance of the searchers to meet them and the female mating probabilities are thus consistently higher than when targets are sedentary (Figs. S3 and S4 in Appendix S2 in Electronic Supplementary Material). Indeed, larger areas than only the newly searched ones are relevant here, as targets may move to the areas already searched. Unfortunately, there is no closed form relationship for the encounter rate when both the searchers and the targets move, even in for the baseline scenario (Hutchinson and Waser 2007).

With moving targets, evolution does not always lead to the straight search. In particular, when targets move at higher rates and population densities are not extremely low, the female mating probability is close to 1. In such cases, the selective pressure on straighter search is lower. However, since we do not consider any costs related to search straightness then unless the targets move very quickly (and hence much faster than the searchers), it is advantageous to move along straighter trajectories. In any case, with increasing the movement rate of targets, evolution to higher values of ρ is slower and the attained evolutionary equilibrium need to reach the value of 1 (Fig. 8b). Moreover, qualitative results of evolution of the mate search rate q stay unchanged when the targets move. Quantitatively, as one

would perhaps expect, lower values of the mate search rate q evolve (results not shown).

Discussion

One of the most important elements of sex-structured population models is a description of mating rate or number of pairs that are formed during a time period (Caswell and Weeks 1986; Dennis 1989; Lindström and Kokko 1998; Boukal and Bercé 2002; Iannelli et al. 2005; Miller and Inouye 2011). A number of models of mating have been proposed, adopting diverse assumptions on the mating process that include a limited male mating potential (Wells et al. 1990), changes in searching efficiency during the mating season (Bercé et al. 2018), or inter-individual heterogeneity in mate search features such as the search rate (Dennis 1989) or the search trajectory (Bartumeus et al. 2008). Mate-finding Allee effects, acknowledging that low population densities are inhibitors of mating, have become a standard output of such models (Dennis 1989; Boukal and Bercé 2002; Courchamp et al. 2008; Gascoigne et al. 2009). Here, we explore and compare the respective influence of many of the underlying determinants of mating success, trying to unravel their commonalities and differences, and how they make a species vulnerable to mate-finding Allee effects. Through developing an individual-based model of mating dynamics that explicitly accounted for spatial search of one sex for the other, we quantified the probability with which a female mated during its mating season, depending

on male and female densities and under a number of relevant mating scenarios. We found that the proportion of females that successfully mated during the mating season increased with male and female densities (hence observing a mate-finding Allee effect), in a decelerating or sigmoid way, that mating could be most efficient at either low or high female densities, that mate search trajectories evolved to be as straight as possible when targets were sedentary, and that the mate search rate underwent density-dependent selection.

Many studies that modeled mating dynamics used an analytical approach. This approach, based on ordinary differential equations and exemplified by the models we develop in Appendix A, assumes that the rate at which males and females meet follows the mass action law. Moreover, depending on the modeled mating characteristics it considers transitions of different types of males and females between various behavioral classes. Thus, males may be always ready to mate in a system with unlimited male polygyny (Dennis 1989), males and females cease to mate after the first mating in monogamous systems (Wells et al. 1990; Veit and Lewis 1996), males may be temporarily or permanently unavailable upon mating (Molnár et al. 2008, this model is a combination of our limited and refractory scenarios), females may enter a gestation period (Ashih and Wilson 2001; Berec et al. 2017a), or emergence of males and females during the mating season need not be synchronized (Blackwood et al. 2012). Because of the mass action contact rate, all the implied female mating probabilities demonstrate a mate-finding Allee effect. Moreover, all increase in a decelerating way as male density or both male and female densities grow large. We use this analytical approach to compare the effects of different mating system characteristics on mating success, demonstrating that this is indeed a valid and flexible way of modeling mating dynamics (see also below).

