

# Lonely hearts or sex in the city? Density-dependent effects in mating systems

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Two very basic ideas in sexual selection are heavily influenced by numbers of potential mates: the evolution of anisogamy, leading to sex role differentiation, and the frequency dependence of reproductive success that tends to equalize primary sex ratios. However, being explicit about the numbers of potential mates is not typical to most evolutionary theory of sexual selection. Here, we argue that this may prevent us from finding the appropriate ecological equilibria that determine the evolutionary endpoints of selection. We review both theoretical and empirical advances on how population density may influence aspects of mating systems such as intrasexual competition, female choice or resistance, and parental care. Density can have strong effects on selective pressures, whether or not there is phenotypic plasticity in individual strategies with respect to density. Mating skew may either increase or decrease with density, which may be aided or counteracted by changes in female behaviour. Switchpoints between alternative mating strategies can be density dependent, and mate encounter rates may influence mate choice (including mutual mate choice), multiple mating, female resistance to male mating attempts, mate searching, mate guarding, parental care, and the probability of divorce. Considering density-dependent selection may be essential for understanding how populations can persist at all despite sexual conflict, but simple models seem to fail to predict the diversity of observed responses in nature. This highlights the importance of considering the interaction between mating systems and population dynamics, and we strongly encourage further work in this area.

**Keywords:** sexual selection; population regulation; Allee effect; extinction; phenotypic plasticity

## 1. INTRODUCTION

A ‘numbers game’ lies at the heart of all sexual selection. The evolution of anisogamy (Parker *et al.* 1972; Bulmer & Parker 2002) leads to the production of a larger number of male than female gametes, with the automatic consequence that not all male gametes will be able to find female gametes. This is the primary reason why females are often choosy about potential mates, whereas males have to compete with each other for access to mates. While factors such as mortality costs of various reproductive activities (Kokko & Monaghan 2001) and quality variation in each sex (Owens & Thompson 1994) may considerably complicate this picture (Forsgren *et al.* 2004), the simple difference in numbers of gametes nevertheless remains a powerful force causing differences in sex roles (Clutton-Brock & Parker 1992; Jiggins *et al.* 2000; Kokko & Monaghan 2001).

Sex-ratio theory provides another example, where the actual numbers of potential mates have a profound influence on evolutionary strategies. If there is a bias in the primary sex-ratio in a panmictic population, any parent investing more in the rarer sex will have a competitive advantage (Fisher 1930). The result is strong selection for equal investment in the two sexes

(reviewed in Seger & Stubblefield 2002). The strongest deviations from 50 : 50 ratios occur when mate competition occurs locally (Hamilton 1967); thus, to understand these deviations, assessing mate density in the local patch is essential (Herre 1987).

The above examples show that the number of potential mates can have potent influences on reproductive strategies. In general, there is no reason to assume that selective pressures should be the same at high and low-density populations (or at varying sex ratios). Conservationists have listed a number of examples, where small populations suffer from deleterious evolutionary processes, such as the accumulation of deleterious mutations and inbreeding (Lynch *et al.* 1995; Saccheri *et al.* 1998). Likewise, for population ecologists, a central question is to understand how competition for resources changes individual fitness at low compared to high densities (e.g. Sutherland 1996; Grant 1997; Rodenhouse *et al.* 1997; Sutherland & Norris 2002), and the result is often a reaction norm that predicts individual adjustment to density (e.g. via dispersal: Travis *et al.* 1999). Competition for mates is unlikely to be fundamentally different from competing for other resources (Emlen & Oring 1977), and thus neglecting density dependence is not justified.

Against this background it is quite surprising that the number, or density, of potential mates has received scant attention when examining evolutionary processes in mating systems, other than anisogamy or sex

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allocation. Much of sexual selection theory is built on either quantitative genetics models (reviewed by Mead & Arnold 2004) or phenotypic game theory models (e.g. Kokko *et al.* 2002; McNamara *et al.* 2003). Even though these techniques—among many others—can be modified to accommodate variation in the number of individuals, the central models that have advanced our understanding of sexual selection do not make explicit references to the number of potential mates (e.g. Lande 1981; Iwasa *et al.* 1991; Kirkpatrick & Barton 1997; Gavrillets *et al.* 2001; Houle & Kondrashov 2002; Kokko *et al.* 2002). The rationale is that relative, rather than absolute, fitness counts in evolution: it is not important that a male with an ornament one standard deviation better than the average improves his mating success from 3 to 6 females; an improvement from 1 to 2 would result in the same selective pressure. Yet, as we shall see below, numbers of potential mates can result in changes in relative fitness too, and this may have profound effects on evolutionary processes.

Currently, there is growing interest in population-level consequences of processes that shape mating systems (Holland 2002; Kokko & Brooks 2003; Rowe & Hutchings 2003; Stenseth & Saetre 2003; Saether *et al.* 2004; Skorping & Jensen 2004). Selection for mate-acquisition traits could lead to deteriorating population-level performance if sexual and natural selection act in opposite directions, but the theoretical aspects of these questions remain largely unanswered to date (Kokko & Brooks 2003), and the empirical evidence appears likewise conflicting (e.g. McLain *et al.* 1995; Badyaev & Ghalambor 1998; Sorci *et al.* 1998; Prinzing *et al.* 2002; Doherty *et al.* 2003; Morrow & Pitcher 2003; Morrow & Fricke 2004; Radwan 2004; Radwan *et al.* 2004). In this review, instead of asking how sexual selection affects population dynamics (e.g. equilibrium population size), we address the opposite causalities: how does population size or density influence evolutionary processes that shape mating systems? However, when investigating this question, we also aim to keep in mind that the eventual goal is to understand the two-way interaction between mating systems and population densities: individual strategies that have fitness consequences should be reflected in growth rates of populations, and the resulting population densities will then feed back to the success of the individual strategies.

In the sections below, we will review current knowledge of density-dependent effects in several different study fields of mating systems. We first consider strategies of the sex whose reproductive success is (more) strongly limited by access to the opposite sex: these are usually males, and tend to be the more numerous sex of the operational sex ratio (but see Kokko & Monaghan 2001; Forsgren *et al.* 2004). Then we proceed to strategies of the limiting sex, which are usually females. Following this, we point out that density variations often impose changes that covary between the sexes, which is important for some aspects of mating systems such as mate searching, mutual mate choice, and parental care. Throughout, we will consider both theoretical and empirical evidence, and investigate two possible scenarios: (i) effects of varying

density on sexual selection if individuals do not possess reaction norms with respect to density and (ii) what happens if they do. We mostly focus on *sparse* (low-density) populations, but where appropriate we also review evidence from *small* populations. The latter consist of a limited number of individuals, but the local density is not necessarily small.

