Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species

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In this paper we examine how the process of mate search, degree of mate choice and degree of mate fidelity may interact to affect long-term population dynamics of sexually reproducing species. In particular, we address the following questions: are degree of mate choice and degree of mate fidelity correlated? How does mate search shape this relationship? How does longevity affect mating behaviour? To resolve these questions, we develop a spatially explicit, individual-based model of a sexually reproducing population with single (i.e. unpaired) males, single females, and pairs as focal individuals. Both this model and its non-spatial approximation give rise to the Allee effect due to lack of mating possibilities, and sufficiently small/sparse populations always go extinct. We quantify combinations of mate choice and divorce rate under which populations persist or go extinct even from high sizes. We thus show that there exist ecological constraints for possible (co)evolution of mate choice and pair maintenance behaviour. Our models also suggest that colonial species with active mate search strategy survive at higher divorce rates than less colonial animals that search for their mates randomly, and that long-lived species sustain at higher degrees of mate choice and lower degrees of mate fidelity compared to the short-lived ones. Connection of these findings to other theoretical results and some empirical observations is discussed.

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Evolution of sexuality and various implications of sexual reproduction are currently in focus of both empiricists and theoreticians. Many aspects of sex have been taken into account: evolution of sex itself, evolution of sex ratio, allocation of resources to sexual versus asexual reproduction in some plants and invertebrates, environmental sex determination, mate search, mating systems, sexual dimorphism, sexual selection, etc. (Andersson 1994, Choe and Crespi 1997, Apollonio et al. 2000, Orzack 2001, Sakai and Westneat 2001, Savalli 2001, Hardy 2002). Search for population-dynamic consequences of these aspects requires explicit modelling of males and females, and cannot be successfully covered by “asexual” models that still prevail in theoretical studies of population dynamics.

In many animals, successful reproduction requires paired individuals and there exist numerous ways pairs are being formed and maintained. Three major processes play a significant role in pair dynamics: mate search, mate choice, and breakup of established pairs. Different taxa use different ways to locate mates; in this paper we use random search, local passive search, and local active search as three generic examples (Berec et al. 2001). Random search is equivalent to a non-spatial modelling framework and may serve as a null model to assess how space and localized mate search strategies affect population viability; it can also reasonably capture movement in many insects (King and With 2002). Local passive search may approximate relatively less mobile individuals in which other aspects of behaviour...
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Many animals are known to avoid or reduce repro-
duction with mates belonging to incompatible or non-
preferred phenotypes; this phenomenon is known as
mate choice (Andersson 1994). Möller and Legendre
(2001) listed many studies that demonstrated mate
choice for mammalian and bird species. Also, animals
vary widely in their fidelity (i.e. pair bond duration).
Dubois et al. (1998) enumerated divorce rate estimates
for 58 species of monogamous colonial waterbirds. In
some species, such as wandering albatross Diomedea
exulans L. and waved albatross D. irrorata Salvin,
individuals tend to maintain life-long pair bonds,
whereas in others, such as grey heron Ardea cinerea L.
and crozet shag Phalacrocorax melanogenis Blyth, birds
experience many partners during their reproductive
lifespan. Choudhury (1995) listed additional examples
of monogamous birds demonstrating various degrees of
fidelity, and critically reviewed current hypotheses that
have been proposed to explain divorce behaviour.

Mate search, mate choice and divorce behaviour are
apparently intertwined. It is now believed and partly
supported by observational evidence that divorce is an
adaptive strategy of an individual to improve its repro-
ductive success; “divorce may simply be an extension of
the mate-choice process, where birds continue to sam-
ples mates and improve on their breeding situation after
initial pairing” (Choudhury 1995). Mate choice is also
tightly related to mate search efficiency. For example,
actively searching individuals may locate many more
potential mates than passive or random searchers in a
given time interval, and thus secure a better mate. Last
but not least, intuition suggests that the lower is divorce
rate of an individual, i.e. the fewer partners it has
during its lifetime, the more carefully it should choose
these partners in order to secure that its genes pass to
the future generations. Needless to say, these processes
have certainly evolved together and strongly shaped the
currently observed mating strategies.