On the other hand, an extensive literature exists on the types of movement (move length and movement angle distributions) and how encounter rate between different types of individuals are affected by these. For example, Viswanathan et al. (1999) looked for an optimal search strategy, in terms of a move length distribution, of predators that follow Lévy flight motion in search of their prey. Similarly, Bartumeus et al. (2005) examined efficiency of searchers following either Lévy or correlated random walks in locating destructive and non-destructive targets, and Bartumeus et al. (2008) explored how various turning angle distributions influenced encounter success in homogeneous vs. patchy target environments. Last but not least, Gurarie and Ovaskainen (2013) presented a framework aimed at investigating how encounter rates were affected by such properties of the encounter process as the encounter kernel, spatial distribution and birth–death dynamics of targets and whether encounters are destructive or not. All these

and many similar studies aim at providing some general predictions regarding the effects of search strategies, irrespective of a specific encounter context (e.g., mating, predation or infection). As a consequence, they leave many details of specific encounter contexts out. In this respect, they are complementary to our approach of selecting a single search strategy (or rather a family of strategies distinguished by the mate search rate q and the search straightness ρ within the correlated random walk modeled via the wrapped Cauchy distribution) and varying details of mating behavior. As a future work, it is certainly worth combining these two topics and examine optimality of mate search under a number of selected mating systems.

Gurarie and Ovaskainen (2013) found that (in the case of hard encounters) the (first) encounter rate was generally proportional to the movement rate, density of targets, and the encounter radius (see also Hutchinson and Waser 2007). Moreover, when holding these variables constant, the (first) encounter rate was found to increase with higher directional persistence of the searchers (that is, straighter movement trajectory). What we reveal in our study is that the corresponding proportionality constant (our scaling factor c) may depend on specific values of these elements, even when their product remains constant. Quantification of this proportionality constant in a scenario akin to our baseline one was attempted by Snyder et al. (2017). Using a truncated uniform distribution of movement angles they showed that this constant did not depend on directional persistence of the searcher's movement, which is in a stark contrast with one of our main results: the factor c scaling the male–female encounter rate in the baseline scenario declines in a non-linear way as the directional persistence of the searcher's movement decreases (Fig. 2d). The exact reason for this and dependence of the scaling factor on search straightness under other movement strategies such as Lévy walks is to be explored.

Intriguingly, although theoretically plausible, we know of no model or mating dynamics that would produce a sigmoid form of the female mating probability as a function of male and female densities, that is, a disproportionately low/high mating probability at low/high densities. Neither we are aware of any data that would support such a form. Except for a short note that the female mating probability cannot be sigmoid unless inter-individual heterogeneity in the area searched per unit time depends on male density (Dennis 1989), literature is silent about this issue. We have therefore attempted to bring in a possible mechanism, building on analogy with predator–prey systems in which predators learn how to catch prey (Real 1977) and with substrate–enzyme interactions in which binding of a substrate to an enzyme increases binding affinity of another substrate to the same enzyme (Klipp et al. 2005). We found that a sigmoid form of the female mating probability as a

function of male and female densities might arise when males learned to search more effectively as a result of previously unsuccessful encounters. We showed this in both the individual-based model and the analytical model, further demonstrating flexibility of the latter approach, and, more importantly, plausibility of the sigmoid form as such. Whether models of two-sex population dynamics produce different results depending on whether the female mating probability is decelerating or sigmoid with increasing male and female densities is certainly a valid query that remains to be explored.

In predator-prey systems, a sigmoid Holling type III functional response can also arise if prey can utilize refuge sites with lessened risk of predation or predators forage optimally on several prey types (Křivan 2013). Can a similar analogy be imagined also for mating systems? In predator-prey systems, there is an absolute prey density around which either prey (by exploiting refuge sites) or predators (by switching prey) modify their behavior, which in turn generates a sigmoid Holling type III functional response. As regards mating, males correspond to prey since the mate-finding Allee effect primarily arises as a response of the female mating rate to male density. To get a sigmoid female mating rate would thus mean that there is an absolute male density around which a male or female behavior changes. Since it is in the interests of both males and females to mate during the mating season, we cannot make out any specific mechanism for such a behavioral change.

Only when the mate search rate was heterogeneous among the searchers did the female mating probability differ depending on whether males or females were the searching sex. Whereas the mean female mating probability does not deviate from when searchers are homogeneous with respect to the mate search rate when males are the searching sex, a difference arises when females are the searching sex. Moreover, the mating probability is always lower when females search as opposed to when males search, and the difference increases as the variance in the mate search rate grows. The apparent reason for this difference, elaborated in Appendix A, is that contributions to the mean female mating probability by males and females differ when one or the other sex is searching. Specifically, when females are the searching sex the mean female mating probability is a mean of individual mating probabilities over all females (Eq. 19 in Appendix A). On the other hand, when males are the searching sex it is the mean of areas searched per unit time over all males that plays the role, since all females now have the same mating probability (Eq. 20 in Appendix A). This distinction has not to have been made in literature so far. Although the form (19) is not new and has been derived by Dennis (1989), he had not assign it clearly to the female search that he had supposed and had not contrasted it to the case when males are the searching sex. In any

case, the observation that under individual heterogeneity in the mate search rate the female mating probability is consistently lower when females search as opposed to when males search may add to the discussion on why male search is the more prevalent pattern in nature (McCartney et al. 2012; Fromhage et al. 2016).