Numbers of potential mates can vary in two fundamentally different ways. Biased (operational) sex ratios increase the mate encounter rate for one sex while decreasing it for the other. Variations in population density, on the other hand, influence mate availability for both sexes in the same direction (although the responses to this may be sex specific). We mainly focus on the effects of density in this review, although it should be kept in mind that a biased sex ratio can amplify any effects of density for one of the sexes; we will refer to examples of this where necessary.

## 2. STRATEGIES OF THE LIMITED SEX: COMPETITION FOR MATES AND MATE ACQUISITION

In the sex (usually males), where reproductive success is limited by access to gametes of the opposite sex, selection generally favours strategies that improve this access. Successful individuals thus gain an upper hand in intrasexual competition, which may correlate with straightforward physical properties such as size, ‘armaments’ such as weaponry, or more subtle characteristics such as the possession of direct benefits valued by females, or display of physical traits that females prefer. Males may also improve their access to mates by ‘sneaking’ fertilizations (Parker 1998), by mate-guarding (Birkhead 1998; Jormalainen 1998), or through forced copulation (Clutton-Brock & Parker 1995).

Many of these determinants of a male’s mating success can depend on population density. The most straightforward case is physical dominance. Theory predicts that all other factors being equal, the chances of dominating many conspecifics become reduced when they are rare (Eshel 1979; Shuster & Wade 2003). Figure 1a shows a simple simulated example, where males interact locally and those of higher resource potential hinder the mating attempts of nearby, inferior males. Only males who do not have a superior male nearby are assumed to be successful; while this is a simplification as spatial locations of females are not explicitly modelled, it illustrates the basic principle that if nearby males interfere with each other’s mating success, interference will increase with density. In this ‘null model’, the proportion of males that do not mate—a simple measure of reproductive skew—drops drastically with lowering population density. Similar ideas could apply to small (rather than sparse) populations, as random processes play a significant role in the evolution in these (Whitlock 2000; see also Kokko *et al.* 1999a; Purse & Thompson 2005).

The consequence of a lower mating skew at low population density is a relaxation of sexual selection. If sexual selection generally becomes relaxed in sparse (or small) populations, one would expect a reduction or loss of ornaments, armaments or the strength of sexual conflict (Gavrillets 2000; Martin & Hosken 2003;

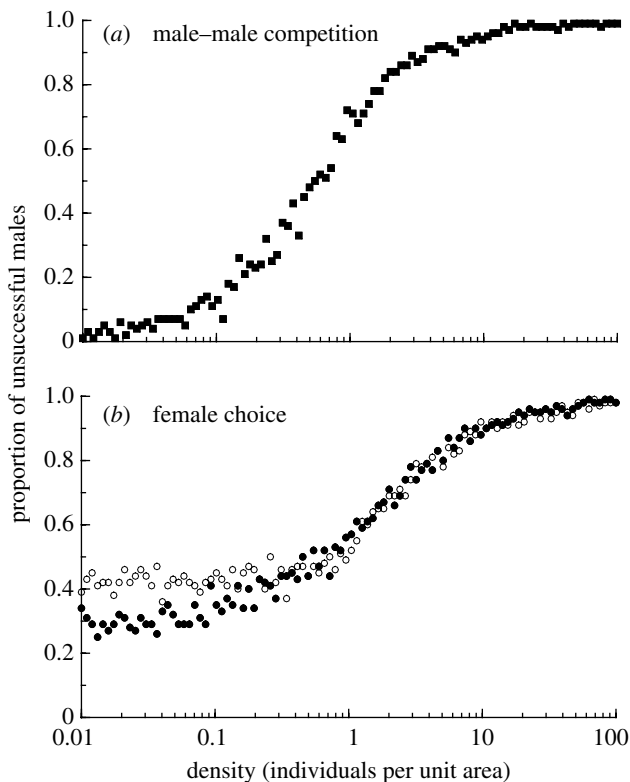


Figure 1. Proportions of unsuccessful males in two simple simulated scenarios. Each dot is an outcome of one simulation run, where locations of 100 individuals were randomly distributed to a square area of two-dimensional space. The size of the area is  $h \times h$  units, where  $h$  leads to the density as indicated on the  $x$  axis (i.e.  $\text{density} = 100/h^2$ ). In (a), males vary in their resource-holding power (RHP), drawn from a normal distribution (mean 0, variance 1). Female locations are not explicitly modelled, but a male is assumed to be unsuccessful in acquiring matings, if there is another male with higher RHP within less than one unit of distance; otherwise he is successful. In the scenario marked with open dots in (b), both males and females are randomly distributed in space, males vary in their attractiveness to females (drawn from a normal distribution, mean 0, variance 1), and every female mates by choosing the most attractive male among those located within one distance unit (if no male is available there, females choose the closest one). The filled dots in (b) mark a similar scenario, but add a component where males follow the distribution of females: after the distribution of females is determined, male locations are recalculated until no male is further away than 0.5 distance units from a female.

Levitan 2004), when populations diminish in density or size. It is interesting to note that according to some (but not all) hypotheses, strong sexual selection should itself lead to lower population size (reviewed in Kokko & Brooks 2003). If this is the case, and low population size then feeds back by diminishing the strength of sexual selection, sexual selection may become self-limiting.

This could help to answer the all too rarely asked question of what limits the negative effects of costly sexual traits, that give their bearer an advantage in intrasexual competition but may be harmful for the reproduction of the population as a whole (Houle & Kondrashov 2002; Kokko & Brooks 2003). Models that track the numbers of individuals, but do not include density-dependent mating skew, produce a

worrying result: nothing necessarily stops sexual selection from driving species extinct (Houle & Kondrashov 2002; Howard *et al.* 2004; but see Whitlock 2000). Behaviours that benefit male mating success can be drastically detrimental for female fitness: examples range from females in guppies *Poecilia reticulata* and solitary bees *Anthophora plumipes* experiencing a 25 and 50% reduction, respectively, in their foraging efficiency when harassed by males (Magurran & Seghers 1994; Stone 1995), to increases of similar magnitude in energy expenditure in water striders (Watson *et al.* 1998), and to deaths of sexually harassed females of feral sheep (Reale *et al.* 1996). Males may also harm direct female fitness by preventing remating, where this would confer direct benefits (Sauter *et al.* 2001).

In a simple model of sexual conflict (Kokko & Brooks 2003), genes that gave males a mating advantage could harm female reproduction to the extent that population growth becomes negative. These genes could spread no matter how low the population density, resulting in evolutionary suicide (Dieckmann & Ferrière 2004). Similar results have been found in a model based on real data on transgenic organisms (Howard *et al.* 2004; see also Price *et al.* 1993; Gavrillets *et al.* 2001; Rowe *et al.* 2005), and there is some empirical support for the threat on population persistence imposed by sexual dimorphism (e.g. Doherty *et al.* 2003; but see Morrow & Fricke 2004). All of this raises the question of why sexual selection does not routinely drive species extinct. A simple modelling exercise (figure 2) shows that the dynamics of persistence may completely change if male ability to monopolize females is density-dependent: first, the harmful alleles spread to an extent that the population fitness is reduced, but the resulting low population density causes matings to become more random, which eventually destroys the 'selfish' selective advantage of harmful alleles long before the extinction threshold is reached.