Tightly coupled with these processes, there is an
ongoing debate in the literature about the relationship
between longevity and mate fidelity (Saether 1986,
Choudhury 1995, McNamara and Forslund 1996). So
far the evidence provided by theoretical models is am-
ivalent and competing hypotheses do exist: some au-
thors have argued that selection may not favour mate
fidelity in species with high mortality rates, yet the
others have suggested that divorce should be expected
mainly in long-lived species, since they gain more in
terms of improving lifetime reproductive success
(Choudhury 1995).

In this article, we study implications of these three
processes for dynamics of a sexually reproducing popu-
lation. We develop a spatially explicit, individual-based
model and its non-spatial approximation to represent
animals occupying exclusive “territories” and exhibiting
a monogamous mating system, and to address three
main questions. First, are degree of mate choice and
degree of mate fidelity correlated? Secondly, how does
type of mate search shape this relationship? Finally,
how does longevity affect mating behaviour? We do not
explicitly model different geno- or phenotypes and sub-
sequent mate choice. Instead, to keep the current mod-
els simple, we work with a monomorphic population
and the probability of successful pair formation upon
male and female encounter (Möller and Legendre
2001).

Methods

We study population dynamics of sexually reproducing
species by means of a spatially explicit, individual-based
model and its mean-field (i.e. spatially homogeneous)
approximation (further referred to as the non-spatial
model). We represent two-dimensional, physically ho-
momogeneous environment as a regular lattice of 200 ×
200 identical square sites, with periodic boundary
conditions. Time runs continuously. At any time in-
stant, each site represents a “territory” that can be
vacant or occupied by a single (i.e. unpaired) individual
or pair, i.e. the environment can host up to 80,000
individuals. Simulations are initialized with a given
number of single males, single females, and pairs, all
being randomly distributed over the lattice. The follow-
ing life history processes determine the fate of each
individual. Due to continuous time, process ordering is
determined by the actual occurrence of particular
events. Further technicalities of this approach are dis-
cussed in Appendix A and Berec (2002).

Males and females die at rates \( d_m \) and \( d_f \), respec-
tively, regardless of their paired status. Dead individu-
als are instantly removed from the lattice. Pairs give
birth to one offspring at rate \( b \). The offspring becomes
male [female] with probability \( \mu \) [1 − \( \mu \)]. Respecting
boundary conditions, it instantly and equiprobably dis-
perses to a parents’ nearest neighbour site and becomes
an adult capable of reproduction. If the chosen site is
already occupied, the offspring dies. If the chosen site is
vacant, the offspring settles there. Pairs separate at rate
\( m_p \), and we assume that divorce (i.e. the act of leaving
the pair) is pursued by males and females equally. The
terminal site of the leaving individual is determined by
a mate search strategy described below. Divorce is
withdrawn if the leaving individual would step on a site
with a pair or same-sex single. As a consequence, contests for mates do not occur. If it would step on a site occupied by a single of the other sex, there is probability \( p_\text{m} \) of a successful pair formation; this probability may quantify, e.g. female choosiness with respect to males. If the new pair is not formed divorce is also withdrawn.

Single males and females move at rates \( m_m \) and \( m_f \), respectively. Again, the terminal site of the disperser is determined by its mate search strategy. Dispersal is discarded if a pair or individual of the same sex occupies the site to which the disperser intends to move. Upon male and female encounter, a pair is formed with probability \( p_q \). If the pair formation is not successful, the disperser does not move. We distinguish two local mate search strategies which may differ for males and females (Berec et al. 2001). First, single individuals are expected to search for their mates passively by moving or leaving divorcing pairs equiprobably to any site on the lattice; second, individuals are assumed to be active searchers through perceiving other conspecifics in a square neighbourhood of side length \( 2s \), centred on their current location. Side length of the neighbourhood may differ for males (\( r_m \)) and females (\( r_f \)). Secondly, individuals are assumed to be active searchers through perceiving other conspecifics in a square neighbourhood of side length \( 2s + 1 \), centred on their current location. A male perceiving only one single female moves directly to her site if two or more unpaired females are perceived, one is chosen equiprobably. If no single female is detected, the male moves to a randomly chosen site in the neighbourhood unless it is occupied by a single male or pair, and stays in the current site otherwise. Analogous rules apply to females. Neighbourhood side length may differ for males \( (r_m) \) and females \( (r_f) \).