Search straightness is an important mate search trait and we find that evolution always goes to maximize it. When search is straight the area newly scanned through per unit time is maximized and the chance to find a sedentary mate randomly distributed in the habitat is the highest. Conversely, the more curved is the movement trajectory, the larger is the overlap between the area searched previously and now. A valid question is what happens when the targets are not sedentary (and/or are not distributed randomly; exploration of effects of non-random target distributions is beyond the scope of this study). Consider an extreme case in which males are the searching sex and females are randomly reshuffled at each time step. Then the area searched previously and not containing any female may now contain a female. As a consequence, it is not the newly searched area per unit time that matters in this case but rather the total area searched per unit time, irrespectively of the search straightness. Hence, in this extreme case, there is no need for search straightness to change as a result of evolution. On the other hand, we do not impose any costs on the degree of search straightness. Hence, unless the targets will move very quickly, it may always be advantageous to move along straighter trajectories. Of course, as the target movement rate will increase, the returns from increasing search straightness will diminish and the evolution to straighter search will be slower, as our simulations confirm. On the other hand, if the target moves much faster than the searcher, there may be likely that the search-target roles would be switched.

The mate search rate q is subject to runaway selection to ever higher values if no costs are imposed on mate search. On the other hand, density-dependent selection occurs, with evolution at higher densities leading to higher initial mate search rates when the search rate decreases as the mating season proceeds and decreases faster in initially faster searchers (i.e., higher initial mate search rate implies lower individual endurance). This selection is stronger when males are the searching sex and when the costs are more step-like such that search effectively ceases at some time. Also, although variance in the proportion of mated females declines with increasing density, variance in the evolutionary trajectories appears to be higher at higher densities. Surprisingly, using an alternative framework to mate search rate evolution, Berec et al. (2018) observed quite opposite results. In particular, they found that even under no mate search costs evolution stabilized when females were the searching sex, that density-dependent

selection did not occur when analogous costs were applied to the searching males, and that variance in the evolutionary trajectories was lower at higher densities. Although the two studies examine the same issue, the respective models differ in many respects. It is hard to suggest why those differences arose, but we hazard to guess that an explicit spatial search and sigmoid trade-off between the initial mate search rate and search endurance considered here, versus an implicit spatial search and exponentially decaying trade-off assumed in Berec et al. (2018) might be promising candidates. In any case, a message from this is that under similar ecological and behavioral scenarios, we can get different evolutionary outcomes if the other model elements differ. In any particular evolutionary study, all elements of the adopted model should thus be specified in detail.

Although individual-based models are a powerful tool to examine how many interacting mating dynamics characteristics may influence the female mating rate, many researchers want to model two-sex (or even one-sex) population dynamics without including the level of detail required by an individual-based model. What explicit recommendations can we give based on our results? And what do our results imply for modeling two-sex dynamics? The two most commonly used “generic” formulations of the female mating rate in presence of the mate-finding Allee effect are the exponential form $1 - \exp(-\beta m)$ for a positive parameter β that has an advantage of being easily fitted to data, and the hyperbolic form $m/(\theta + m)$ for a positive parameter θ that has an appeal from a mathematical analysis perspective (Dennis 1989; Boukal and Berec 2002) but can also naturally arise under some circumstances (Dennis 1989; Berec et al. 2017a). Both these forms are decelerating as male density increases and are independent of female density.

We find that many of our scenarios result in the female mating probability curves that are concave functions of male density and are nearly independent of female density. Hence, those two “generic” formulations can be used as their phenomenological description, especially in populations models where details of mating dynamics are not of the primary interest, such as for example in a predator-prey model with a mate-finding Allee effect in predators (Terry 2015). Based on our results, we add to this a “generic” form $m^k/(\theta^k + m^k)$ that for some $k > 1$ may be thought of as a phenomenological description of scenarios giving rise to sigmoid female mating rates. Ability of all these functions to fit results of many of our mating scenarios thus lends them a credit for continuing use in many strategic population models, including the sexually unstructured ones in which an assumption that males and females share equal life histories is made. Indeed, mating dynamics needs to be considered also in such cases or if the population is composed just of simultaneous hermaphrodites.