This hypothetical example (figure 2) shows that incorporating density effects can produce fundamentally different outcomes for male trait evolution, making a dramatic difference to population existence. While the example remains hypothetical, it is worrying how rarely models of mate acquisition strategies, including those addressing the evolution of sexual displays, are explicit about the feasibility of a suggested solution: can a viable population persist, given the proposed strategy? Our simple model (figure 2) may in fact underestimate the importance of density dependence. If high mating skew leads to low effective population size, density-dependent reductions in mating skew will play a larger role for population persistence than envisaged in figure 2.

#### (a) From individual behaviour to population dynamics (and back)

Is there any evidence for the process of figure 2? The empirical task of examining mating skew at different population densities is not easy as measures of mating skew tend to respond to the average number of matings, even if the underlying distribution of matings remains unchanged (for a debate on the best measure,

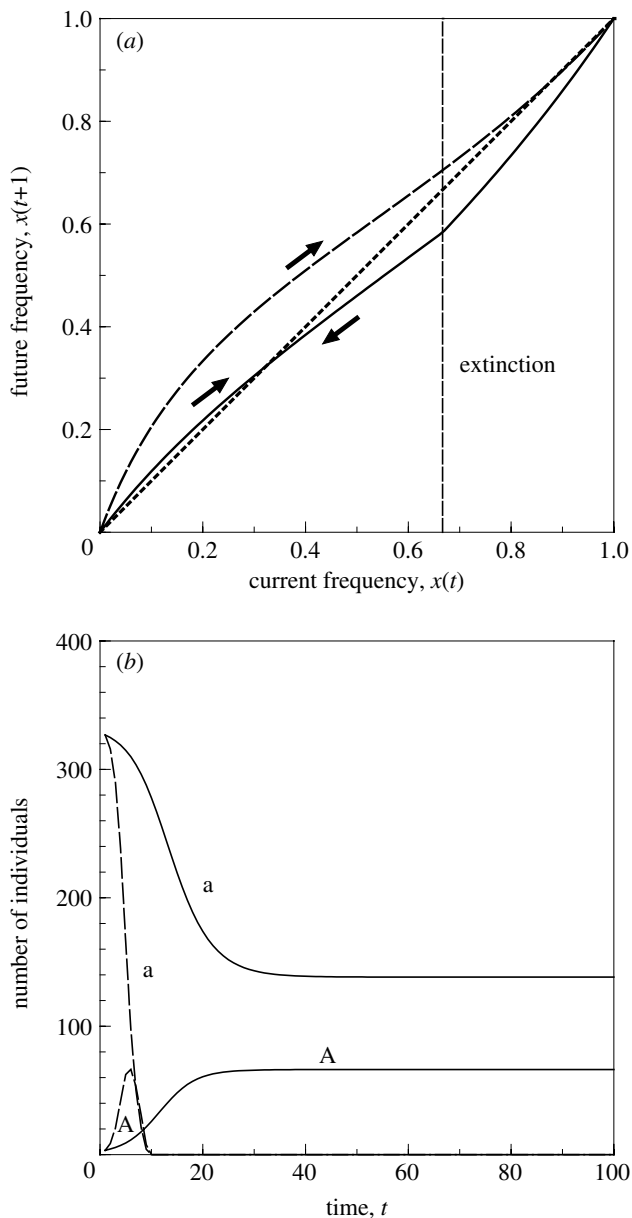


Figure 2. Evolution can increase the proportion of coercive males,  $x$ , beyond the extinction boundary if mating skew is not allowed to depend on population density. (a) Future frequency of the A allele,  $x(t+1)$ , against current frequency,  $x(t)$ ; see Appendix for allele definitions. If mating skew depends on density, the advantage of coercive males disappears faster (i.e. the solid line approaches and crosses the diagonal, which is marked as the dotted line). The process stabilizes at an equilibrium  $x^* = 0.324$ , which allows population persistence (solid line). Density-independent mating skew increases  $x(t)$  up till the extinction threshold (dashed line). (b) Evolution over time, showing the numbers of individuals carrying the 'a' or 'A' allele, if mating skew depends (solid lines) or does not depend (dashed line) on density. The results are derived according to the model in the Appendix, which assumes 'fast-slow' dynamics, where evolutionary equilibria are approached at a slower pace than ecological equilibria. However, results do not change qualitatively if these two timescales are equal (not shown). Parameter values:  $m_{\max} = 5$ ,  $f = 0.5$ ,  $F = 1.5$ ,  $k = 0.001$ ,  $K = 1000$ , which implies that extinction occurs when  $x \geq 2/3$ .

see Kokko *et al.* 1999a; Nonacs 2000; Fairbairn & Wilby 2001; Tsuji & Kasuya 2001; Jones *et al.* 2002). Nevertheless, it is intriguing that some studies cast strong doubt on the assumption that skew should

diminish at low population size, which was necessary for preventing evolutionary suicide in figure 2. For example, in several density treatments of guppies *P. reticulata*, Jirotkul (1999) found that an index of the mating skew, the opportunity for sexual selection ( $I$ ), decreases with density—i.e. the opposite of what figure 2 predicts. This was due to changes in male behaviour: high-density populations exhibited less courtship and more movement, and interference behaviours were most common at intermediate densities.

A study on bitterlings *Rhodeus sericeus* (Reichard *et al.* 2004a) similarly points out that biological details can matter, and produce predictions that differ from abstract null expectations such as that of figure 2. Bitterlings are fish that spawn in mussels, and males defend breeding sites aggressively. Interference competition by intruding males causes major disruption and often prevents spawning, but high male density was not found to lead to most disruption. Instead, at high density territoriality broke down as defending paternity against too many intruders became increasingly difficult (see also Reichard *et al.* 2004b), and in the absence of territorial aggression spawning disruptions became rarer (Reichard *et al.* 2004a). Similarly, in a seed bug *Neocoryphus bicrucis*, resource defence polygyny collapsed, rendering large males unable to monopolize females, when population density peaked (McLain 1992).

To complicate matters further, population density variations may also treat sexes differently, making densities and sex ratios covary. Regarding sexual selection, the most important measure of density for a given sex is not absolute density but the relative density of the opposite sex, and this offers another way to override the effects outlined in figure 2. Clutton-Brock *et al.* (1997) showed that increases in population density in the red deer *Cervus elaphus*, following a cessation of culling, led to a strongly female-biased sex ratio: males tend to starve first as the carrying capacity of the environment is approached. As a result, high-density conditions had low male density relative to the resource (females). Clutton-Brock *et al.* (1997) found that sexual selection was relaxed under those conditions, as a higher proportion of males fathered offspring. As noted by these authors, resource limitation reduces antler growth in ungulates more than growth of other traits, and there are two good reasons: resource limitation in ungulates predicts higher male than female mortality, which means low mating skew, which in turn reduces the benefits of large antlers. These same difficult conditions also increase the risks of developing excessive secondary sexual characteristics.