The non-spatial model is extracted from the above spatially explicit, individual-based model by assuming an infinite lattice, random initial condition, and random search strategy (i.e. dispersal of all individuals, including offspring, equiprobably to any site on the lattice); see Appendix A and Berec (2002) for a conceptual approach. Then, densities of single males \( (v_m) \), single females \( (v_f) \), and pairs \( (v_p) \) obey the following system of ordinary differential equations,

\[
\begin{align*}
\frac{dv_m}{dt} &= -d_m v_m - p_m (m_m + m_f) v_m v_f + d_m v_p \\
&+ (m_p + b_p) (1 - v_m - v_f - v_p) v_p \\
\frac{dv_f}{dt} &= -d_f v_f - p_f (m_m + m_f) v_m v_f + d_m v_p \\
&+ (m_p + b(1 - \mu)) (1 - v_m - v_f - v_p) v_p \\
\frac{dv_p}{dt} &= p_f (m_m + m_f) v_m v_f - (d_m + d_f) v_p \\
&- m_p (1 - v_m - v_f - v_p) v_p
\end{align*}
\]

(1)

The male and female equations consist of five terms. From left to right, these correspond to the death of a single individual, formation of a pair when two singles meet, death of a paired individual, divorce, and birth of an offspring. Pair dynamics are driven by formations of new pairs, deaths of constituent members, and divorces.

The non-spatial model (1) was analysed using the software package Content (Kuznetsov 1998). We examined a number of scenarios differing in values of pair divorce rate \( m_p \) and probability of successful pair formation \( p_q \). For stochastic simulations of the spatially explicit, individual-based model, one replicate run (5000 time units) was performed for each parameter combination, with densities during the last 200 time units averaged to get an equilibrium estimate. For each parameter combination, population dynamics were summarized into three single numbers: total population sizes in the two non-zero equilibria (set to 0 if the equilibria did not exist), and time to extinction (time at which the total population density falls below a predefined value \( \epsilon \)). We could not locate the non-zero unstable equilibria in simulations of the spatially explicit model; hence, we compared these simulations to the behaviour of model (1), using only total population sizes in the non-zero locally stable equilibria.

**Results**

**Non-spatial model**

First, the origin \( E^0 = (0,0,0) \) is always a locally stable equilibrium in model (1); if the male, female and pair densities are sufficiently close to zero, the population will inevitably go extinct. This is an obvious manifestation of the Allee effect due to lack of mating possibilities in a sexually reproducing population. Moreover, model (1) has zero, one or two non-zero equilibria depending on parameter values (Boukal 2001). If two non-trivial equilibria exist, the equilibrium \( E^0 \) that is closer to the origin is unstable, while the distant equilibrium \( E^* \) is locally stable; such a bi-stable regime is often characteristic of an Allee effect (Boukal and Berec 2002). Equilibria \( E^0 \) and \( E^* \) are separated by a three-dimensional extinction boundary (Fig. 1); populations starting below it go extinct, while those starting above it establish and equilibrate at \( E^* \). If no pairs are initially present, a sufficient number of single males and single females are needed for a population to persist. If singles are absent on the other hand, a minimum number of breeding pairs is required to secure population survival. Fig. 1 shows that the minimum number of breeding pairs necessary for population survival is lower than the minimum number of single males plus single females; paired individuals do not need to search for mates and may immediately start to reproduce.