If a more detailed, mechanistic mating model is required then a continuous-time model of seasonal mating dynamics following philosophy outlined in Appendix A can be used. Parameters driving an inspected mating behavior are then directly available, including the rate at which males and female encounter and mate. These analytical models can also easily be generalized to situations where the processes of mating, reproduction and mortality are supposed to mix, as we exemplify in Appendix B, further extending their utility for modeling two-sex population dynamics. What we emphasize here is that the parameter scaling the mass action mating rate in these models (named β in our case) is a complex function of search strategy: it increases with increasing mate search rate but declines with decreasing search straightness. Sensitivity of results of these analytical models to this parameter should thus always be examined. Needless to say, individual-based models provide the highest flexibility in describing mating dynamics, but suffer from a couple of well-known issues, including often long computation time, necessity to run multiple simulation replicates to unravel expected dynamics, need to set values and explore sensitivity to many parameters, and lack of general insight into model behavior. In any case, we believe that the current study provides a useful insight into modeling mating in two-sex (but also one-sex) population models.

Funding Information This study was funded by the Grant Agency of the Czech Republic (15-24456S) and institutional support RVO:60077344

Compliance with Ethical Standards

Conflict of interest The author declares that he has no conflict of interest.

Appendix A: Continuous-time models of mating dynamics

Let each female encounter males at rate βm , for a positive constant β . This means that individual searchers scan a new area β each time unit. Moreover, the rate at which females mate equals $\beta m f$ and thus follows the mass action law.

Scenario 1: Baseline When males are not limited in their mating potential, the corresponding model of seasonal mating dynamics, assuming a large enough habitat area H^2 , is

$$\begin{aligned} \frac{dm}{dt} &= 0, \\ \frac{df}{dt} &= -\beta m f. \end{aligned} \quad (12)$$

Since male density m is constant, the density of unmated females declines exponentially as $f(t) = f_0 \exp(-\beta mt)$ for an initial female density f_0 . Therefore, the proportion of females mated at the end of the mating season of length ϕ is

$$P(\phi; m) = 1 - \exp(-\beta m\phi). \tag{13}$$

Scenario 2: Limited Denoting by n_m the male mating potential (i.e., the maximum number of matings any male may have during the mating season) and by m_i , $i = 1, \dots, n_m$, the densities of males that have already mated i times, then males of class i go to class $i + 1$ at rate $\beta m_i f$, and become unavailable for mating after making n_m transitions (i.e., after mating n_m times). Therefore, under a limited male mating potential the baseline continuous-time model of mating dynamics (12) changes to

$$\begin{aligned} \frac{dm}{dt} &= -\beta m f, \\ \frac{df}{dt} &= -\beta m f - \beta m_1 f - \beta m_2 f - \dots - \beta m_{n_m-1} f, \\ \frac{dm_1}{dt} &= \beta m f - \beta m_1 f, \\ \frac{dm_2}{dt} &= \beta m_1 f - \beta m_2 f, \\ &\dots \\ \frac{dm_{n_m-1}}{dt} &= \beta m_{n_m-2} f - \beta m_{n_m-1} f. \end{aligned} \tag{14}$$

We note that $n_m = \infty$ corresponds to unlimited polygyny (scenario 1). On the other hand, $n_m = 1$ corresponds to male monogamy and the model (14) then reduces to

$$\begin{aligned} \frac{dm}{dt} &= -\beta m f, \\ \frac{df}{dt} &= -\beta m f. \end{aligned} \tag{15}$$

This model can be solved analytically. Indeed, Wells et al. (1990) showed that the female mating probability P depends on both male and female densities as

$$P(\phi; m) = \begin{cases} \frac{m \exp[(m - f)\beta\phi] - m}{m \exp[(m - f)\beta\phi] - f} & \text{if } m \neq f, \\ \frac{\beta m\phi}{1 + \beta m\phi} & \text{if } m = f. \end{cases} \tag{16}$$

Scenario 3: Refractory Denoting by m_s and m_r the densities of searching males and males currently in the refractory state, respectively, searching males enter the refractory class at the rate $\beta m_s f$ and leave it at the rate m_r/T , where