A multitude of sexual selection models predict runaway evolution towards infinitely large traits, and we lack sufficient knowledge of the ecological feedback mechanisms that help us to predict more realistic equilibria that take the ecology of resources, population sizes and sex ratios into account. Figure 2 on the one hand, and the scenario outlined by Clutton-Brock *et al.* (1997) on the other, both possess a feedback mechanism that eventually stops trait exaggeration, but these are rather different. In the former scenario, the evolving

trait causes harm to females and diminishes population density, which again diminishes the mating skew and stops the evolution of the trait. In the latter scenario, sex-specific expression of the trait causes male density to drop (while female density increases), and poor food availability at high densities, combined with high female availability, undermines the benefits of further trait exaggeration. Our current inability to say much about which scenario is more likely (or if some other ecological mechanism should kick in first) highlights that much more theoretical and empirical effort should be spent asking what determines the ecological and evolutionary equilibrium towards which sexual selection drives a species.

Two examples underline our lack of general predictions regarding strength of sexual selection in different densities. First, Pröhl (2002) describes a situation in dart-poison frogs *Dendrobates pumilio* which resembles that of the deer: high density leads to female-biased sex ratios and much less opportunity for sexual selection. Yet, Pröhl (2002) did not attribute the change to density-dependent male mortality (which was not measured), but to the female habit of aggregating around tadpole-rearing sites, which are more numerous in high-density populations. Second, an opposite pattern to that of Clutton-Brock *et al.* (1997)—i.e. increasing sexual selection with density—has been documented for the very same species, red deer, when density was considered at the local scale of a herd (Bonenfant *et al.* 2003). The study population of Bonenfant *et al.* (2003) lived in a forested habitat, leading to much smaller group sizes than in more open habitats.

The study of Bonenfant *et al.* (2003) is one of many that highlight that the population structure and the strength of sexual selection can be modified by environmental factors, such as variations in visibility (Seehausen *et al.* 1997; Seehausen & van Alphen 1998; Järvenpää & Lindström 2004) or the availability of nest sites or other necessary resources for reproduction (Simmons 1992; Forsgren *et al.* 1996; Borg *et al.* 2002; Debus *et al.* 2003). Low-visibility scenarios mimic low population density if individuals detect each other visually. As environmental factors often are easy to manipulate, they could be used to investigate effects of population density too—although, obviously, the analogy is incomplete: visibility is not a result of reproductive output in the population in the same way as population density is.

Regarding this feedback, it is notable that studies often consider a link between some environmental conditions (such as nest site availability) and the numbers of individuals competing for the relevant resource (e.g. Forsgren *et al.* 1996; Borg *et al.* 2002), but they very rarely consider the full demographic loop: the behaviour of the two sexes leads to a particular pattern of reproductive output, which then determines population structure and thus feeds back to the behavioural options experienced by individuals (but see e.g. Sinervo *et al.* 2001; Horth & Travis 2002). Operational sex ratios are not the only demographic factors that respond to nest site availability (Ahnesjö *et al.* 2001), the overall density of a population should follow from density-dependent reproduction too,

assuming that, for example, nest sites are in short supply (Rodenhuse *et al.* 1997).

It is perhaps understandable that behavioural studies rarely examine the full density-dependent feedback. Detecting density dependence is not a trivial exercise, and findings can be strongly scale dependent (Ray & Hastings 1996). Hence, local variations in density may appear to be caused by chance environmental factors rather than the possibly large-scale processes that ultimately operate in population regulation. Spatial structure may also complicate the picture by introducing gene flow that has the potential to hinder local adaptation (Holt 2003, and references therein). But instead of being insurmountable obstacles, such factors could be seen as exciting challenges. For example, we know that gene flow and spatially varying selection can aid in maintaining genetic variation required in many models of sexual selection (Barton 1999). If variations in local density are responsible for spatially varying selection on male traits (Arnqvist 1992a), exciting empirical avenues follow immediately. The 'large-scale' questions, such as whether density dependent processes have a significant influence on the evolutionary outcomes of sexual selection, are so fundamentally important that we strongly encourage attempts to link the various scales from local behavioural interactions to questions of population-level persistence. In short, behavioural ecologists should pay more attention to processes that determine the dynamics of populations (Sutherland 1996).

#### (b) Reaction norms and alternative mate acquisition strategies

The simple two-allele, one-locus model of figure 2 shows frequency-dependent selection: the 'aggressive' male genotype performs relatively less well when common. Importantly, frequency dependence in this example is enhanced when density-modifying effects of alleles are taken into account (figure 2, solid lines): a higher proportion of A alleles leads to lower population size, which steepens the decline in the relative fitness of A. There is nothing in the definition of frequency dependence that excludes effects mediated by density. Thus, our example (figure 2) shows that the common experimental practice to standardize density, when studying frequency dependence, may lead to underestimating the strength of the very process one is interested in.

If one was to develop figure 2 further, allowing for a continuous distribution of possible trait values, one would probably have observed a single best genotype, where males are optimally coercive given their own biotic environment (i.e. strength of competition, importantly including both the number and the coerciveness of competitors). Optimal levels of male coerciveness—or any other trait related to mate acquisition—will then evolve according to density. This could be achieved in two ways (Hazel *et al.* 2004; Plaistow *et al.* 2004): strategies may be directly dependent on the individual's genotype, and the genotypes that produce the appropriate response in a given population density become common; alternatively, reaction norms may evolve, allowing individuals

to adjust to whatever density they will find themselves in (assuming that different densities are sufficiently commonly experienced by the population; Shuster & Wade 2003, p. 174). The latter alternative, phenotypically plastic mating strategies, should be particularly likely in fine-grained environments, where significant variations in density occur over a shorter timescale than the lifespan of an individual (Levins 1968; Schlichting & Pigliucci 1998). It may also be more likely if the mating skew is low (Plaistow *et al.* 2004).

Alternative mating strategies can also be clearly distinct: examples include residents and satellites on ruff *Philomachus pugnax* leks (Lank *et al.* 1995), winged and unwinged males in fig wasps (Cook *et al.* 1997) and 'sneaking' (Parker 1998) or female-mimicking (Hanlon *et al.* 2005) males in many taxa. If, as we argue throughout the paper, the relative fitness of strategies in mating systems is likely to depend on density, then the equilibrium proportion of individuals using each strategy should also be density dependent. As in the case of continuous trait variation, there are two possibilities for how an equilibrium is reached: different genotypes producing a fixed phenotype may compete, or reaction norms allow individuals to develop the appropriate response to each density.