The locally concave shape of the extinction boundary leads to a somewhat counterintuitive result: for a specific range in the number of pairs (pair density around 0.1), and no or very few single males, a population goes...
extinct if there are either few (female density less than about 0.2) or many (female density around 0.85) single females (Fig. 1). In the former case, the population dies out due to low chances of singles to find mates. If the number of single females is sufficiently high, there are nearly no vacant sites to place newborns and male population thus cannot increase; minimum number of pairs needed for the population to survive thus has to be higher than for intermediate densities of single females (Fig. 1, female densities around 0.3–0.8). Analogous reasoning may hold for males and females interchanged.

To assess population-dynamic implications of the degree of mate choice and the degree of mate fidelity, we plot selected ecological characteristics of model (1) as functions of the probability of successful pairing $p_s$ and the divorce rate $m_p$ (Fig. 2). While total population sizes in the non-zero model equilibria (Fig. 2A,B) give insight into the bi-stable Allee dynamics (small populations go extinct, large ones survive), time to extinction (Fig. 2C) illustrates parameter combinations for which the Allee effect is too strong (i.e. the origin is globally stable) and populations go extinct from any initial condition. Fig. 2 shows that the degree of mate choice and the degree of mate fidelity are strongly correlated.

For a population to survive, the room for mate choosiness decreases with increasing divorce rate, while the room for divorce rate increases with decreasing mate choosiness (i.e. increasing $p_s$). The boundary separating parameter region with the bi-stable regime from that with the globally stable origin (we call it the bifurcation boundary further on) intersects the axes $m_p = 0$ and $p_s = 1$ in points $p_s = p_s^*$ and $m_p = m_p^*$, respectively.

Fig. 1. The Allee-effect: hyperbolic-shaped extinction boundary separating the areas of attraction of the origin and the non-zero locally stable equilibrium in the bi-stable regime of model (1). Parameters: $d_m = 0.01$, $d_f = 0.02$, $b = 0.2$, $\mu = 0.5$, $m_m = 0.2$, $m_f = 0.2$, $p_s = 0.6$, $m_p = 0.15$. We run the model for 5000 time units and considered the population extinct if the total population density at the end of simulation decreased below $\epsilon = 0.001$.

Fig. 2. Three currencies characterizing population dynamics of model (2) as functions of the probability of successful pairing $p_s$ and the divorce rate $m_p$. (A) Total population size in the non-zero locally stable equilibrium. (B) Total population size in the non-zero locally unstable equilibrium. (C) Time to extinction for a specific initial condition: lattice full of pairs. We run the model for 5000 time units and considered the population extinct if the total population density at the end of simulation decreased below $\epsilon = 0.001$. Other parameters as in Fig. 1.
These points represent the minimum mate acceptance and the maximum divorce rate under which populations can persist.

Note that the bi-furcation boundary is a straight line (apparent dents in Fig. 2 are visualisation artifacts). This follows from the simple way parameters $m_p$ and $p_s$ enter the model; we observed a curved (but qualitatively identical) boundary for a slightly different formulation of the life-history processes (Berec and Boukal, unpubl.). The initial condition used in Fig. 2C (lattice initially full of pairs) leads to the slowest extinction rates. Starts from other initial conditions give similar results; in general, the farther we start from the bifurcation boundary and the smaller is the initial condition we start with, the faster extinction occurs.

Local mate search strategies

Simulations show that on the population level, behaviour of the spatially explicit, individual-based model does not differ qualitatively from that of the non-spatial model. Quantitative differences, however, do exist. Fig. 3 compares results obtained with all three mate search strategies. In Fig. 3A, the divorce rate $m_p$ is fixed at 0.05, and the total population size in the non-zero locally stable (quasi-)equilibrium (recall the intrinsic stochasticity of the spatially explicit model) is calculated for various values of the successful pairing probability $p_s$. Relative to random searchers, we observe that the equilibrium population size increases and the bi-furcation point (i.e. the point at which the global population extinction is replaced by the bi-stable Allee dynamics) shifts towards lower values of $p_s$ if active mate searchers form the population. The active searchers thus survive at higher degrees of mate choice compared to the random searchers. An opposite effect occurs if the passive mate search strategy is adopted: the room for mate choosiness shrinks for the passive searchers, as compared to that belonging to the random ones. Behaviour of the passive searchers approaches that of the random searchers when increasing the maximal distance $r$ of passive search (not shown). Fig. 3B fixes the degree of mate choice $p_s$ at 0.8 and varies the divorce rate $m_p$. As a result, populations composed of locally active mate searchers survive at much higher divorce rates than populations composed of individuals that use either random or local passive search to locate mates.