T is the (mean) length of refractory period. Therefore, modification of the baseline model (12) that accounts for the refractory period of males after each mating is

$$\begin{aligned} \frac{dm_s}{dt} &= -\beta m_s f + \frac{1}{T} m_r, \\ \frac{df}{dt} &= -\beta m_s f, \\ \frac{dm_r}{dt} &= \beta m_s f - \frac{1}{T} m_r. \end{aligned} \tag{17}$$

Scenario 4: Learning Denote by m_i and m_e the densities of inexperienced and experienced males, respectively. Both types of males search for females at rate β . Moreover, inexperienced and experienced males mate with probability p_0 and p_1 upon encounter, respectively. After n_t encounters with females, inexperienced males become experienced. With these assumptions, the baseline model (12) can be extended as

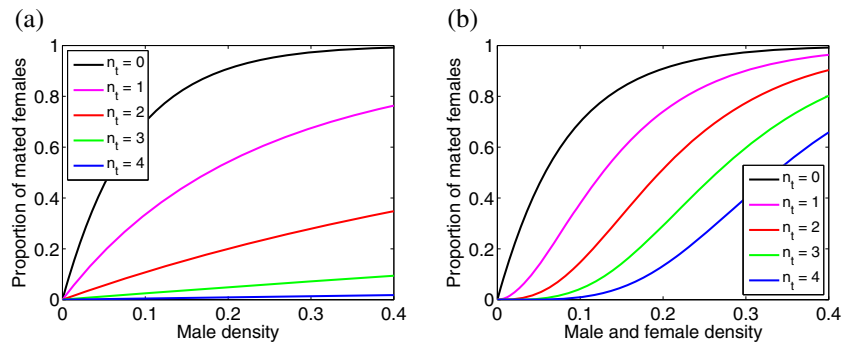
$$\begin{aligned} \frac{dm_i^1}{dt} &= -\beta m_i^1 f, \\ \frac{dm_i^k}{dt} &= \beta m_i^{k-1} f - \beta m_i^k f, \quad k = 2, \dots, n_t \\ \frac{df}{dt} &= -p_0 \beta \left(\sum_{k=1}^{n_t} m_i^k \right) f - p_1 \beta m_e f, \\ \frac{dm_e}{dt} &= \beta m_i^{n_t} f. \end{aligned} \tag{18}$$

By analogy with predator-prey theory and cooperative enzyme dynamics (see the main text), this learning scenario is expected to produce a sigmoid form of the female mating probability. While a sigmoid form is hardly seen to non-existent when only the male density m varies (Fig. 12a), it is clearly seen when both male and female densities change and are kept at a constant ratio (Fig. 12b).

Scenario 5: Heterogeneity The searchers may be heterogeneous in various ways. We return here to the baseline scenario and assume that males are not limited in their mating potential. Hence, each female’s mating probability at time t is $P(t; m) = 1 - \exp(-\beta mt)$. However, we let the parameter β differ among individual searchers, due to varying mate search rate. When females are the searching sex then the female mating probability becomes

$$P_F(t; m) = \int_0^\infty (1 - \exp(-\beta mt)) f(\beta) d\beta, \tag{19}$$

Fig. 12 The mate-finding Allee effect for the learning scenario model (18) and for parameters $\beta = 3$, $p_0 = 0$, and $p_1 = 1$; the length of mating period $\phi = 4$. Initial female density $f = 0.08$ in panel (a)



where $f(\beta)$ is a probability density function on β . On the other hand, when males are the searching sex then the female mating probability is

$$P_M(t; m) = 1 - \exp\left(-mt \int_0^\infty \beta f(\beta) d\beta\right) = 1 - \exp(-\mu_\beta mt), \tag{20}$$

where μ_β is the mean value of β .

Assuming a Gamma-distributed search area β per unit time,

$$f(\beta) = \frac{\theta^\tau \beta^{\tau-1}}{\Gamma(\tau)} \exp(-\theta\beta), \quad 0 < \beta < \infty, \tag{21}$$

and we get

$$P_M(t; m) = 1 - \exp\left(-\frac{\tau}{\theta} mt\right) \tag{22}$$

and (Dennis 1989)

$$P_F(t; m) = \frac{(\theta + mt)^\tau - \theta^\tau}{(\theta + mt)^\tau}. \tag{23}$$