Excitingly, several studies document phenotypic plasticity with respect to density in mate acquisition traits, in either continuous or discrete sets of traits. As an example of (fairly) distinct alternative mating strategies, Tomkins & Brown (2004) report conditional strategies in the European earwig *Forficula auricularia*. Males are dimorphic, differing in forceps length. The 'macrolabic' morph with long forceps is competitively superior in male–male fights, while the 'brachylabic' morph sneaks copulations. Poor nutrition during development leads to the development of sneaker males. But if fighting is a stronger determinant of mating success when density is high than if it is low (see figure 1a), then one expects the switchpoint to depend on population density. This was confirmed by Tomkins & Brown (2004): high-density island populations had greatly elevated proportions of the fighter morph. Do earwigs assess a density cue during development, or are the morphs inherited, combined with frequency-dependent selection on each island? In an earlier laboratory study (Tomkins 1999) found no effects of rearing density on forceps length, but we are not aware of studies on morph inheritance in this species.

Some laboratory studies, mostly on insects, provide direct evidence for plastic life-history decisions in mate acquisition traits. Both continuous and discrete mate acquisition have been shown to respond to larval density. As an example of the former kind, Gage (1995) describes that males of the moth *Plodia interpunctella* are sensitive to population density during larval development. Sperm competition is more intense at high densities, thus males reared at high densities take longer to develop and invest more heavily in the size of testes and ejaculates than males reared at low densities. Similar results have been reported in dung flies *Scatophaga stercoraria*, where high-density larval populations developed larger testes, and high-density populations showed signs of a trade-off between

investment in sperm competition and mate searching (Stockley & Seal 2001; but for negative results on other species, see e.g. Evans & Magurran 1999; Schaus & Sakaluk 2001). In the mite *Sancassania berlesei*, density cues occur during development (Tomkins *et al.* 2004) but operate in the opposite direction from the above examples: investment in intrasexual competition (here, in the form of a fighter morph) only appears to pay off in low-density colonies, where fighters can monopolize resources. High-density colonies suppress fighter morph production pheromonally, and instead invest in 'scramblers' (Radwan *et al.* 2002).

Plastic responses to densities can occur over behavioural time too, and thus they need not be fixed during early development. Behavioural changes are often simple to explain: it is so obvious that a lekking black grouse *Tetrao tetrix* should display more intensely when females are present on the lek, that the more challenging question becomes why display continues in their absence too (Kokko *et al.* 1999b; Rintamäki *et al.* 1999). While behavioural adjustments of this kind are often relatively easy to explain, they become evolutionarily interesting if they lead to consistently different mating patterns in high or low-density populations.

Male paternity guards such as mate guarding or copulation frequency provide examples of behavioural traits that intensify as a plastic response to the density of conspecific competitors (Komdeur 2001). This may lead to consistent differences in behaviour between breeding sites of different densities, as shown, e.g. in raptors (Mougeot 2000, 2004). Because males can usually guard only one mate at a time, the effect of mate guarding should resemble the scenario in figure 1b, where males move close to individual females and thereby diminish the mating skew. If population density intensifies male–male competition, the frequency or intensity of mate guarding will increase too (Davis & Brown 1999; Härdling *et al.* 2004; also see Sinervo 2001 for selection between genetically determined mate-guarding morphs), and this should counteract any density-related increases in skew. The net effect is unclear, however, because paternity is a complicated outcome of behavioural interactions (Thusius *et al.* 2001; Westneat & Stewart 2003). In vertebrate mating systems, increased efficiency of mate guarding is generally not expected to fully compensate if female tendencies for infidelity change (Kokko & Morrell 2005). For example, in barn swallows *Hirundo rustica*, stronger mate guarding effort in high densities did not compensate for a density-dependent increase in extra-pair copulation rates (Møller 1991). In invertebrates that often maintain close physical contact during mate guarding, the potential for density-related and guarding-mediated changes in paternity appear stronger. In the snapping shrimp *Alpheus angulatus* population density did not appear to influence pairing behaviour (Mathews 2002), but guarding durations have been found to increase with density in two other crustaceans, *Gammarus pulex* and in *Eogammarus oclairi* (reviewed in Jormalainen 1998). Quantifying density-dependent paternity patterns would be an obvious next step.

An extensive meta-analysis of effects of density on the multitude of possible alternative mating tactics is beyond the scope of our current paper. Given that our

modelling effort shows how crucially population persistence may depend on the ways different male types benefit from high or low density, we strongly encourage conducting such studies in the future. If density interacts with the evolution of sexual traits, population-level consequences for persistence or genetic diversity are almost inevitable. One trait that is of particular interest here is mate searching, which obviously needs to be performed by at least one of the sexes to guarantee population viability; we will return to this question in §4, below.

### 3. STRATEGIES OF THE LIMITING SEX: CHOOSINESS, RESISTANCE, AND MULTIPLE MATING

The limiting sex is generally not assumed to suffer from lack of potential mates, and the mating strategies are accordingly shaped by selection to either distinguish between several potential mates, or to thwart the attempts of too eager opposite-sex individuals if these impose net costs (sexual conflict in the strict sense, e.g. Chapman *et al.* 2003). Before asking how density variations may alter such behaviours, it is instructive to build a null model on how the behaviour of females (i.e. the usual limiting sex) influences mating skew, if their behaviour does not change with density.

Figure 1*b* shows that the effects are similar to lowering density in male–male competition. If females choose the best male that they can easily observe—i.e. one within a fixed distance—then this corresponds to a larger  $n$  in a best-of- $n$  rule if density is high; as a consequence, the mating skew is much more pronounced at high population densities (figure 1*b*). In other words, the same mate choice rule leads to stronger sexual selection at high density and, for example, evidence that extra-pair paternity correlates with breeding density could be seen to support this null model (this correlation appears to hold in within- but not across-species comparisons, Westneat & Sherman 1997; Griffith *et al.* 2002; Charmantier & Perret 2004). Note also that at lowest densities, the skew no longer changes with density (figure 1*b*), as females simply mate with the closest male regardless of the distance involved.

The overall density of individuals may perform poorly as a measure of local density, if individuals move in order to facilitate mating and breeding. Mating aggregations (leks) are a common phenomenon in diverse taxa (Höglund & Alatalo 1995), and males in non-lekking species often perform extensive mate searching, which will improve encounter rates for females. Spatial clumping increases the opportunity for sexual selection (Shuster & Wade 2003), but one should not carelessly argue that all situations, where individuals move closer to each other end up resembling high-density populations. In the case marked with filled dots (figure 1*b*), female distributions in space remain random, while males move until no male is far away from a female. The result is not high skew as in high-density populations, but a further lowering of skew compared to random locations of males. This is because monopolization of many females is very difficult when males search for females who remain

scattered in space (Emlen & Oring 1977; Blanckenhorn *et al.* 2003; Shuster & Wade 2003). Thus, while one can imagine dispersal rules that lead to high-density aggregations in both sexes, the example of figure 1*b* shows that the details of adaptive mate searching rules can retain, or even accentuate, the effects of low density. The need of females to adapt to situations of high or low mate availability should, therefore, not be immediately dismissed (Kokko & Mappes 2005).