Longevity and mating strategies

Obviously, life-history constraints are different in short-lived and long-lived animals. The role of longevity is summarized in Fig. 4 that shows the total population size in the non-zero locally stable equilibrium under the random search strategy. There is a limit on longevity such that populations composed of very short-lived individuals go extinct from any initial condition. Besides the birth rate $b$, this limit is affected by both the successful pairing probability $p_s$ (Fig. 4A) and the divorce rate $m_p$ (Fig. 4B). Fig. 4A shows that all else being equal, a long-lived species survives (and reaches the same equilibrium population size) with more stringent mate choice than the short-lived one. In the same vein, Fig. 4B shows that all else being equal, a long-lived species survives (and reaches the same equilibrium population size) at higher divorce rates than the short-lived one. We observed the same trends for the two local mate search strategies (not shown).
Sexual reproduction and the Allee effect

We discover that populations demonstrate the Allee effect for any combination of parameter values, presumably due to the lack of mating possibilities at low population densities: extinction is always a locally stable event (Courchamp et al. 1999, Stephens and Sutherland 1999). If the Allee effect is too strong, extinction is inevitable for populations starting from any size. For a weaker Allee effect, two non-zero equilibria (one unstable and one locally stable) arise, and populations either go extinct or establish at a carrying capacity. The Allee effect emerges internally from demographic and dispersal processes, and our model thus differs from those that consider the “Allee threshold” as an external model parameter (Boukal and Berec 2002).

In the non-spatial, deterministic model, a hyperbolic-like extinction boundary strictly separates population sizes leading to extinction or establishment (Fig. 1): populations starting below the boundary face certain extinction, whereas those starting above it persist at a carrying capacity. The spatially explicit, individual-based model is stochastic: randomness in the number of births and deaths gives rise to fluctuations known as demographic stochasticity. Demographic stochasticity and the Allee effect appear to be alternative explanations for small population extinctions. Although Lande (1998) claimed that demographic stochasticity itself can generate an Allee-like effect, his results are difficult to interpret in biological terms (Stephens et al. 1999, Boukal and Berec 2002, Dennis 2002). On the other hand, Dennis (1989, 2002) showed that the threshold-like extinction probability, characteristic of the Allee effect in deterministic population models, becomes “blurred” into a sigmoidally decreasing function of population size if demographic stochasticity starts to operate. In that case, even small populations may establish and survive, while bad chance may sometimes wipe out a large population. We observe this behaviour in our spatially explicit model.

Møller and Legendre (2001) demonstrated that mate choice is an important force generating the Allee effect, and showed that probability of a female being mated increases (with a decreasing rate) as a function of population size when there are genetic incompatibilities or mating preferences between males and females. When put into a proper dynamic framework, this probability generates the bi-stable regime typical of the Allee effect (Boukal and Berec 2002). In our models, the primary cause of the Allee dynamics is the lack of mating possibilities at low population sizes. However, mate choice adds an important component to it. We show that all else being equal, an increase in mate choice leads to a decrease in population viability; the two non-zero equilibria in the bi-stable regime converge one to another and eventually disappear, thus making the population increasingly vulnerable to chance fluctuations.