Here, τ is a shape parameter and θ is a rate parameter of the Gamma distribution which are related to mean μ_β and variance $\text{var } \beta$ as $\tau = (\mu_\beta)^2 / \text{var } \beta$ and $\theta = \mu_\beta / \text{var } \beta$. For $\tau = 1$, the Gamma distribution becomes an exponential

distribution and $P_F(t; m) = m / (\theta + m)$, one of the forms most commonly used to describe the female mating rate in population models accounting for a mate-finding Allee effect (Dennis 1989; Boukal and Berec 2002; Terry 2015). On the other hand, letting $\tau \rightarrow \infty$ and $\theta \rightarrow \infty$ such that $\tau / \theta \rightarrow \beta$ the baseline model $P(t; m) = 1 - \exp(-\beta mt)$ is recovered (Dennis 1989).

Summary of Scenarios 1–5 Figure 13 summarizes how density of mated females increases in time or with male and female densities for the five examined mating scenarios. The monogamy scenario (i.e., the limited scenario with $n_m = 1$) is the worst scenario when the mating season is relatively long as the other scenarios allow males to mate multiply and hence increase the chance of females to meet at least one male. On the other hand, the learning scenario is the worst scenario if the mating season is relatively short as it catches up with male polygyny only when a majority of males are experienced. As we know from above, small refractory period and large male mating potential behave similarly to the baseline scenario with unlimited male polygyny. We also know from our individual-based simulations that heterogeneity in the mate search rate when females are the searching sex produces consistently lower female mating probabilities relative to the baseline scenario,

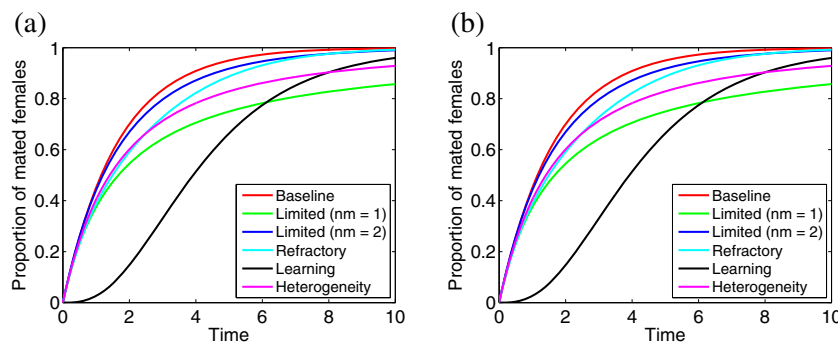


Fig. 13 Dynamics of analytical models of mating dynamics corresponding to Scenarios 1–5. The heterogeneity scenario here considers mate search rate heterogeneity in females; mate search rate heterogeneity in males would give results identical to the baseline scenario.

The female mating probability is plotted as a function of **a** time, with $m_0 = f_0 = 0.2$, and **b** male and female density, with $\phi = 4$, for parameters $\beta = 3$, $n_m = 2$, $T = 2$, $p_0 = 0$, $p_1 = 1$, $n_t = 2$, and $\text{var } \beta = 5$

while the results under heterogeneity in the mate search rate when males are the searching sex coincide with those for the baseline scenario.

Appendix B: Derivation of a simple continuous-time two-sex model

Here, we exemplify a sex-structured population model in which the processes of mating, reproduction, and mortality occur simultaneously. We assume that when a male and a female encounter one another they mate. Upon mating, the female enters a gestation period of length t_F after which it gives birth to b offspring following a 1:1 sex ratio and then resumes mate search. Mated males are assumed to enter a refractory period of length T . Moreover, males and females die at rates m_M and m_F , respectively. We distinguish four state variables: searching males M_s and females F_s , and resting males M_r and females F_r . A continuous-time two-sex model may then be as follows:

$$\begin{aligned}\frac{dM_s}{dt} &= -\beta M_s F_s - m_M M_s + \frac{1}{T} M_r + \frac{b}{2} \frac{1}{t_F} F_r, \\ \frac{dF_s}{dt} &= -\beta M_s F_s - m_F F_s + \frac{1}{t_F} F_r + \frac{b}{2} \frac{1}{t_F} F_r, \\ \frac{dM_r}{dt} &= \beta M_s F_s - \frac{1}{T} M_r - m_M M_r, \\ \frac{dF_r}{dt} &= \beta M_s F_s - \frac{1}{t_F} F_r - m_F F_r.\end{aligned}\quad (24)$$

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