Females of different species can face completely different problems related to mate availability. Let us first consider the case where superfluous matings are harmful to the female and the need to fend off unwanted males may be a major fitness cost for females. In some cases the least costly option for a female is to give up resisting unwanted mating attempts, but it is not obvious whether this ‘convenience polyandry’ (Rowe 1992; Lee & Hays 2004) is more likely at high or low mate encounter rates. The accumulating costs of superfluous mating can be considerable if the mate encounter rate is high, but this scenario could also mean that there is little point in resisting male mating attempts, as another male will soon arrive even if the current one is successfully rejected (Arnqvist 1992*a,b*; Rowe *et al.* 1994). A model by Härdling & Kaitala (2005) assumes that females gain enhanced fecundity but also suffer mortality costs when mating multiply, and predicts that females remate more willingly when population density is low, but the larger number of mating attempts by males in high-density populations compensates for this. The overall level of polyandry is, therefore, predicted to be independent of density, which also means that sperm competition is not necessarily strongest at high population density.

Experimental manipulations of density in water striders *Aquarius remigis* (Lauer *et al.* 1996) and dung flies *Sepsis cynipsea* (Martin & Hosken 2003) offer partial support for this idea. In the dung flies, females resisted male mating attempts more in high-density treatments, and the overall level of sexual activity was higher at high density (Martin & Hosken 2003). In water striders, female resistance and male mating behaviour both changed with density, yet male mating frequency was independent of male or female density; female mating frequency, however, was positively correlated with male density (Lauer *et al.* 1996). In natural conditions, mating frequencies of both sexes should obviously covary (Kokko & Jennions 2003; Arnqvist 2004). Using existing results as a proper test of a model, however, requires scrutiny of the assumptions, not merely of the predictions; for example, if matings are truly superfluous for the female, the reason to remate disappears, unless resisting harassment is more costly than accepting a mating. Such factors were not explicitly included in the model by Härdling & Kaitala (2005), although it did predict that a general increase in female mortality due to harassment should produce less resistance. Further theoretical and empirical work distinguishing between the costs of mating and the costs of experiencing mating attempts by males would clearly be fruitful.

Multiple mating is not always a case of convenience polyandry, but it may also be adaptive for the female

(Jennions & Petrie 2000). Whether a female is 'shopping for the best genes' (Evans & Magurran 2000; Bernasconi & Keller 2001; Hosken *et al.* 2003; Ivy & Sakaluk 2005) or compatible genes (Tregenza & Wedell 2002), 'trading up' to find the best genetic or social mate (McNamara & Forslund 1996; Jennions & Petrie 2000), or mating with as many mates as possible (Takakura 1999) or with some intermediate optimum number (Houston *et al.* 1997) for the sake of direct benefits, density can in every case influence the best strategy. In some cases, female mate preferences should change with density, not only in terms of the strength of the preference, but also its direction: males giving long or short calls should be preferred depending on density in grey tree frogs *Hyla versicolor* (Welch 2003), and female preferences in side-blotched lizards *Uta stansburiana* should likewise depend on the phase of the population cycle, as reproductive success of males depends on the types of morphs present in the population (Alonzo & Sinervo 2001; Sinervo & Zamudio 2001). It remains to be seen if females really do follow these cues.

Theoretical studies explicitly devoted to the study of density-related changes in mate choice rules appear rare, even though incorporating a proxy for density is easy: this is achieved by specifying a parameter 'mate encounter rate' that influences how quickly females can find another potential mate if they have rejected one. Unsurprisingly, models that incorporate mate encounter rates generally predict that females become less selective when mate availability is low (Hubbell & Johnson 1987; Crowley *et al.* 1991; Kokko & Monaghan 2001; Härdling & Kaitala 2005; Kokko & Mappes 2005), yet few studies have predicted the net effect on the rate of multiple mating (but see Härdling & Kaitala 2005). A less direct way to assess the effects of density is achieved by varying the cost of mate sampling: low density corresponds to high costs of locating another male. Such models, again, produce a higher willingness to mate indiscriminately when densities are low (Kokko *et al.* 2002; Hutchinson & Halupka 2004; but see Johnstone 1997).

Some empirical support exists for the idea that the limiting sex, in cases where it can be choosy, becomes more selective at high population density or when the relative density of the opposite sex is high (e.g. Gwynne 1984; Palokangas *et al.* 1992; Souroukis & Murray 1995; male choice, Shelly & Bailey 1992; Berglund 1995). But again, an interesting counterargument applies to some cases: female choice may be made more difficult at high density, because of cognitive constraints that make it difficult to choose from many options (Gerhardt & Klump 1988; Johnstone & Earn 1999; Cooley & Marshall 2001; Hutchinson 2005). Also, in some cases male resource defence or lekking may break down at high density, and give way to scramble-competition polygyny (Grant *et al.* 1995; Byrne & Roberts 2004), which again may make female choice difficult at high density.

In small (as opposed to sparse) populations, there is another constraint to mate choice evolution. Drift reduces genetic variability in small, isolated populations (Frankham 1997), and if females are seeking indirect benefits, less variation inevitably diminishes

the benefits of choice (Petrie & Lipsitch 1994). Extra-pair paternity in birds is often thought to reflect indirect benefits (but not solely, see Westneat & Stewart 2003), and island-mainland comparisons indeed reveal lower extra-pair paternities in island species or populations (Griffith *et al.* 1999; Griffith 2000). It is intriguing for the topic of our review that phylogenetic comparisons seem to support the island-mainland correlation better than the hypothesis that variations in breeding density explain interspecific variation in extra-pair paternity (Griffith *et al.* 2002).

Whether evolution of female behaviours have similar drastic effects on evolutionary equilibria as in the male case (figure 2), remains to be studied. In principle, one can argue that if excessive investment in ornaments caused low density, and low density increases costs of mate choice, then sexual selection again becomes self-limiting. Whether such a feedback has any practical significance, however, is not clear. What is clear is that there are good reasons to believe that female behaviours can lead to very different sexual selection at varying densities, and this does not necessarily require particularly sophisticated reaction norms. For example, females often mate relatively indiscriminately when they first mate (Jennions & Petrie 2000; Kokko & Mappes 2005). This makes sense: compared to the often slight effects of male quality, it makes a large difference to female fitness whether she can commence reproduction at all. Such an adaptation may not seem spectacular, but it automatically leads to a relaxation of sexual selection at low densities, i.e. conditions under which females cannot mate many times (Kokko & Mappes *in press*).