Discussion

This paper provides one of the attempts that try to link individual behaviour to population dynamics. In particular, we develop a spatially explicit, two-sex, individual-based model with strictly separated processes of pair formation and pair maintenance, and use the model and its non-spatial approximation to study implications of pair bond duration, mate choice, and several generic mate search strategies for population dynamics of sexually reproducing species. Apart from the species-specific model of alpine marmots (Stephens et al. 2002) and our previous model (Berec et al. 2001), the current model is the only individual-based, population-dynamic model of sexual reproduction that we are aware of.
The explicit consideration of the three processes of mate search, mate choice and divorce, together with an intrinsic appearance of the Allee effect due to the lack of mating possibilities (Dennis 1989, Courchamp et al. 1999, Stephens and Sutherland 1999, Boukal and Berec 2002), distinguish our models from nearly all existing population-dynamic models of sexually reproducing species, which either do not explicitly model pair dynamics (Hopper and Roush 1993, Berec et al. 2001), or do not demonstrate the Allee effect (Fredrickson 1971, Dietz and Haderler 1988, Castillo-Chavez and Huang 1995, Hsu Schmitz and Castillo-Chavez 2000), or lack both phenomena (Smouse 1971, Caswell and Weeks 1986, Lindström and Kokko 1998, Legendre et al. 1999, Ranta et al. 1999). In technical terms, most two-sex models with pair formation considered a degree-one homogeneous pair formation function. Pair formation function in model (1) is degree-two homogeneous and thus inevitably leads to the Allee effect (see Appendices A and B, Boukal 2001). Non-homogeneous pair formation functions with similar properties have been used by Hsu and Fredrickson (1975) and Ashih and Wilson (2001).

Interplay between mate fidelity and mate choosiness

As the main result of this paper, we demonstrate for the first time how population dynamics put (quantifiable) constraints on mate choice and mate fidelity. More precisely, we show that some trait combinations cannot exist because they would lead to extinction. We do this only by comparing population viability following from fixed traits; evolutionary dynamics of the inspected traits under selection pressures will be examined elsewhere.

Here we show that the degree of mate choice and the degree of mate fidelity are strongly correlated. All else being equal, populations composed of individuals with longer pair-bonds (lower divorce rates) persist at higher degrees of mate choosiness compared to those that keep shorter pair-bonds; i.e. the room for mate choosiness decreases with increasing divorce rate for a population to survive under given life history. Formulated the other way round, individuals with higher acceptance of potential mates can still form a viable population, while maintaining shorter pair bonds.

In a monomorphic population described by our models, lifetime reproductive success of an individual is likely to be determined by the fraction of lifespan the individual spends paired. Thus, the link between the degree of mate choice and the degree of mate fidelity is mediated by a third factor: search costs. As an example, let females both initiate divorce and choose males. Increased divorce rate as well as increased female choosiness (i.e. decreased probability of successful pairing) increase the time female spends searching as a single and decrease its lifetime reproductive success. If, moreover, an increased mortality rate is associated with its single (i.e. searching) status, or a temporarily decreased reproductive output follows shortly after establishment of a new pair (Choudhury 1995), the female’s lifetime reproductive success decreases even more.

Effects of longevity

There is an ongoing debate in the literature about the relationship between longevity and mate fidelity (Saether 1986, Choudhury 1995, McNamara and Forslund 1996). The evidence provided by theoretical models is ambivalent and competing hypotheses do exist. For example, it has been hypothesized that “in short-lived [migratory] species with high mortality rates, the probability that both pair members will survive to the following season will be low; selection may therefore not favour mate fidelity, since the costs of waiting for a mate that will not return are likely to be high” (Choudhury 1995). On the other hand, “some authors have argued that divorce should be expected mainly in long-lived species, since they gain more in terms of improving lifetime reproductive success” (Choudhury 1995). It seems that longevity may shape the subtle relationship between mate choice and mate fidelity in various ways.

We add to this discussion by showing that all else being equal, long-lived species persist with a more stringent mate choice and shorter pair bonds than short-lived ones. This result is, however, in contradiction with the findings of Saether (1986), who showed in a very simple model based on lifetime reproductive success that a promiscuous mating system (i.e. a system with a high divorce rate) is more likely to evolve when the adult male mortality is high (i.e. in a short-lived species). McNamara and Forslund (1996) modelled divorce decisions of a single female over her lifetime and showed how different costs determine divorce rate in long-lived and short-lived species. Their arguments point to both directions: longevity and mate fidelity may be both positively and negatively correlated. Among other things, McNamara and Forslund showed that “a long-lived female can afford to be more discriminating in her choice of a lifetime mate because she will typically spend a long time with him once he has been chosen (female choosiness increases with longevity)”. Our approach creates a mechanical basis for this result.

Effects of mate search

All three mate search strategies we have studied preserve the qualitative results outlined in the previous two
sections. However, they affect the exact location of both the extinction boundary in the space of population densities and the bi-furcation boundary in the parameter space. Active mate search by both sexes makes populations much less extinction-prone compared to passive search, and the random search strategy yields intermediate results. This “ranking” follows from the complex interplay of mate search, pair maintenance, and offspring placement on the lattice. Spatial clumping, as a result of local mate search and local interactions, plays an important role in the spatio-temporal dynamics (Tilman et al. 1997, Berec et al. 2001) and hence in the strategy ranking. It increases chances of an individual to find a mate relative to random search, with the active mate searchers being most successful. On the other hand, due to local overcrowding, spatial clumping decreases chances of local searchers to place newborns into parent neighbour sites. Relative to local passive search, local active search leads to faster pair formation and in turn to faster appearance of vacant sites.

Dubois et al. (1998) hypothesized that opportunities for finding a better mate are likely to increase with the colony size and density because close proximity with conspecifics makes it easier for individuals to assess the quality of more potential partners, and showed that waterbird species forming large and dense colonies had on average higher divorce rates compared to species forming small or loose aggregations. Our results are consistent with these observations since colonial birds usually employ active mate search (visual contact, songs). For a fixed degree of mate choice, we showed that actively searching, clustered animals survive at higher divorce rates than animals searching randomly for mates that are randomly distributed within the habitat.

Extending the present analysis

Despite the fact that this paper does not address evolutionary dynamics of examined individual traits and considers a non-evolving monomorphic population, we believe that it provides a solid basis for further extensions and is able to address a number of current ecological issues. We showed that ecological constraints set up by population dynamics may limit evolutionary phenomena in pairing behaviour. As a consequence, our results suggest that selection leading to more choosy and/or more frequently divorcing individuals could result in evolutionary suicide, i.e. an evolutionary process where a currently viable population adapts in such a way that it can no longer persist (Geritz et al. 2002, Gyllenberg et al. 2002). Gyllenberg et al. (2002) showed that a discontinuous transition to extinction is a necessary condition for evolutionary suicide to occur; Allee effects demonstrate such a behaviour. With these observations in mind, studies of competition between genotypes that differ in a heritable strategy (mate search strategy, pair divorce rate, etc.) are highly relevant and can be well studied under the current framework.

In this paper we have refrained from inclusion of population structure. There is no doubt, however, that population structure related to age, size etc. and resulting differences in mate quality can make the model more realistic; empirical studies by Jouventin et al. (1999) and Mills (1973) showed the importance of age in mate choice in several seabirds. Also, change of mate, whether by divorce or death of the previous partner, results in many species in a temporary reduction in breeding performance and/or decrease of survival probability due to search costs (Choudhury 1995). Incorporation of these processes may shed further light on ecological as well as evolutionary implications of mating behaviour.

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References


**Appendix A: Derivation of the non-spatial model (1)**

To understand how model rules describing individual behaviour translate into the population-dynamic model (1), it is necessary to give a brief outline of how simulations of the individual-based model formally run; see also Berec (2002). Events are said to occur at rate \( a \) if the event occurrence times are described by a Poisson process with the parameter \( a \). The model rules require that a number of Poisson processes run for each individual (mortality, reproduction, divorce, and dispersal). Fortunately, a “thinning” technique exists that keeps one background Poisson process only (Durrett 1995). This single process generates time instants at which events may occur. Let \( S \) be the number of lattice sites and let the background Poisson process generate time instants at rate \( cS \). Upon each generated time instant, a site is randomly chosen. Thus, each site is independently trying to change at rate \( c \), as \( \lambda S \times 1/S = c \), with 1/S being the probability that a particular site is randomly chosen. If the chosen site is occupied by a single male [female], the male [female] dies with probability
To derive a mean-field approximation of the spatially explicit, individual-based model, we assume an infinite lattice, a random initial condition, and dispersion of all individuals, including offspring, being equiprobable into any site on the lattice (these conditions are often referred to as the mass action law or the homogeneous mixing conditions). Now, we need to consider one by one all processes corresponding to single males, single females, and pairs, and calculate how they affect current population size. As an example, consider single male sub-population. Its size may be decreased by a male death or formation of a new pair, and increased by death of a paired female, divorce or production of a male death or formation of a new pair, and increased male sub-population. Its size may be decreased by a rent population size. As an example, consider single females, and pairs, and calculate how they affect cur-
one all processes corresponding to single males, single mixing conditions). Now, we need to consider one by