An interesting question for further study is whether female strategies that actively improve mate encounter rate (e.g. female pheromones, Greenfield 1981; Phelan 1997), evolve more readily at low density or when the temporal distribution of mate availability varies unfavourably for females (Calabrese & Fagan 2004) and makes at least some females sperm-limited (Wedell *et al.* 2002; Preston *et al.* 2003). Levitan (2004) describes a continuum of selective regimes in a broadcast-spawning sea urchin *Strongylocentrotus franciscanus*. Both sexes are under selection to improve fertilization success if local densities are low; males compete for fertilizations at intermediate densities; and high-density situations were characterized by sexual conflict and selection on females to avoid polyspermy. Only the case of intermediate density corresponds to 'standard' sexual selection theory, once again emphasizing the crucial role that density can play in the evolution of mating systems.

#### 4. INTERACTIONS BETWEEN THE SEXES: MATE SEARCHING, PARENTAL CARE AND MUTUAL MATE CHOICE

Before, we have assigned the role of the limited sex to males, and limiting sex to females, with the corresponding sex roles: one sex competes for mates, the other rejects superfluous mating attempts. There are, however, many aspects of reproduction that can be performed by either of the sexes, and of those we will



treat here: mate searching, mate choice, and parental care.

**(a) Mate searching: which sex?**

For successful fertilization, gametes must find each other. Mate searching in one form or another must, therefore, be performed by at least one of the sexes. Although the simplest form of searching—the release of huge numbers of gametes in broadcast spawners—shows that the male strategy of producing many small gametes is often automatically directed towards the searching role, the searching sex need not always be the male. If one of the sexes performs more searching, the need to search in the other is reduced (Hammerstein & Parker 1987). The game-theoretic nature of the problem means that the burden of searching may shift from one sex to the other. Density, by influencing search costs, could obviously be a factor responsible for shifts between the sexes, and this is nicely demonstrated by a study on fiddler crabs *Uca beebei* (deRivera *et al.* 2003). In this species, search costs are presumably lower in high-density areas, where burrows for shelter are easily found. Female searching for mates increased in these areas, while the male response was to reduce searching. An intriguing question, currently unanswered, is why females responded to reduced costs of searching while males appeared to respond to female behaviour, and not vice versa. A comparative study on fiddler crabs gives generality to these findings: easy searching conditions (high burrow density) were found to favour female searching (deRivera & Vehrencamp 2001). A similar pattern is documented in Lepidoptera (Greenfield 1981).

In anurans (Wells 1977) and Orthoptera (Alexander 1975), however, high density appears to favour male searching. Likewise, conditions of high population density and easy flight make male California patch butterflies *Chlosyne californica* switch to patrolling (mate searching), instead of waiting for females to arrive on their territories (Alcock 1994). Wickman & Rutowski (1999) have argued that high density favours male mate searching in insects in general: males search by default because it is this sex that benefits most from multiple mating (Hammerstein & Parker 1987; Wickman & Rutowski 1999), and it is only at low density that females become limited by mate availability, and they will then be selected to minimize time without sperm and begin searching themselves (Wickman & Rutowski 1999). To our knowledge, this argument has not been explicitly modelled. Theory predicts, however, that mate-locating games may change from one type (e.g. males search, females remain sparsely distributed) to another (e.g. males lek, females visit leks) based on fairly subtle changes in sex-specific costs of either activity (Ide & Kondoh 2000). Given the somewhat messy state of empirical data, further clarifying work aiming at predictive models of sex roles in mate searching is clearly needed.

A recent model (Lehmann & Perrin 2003) considers an additional reason for why males perform the majority of searching in most species: inbreeding avoidance. Inbreeding is easily avoided if one sex disperses, thus again either of the sexes could do all the work. But if choosy females avoid mating with kin,

males will have higher mating success if they move and their dispersal is consequently favoured (Lehmann & Perrin 2003). Mobile males would then be predisposed to do mate searching too. Whether this effect helps to explain variation in mobility, and whether correlations with population size or density would be expected, remains to be studied (small populations are often inbred, but may also have undergone genetic purging, Glémin 2003).

**(b) Mate searching: selection for mate-location ability**

Figure 1b predicts that sexual selection is weak if females are sparsely distributed. While this may (as a broad generalization) be true for conventional secondary sexual traits, it is certainly not the case for mate-location ability. The strength of selection for male mate-location ability is perhaps best exemplified by the impressive sensitivity of male moths to female pheromones: six molecules of olfactory cues used by the cotton leaf worm moth *Spodoptera littoralis* are sufficient to trigger a response in males, which is well below the sensitivities reported earlier for any organism (Angioy *et al.* 2003). Not many studies have documented variation in male ability to search for females, perhaps because this is difficult to achieve in a controlled manner in a confined area, particularly so if female density is low. However, in wolf spiders *Hygrolycosa rubrofasciata*, sexual selection was found to favour active mate searching, while natural selection—selected against it (Kotiaho *et al.* 1998). In line with the assumption that selective pressures for male mobility are strongest at low densities, it has been argued that difficulties in locating females and the consequent selection for small, highly mobile males lies behind male dwarfism in crab spiders *Misumena vatia* that live at low densities (Legrand & Morse 2000).

Yet, the same biological caveats that cast doubt on the null model of diminishing sexual selection at low densities (§2), appear in the context of mate searching too. A number of studies have investigated trade-offs between male mate searching and other components of his fitness, and found that it is not always the case that low density produces highest searching effort. As the population density increases, males may reduce courtship and increase movement instead (Hack 1998; Jirotkul 1999; Byrne & Roberts 2004); in these conditions cognitive constraints (Hutchinson 2005) or interference by males may prevent free expression of female choice, and high-density situations end up resembling scramble-competition polygyny instead (Grant *et al.* 1995). Scramble-competition polygyny may also result from a breakdown of territorial defence or other competitive hierarchies that aim to monopolize resources: too frequent challenges in high-density populations make monopolization of resources uneconomical (Radwan 1993; Byrne & Roberts 2004). In systems with residents and satellites, or territory owners and sneakers, high density may similarly favour the mobile male alternative (Reichard *et al.* 2004a). The possibility that increased movement in high-density conditions is not related to sexual selection, but reflects an adaptation to disperse from

high-density patches (Travis *et al.* 1999), should also be kept in mind when interpreting data on mobility, as well as possibly different scales of the searching processes: searching within a mating aggregation is different from searching the entire population.