\[
\begin{align*}
\text{Letting } S &\to \infty \text{ and } x \to \infty \text{ so that } x/S \text{ is (or converges to) a constant density } v, \text{ (}^* \text{ stands for } m, f, \text{ and } p), \text{ one may show that variance in the number of single male individuals tends to zero as } h \to 0. \text{ Hence, dynamics of the single male population density } v_m \text{ converges to the solution of ODE}
\end{align*}
\]

\[
dv_m/dt = -d_m v_m - p_m (m_m + m_f) v_m v_f + d_f v_p + (p_m + b_m)(1 - v_m - v_f - v_p) v_p
\]

Equations for single female and pair densities follow an analogous derivation.

Rewriting model (1) in terms of total male \((v_M = v_m + v_p)\) and total female \((v_F = v_f + v_p)\) densities, we arrive at the system

\[
\begin{align*}
\dot{v}_M &= -d_m v_M + b_M (1 - v_M - v_F + v_p) v_p \\
\dot{v}_F &= -d_f v_F + b (1 - \mu)(1 - v_F - v_M + v_p) v_p \\
\dot{v}_p &= -(d_m + d_f) v_p - \sigma (v_M, v_F, v_p) v_p + \Phi (v_M - v_F, v_F - v_F, v_F, v_p)
\end{align*}
\]

The functions \(\sigma (v_M, v_F, v_p) = \mu (1 - (1 - \mu) / 2) v_M - (1 - \mu) / 2 v_F + (1 - \mu) v_p)\) and

\[
\Phi (x, y, z) = p_d (m_m + m_f) x y + m_p (p_f / 2) (x + y) z
\]

can be interpreted as the divorce rate and the pair formation function, respectively, which have been used in other pair formation models (Dietz and Hadeler 1988, Castillo-Chavez and Huang 1995, Boukal 2001). Note that the case when the divorcing individual ends up in a site containing an individual of the other sex is composed of two simple events: divorce of the old pair and formation of a new one.

### Appendix B: Homogeneity of the pair formation function

Fredrickson (1971) proposed that any pair formation function \(\Phi (m, f, l)\), relating the male \((m)\) and female \((f)\) population sizes to the rate of pair formation, should satisfy the following properties for all \(m, f, u, v, x, y, z \geq 0\):

\[
\begin{align*}
&\Phi (m, f) \geq 0 \\
&\Phi (m + u, f + v) \geq \Phi (m, f) \\
&\Phi (x, y, z) = \phi \Phi (m, f) \\
&\Phi (m, 0) = \Phi (0, f) = 0
\end{align*}
\]

Both the monotonicity (line two) and degree-one homogeneity \((k = 1 \text{ in line three})\) properties of \(\Phi (m, f)\) have been used as an important tool in the analysis of pair formation models by subsequent authors.
hand, the pair formation function $\Phi(m,f,p)$ arising in model (4) and given by Eq. (5) depends also on the number/density of pairs; it moreover satisfies conditions analogous to (6) except that it is degree-two homogeneous ($k = 2$ in line three). Degree-one homogeneity of the pair-formation function has been advocated by several authors (Fredrickson 1971) as the only reasonable alternative that would, among other things, assure at most exponential population growth. In model (4), finite population growth and size is mediated via environmental carrying capacity and density-dependent growth rates.