Selection for male mobility, particularly if it occurs in low-density populations, could help populations avoid an Allee effect (reduction of growth at low population size that may result, e.g. from mate-locating difficulties; Courchamp *et al.* 1999; Stephens & Sutherland 1999) and hence improve population viability. However, we must stress that the above examples do not appear to give clear evidence that mobility is most favoured in sparse populations. There are also other reasons why male mate-locating behaviour does not necessarily benefit population viability. Competition to find maximally many mates can lead to protandry, i.e. earlier arrival or emergence of males compared to females (reviewed in Morbey & Ydenberg 2001), and this may leave some (late) females unable to find a mate (Calabrese & Fagan 2004). Female responses to this scenario have not been studied. Once again, this is a situation where one expects coevolutionary responses of females and males to each other's strategies of movement both in space and time.

### (c) Parental care, mutual mate choice and divorce

Of all the aspects of mating systems treated here, parental care is perhaps the field with the strongest recent advances in considering population-level feedbacks. Should an individual stay and care for the current brood, or desert in the hope that the other sex cares? Early models studied this problem as a game between the sexes (e.g. Maynard Smith 1977), which takes into account that the payoff from the current brood depends on what the other sex (the pair mate) does. However, these simple games did not take into account that the payoffs from *future* broods also depend on what the others do: whether an average member of the same or the opposite sex deserts will have a large effect on the availability of future mating partners. Models that fail to take this into account are not self-consistent (Houston & McNamara *in press*). There is ample empirical support that low availability of mating partners can constrain the benefits of deserting the current brood (Magrath & Komdeur 2003; Wiebe 2005; see also Härdling & Kaitala 2004). Self-consistent models incorporate the feedback between the behaviour of individuals in the population and the numbers available as mating partners in the population, to produce predictions on frequency dependent selection (reviewed in Houston *et al.* 2005). Such feedbacks can be essential, e.g. for explaining variability in care and desertion patterns (Webb *et al.* 1999). The density of potential mates can vary not only because of individual decisions of same- or opposite-sex individuals, but also because of overall population density. Indeed, it has been shown that male-only care in birds covaries with strong constraints on remating, measured as low population density (Owens 2002).

In species with biparental care, high reproductive effort by both sexes may favour mutual mate choice (Johnstone *et al.* 1996). The solution derived from a

self-consistent model (Kokko & Monaghan 2001) predicts choice evolution to be highly sensitive to mate encounter rates. Typically, solutions move from no choice by either sex, via choice in one sex only, to mutual choosiness, as the mate encounter rate increases (fig. 3 in Kokko & Johnstone 2002); the exact threshold values depend on the degree to which the costs of parental care are egalitarian, or very different (the latter favours choosiness in one sex only). Clearly, mutual mate choice should be most prevalent in high densities, and although we are not aware of any comparative studies testing this prediction, it is perhaps no coincidence that many studies on mutual mate choice are conducted in large seabird colonies (Jones & Hunter 1993; Velando *et al.* 2001; Childress & Bennun 2002; Daunt *et al.* 2003; Torres & Velando 2003, 2005).

A special form of mutual mate choice is divorcing a mate after he or she has performed unsatisfactorily (Dubois & Cézilly 2002). Since the benefits of divorce again depend on future mating opportunities, one would expect less frequent divorce in low-density populations, all other factors being equal. A comparative study on waterbirds lends support for this prediction (Dubois *et al.* 1998), in that colonial species had a higher divorce rate than solitary nesters. If divorce leads to lost breeding opportunities for divorce victims (Moody *et al.* 2005), lowering of divorce rates at low population density could mean improved population growth which, once again, is a candidate mechanism for counteracting Allee effects.

## 5. CONCLUSIONS

Behavioural ecologists sometimes appear to think of populations as no more than a convenient source of individuals for their experiments. It is time to realize that this is not sufficient: density dependence is the fundamental process through which populations reach their ecological equilibria. Since fitness of an individual is nothing but a measure of the demography of its offspring, it should be obvious that selective pressures can be influenced by density-dependent processes. For evolutionary processes other than sexual selection, it is perhaps more often realized that there is an important feedback that leads from individual behaviour to the demographic process, and then back to the level of the individual, as payoffs associated with individual actions change with density. To mention just one example, dispersal rates may sometimes be selected to increase when the mortality cost of dispersal increases (Heino & Hanski 2001). This is because high mortality of dispersers leaves many habitat patches empty, offering potentially spectacular success for a disperser who survives the journey and is able to commence reproduction in a virgin environment.

In this review, we have highlighted many ways in which mating systems may function differently in high or low-density populations. We have also developed a simple theoretical argument why this may, in some cases, truly matter for the persistence of sexually selected organisms. Empiricists should beware that phylogenetic studies that investigate whether sexual selection influences extinction risk (e.g. Morrow & Pitcher 2003; Morrow & Fricke 2004) provide

correlational evidence, and different possible directions of causality should, therefore, be considered. The low density of extinction-prone populations may have been the factor influencing sexual selection, rather than vice versa. Since there appears to be no consensus on how sexual selection influences population-level adaptation and extinction risk (e.g. Doherty *et al.* 2003; Lorch *et al.* 2003; Morrow & Fricke 2004), drawing conclusions about directions of causalities would be premature too. However, this highlights the need for manipulative experiments on population consequences of sexual selection—which intriguingly have so far produced conflicting evidence too (Holland 2002; Radwan 2004; Radwan *et al.* 2004).

Empirical data seem to offer many counterexamples to the assumptions of our models, yet this only proves the point that we have a question without good, general answers at the moment. The question in a nutshell: if it is conceivable that sexual conflict at least sometimes is detrimental for reproductive output at the population level, is there something intrinsically self-limiting about this harm, or is it a matter of pure luck that some species survive the battle, and others do not (Webb 2003; Dieckmann & Ferrière 2004; Rankin and López-Sepulcre 2005)? Either option opens up the possibility of highly intriguing and unexplored evolutionary processes, while a third (more boring) alternative is that major demographic effects of conflicts are exceptions, not the rule. But because of the close link between fitness and demography, this alternative would also mean that sexual selection has very little effect on individual reproductive success, and we consider this unlikely. Empirically, there seems indeed to be a bewildering variety of options of how competition for mates, mate searching, mate choice, sexual conflict and parental care can respond to density. Some work needs to be done before we have a framework to organize all this diversity.

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## APPENDIX

Kokko & Brooks (2003), in their figs 2 and 3, develop a one-locus, two-allele model of sexual conflict, where an allele A makes males more able to monopolize females (e.g. using coercion), but when A is expressed in females it brings about a fecundity reduction. The relative mating advantage to males is  $m$ , and female fecundity is  $F$  with the  $a$  allele, and  $fF$  with the A allele, where  $f < 1$ . The probability that a mating male has the A allele is  $y = mx/(mx + (1-x))$ , where  $x$  is the frequency of the A allele in the population. Assuming haploid inheritance, the dynamics of  $x(t)$  is given by (see Kokko & Brooks 2003 for a more detailed

derivation)

$$x(t+1) = x(t) \frac{(f+m)(1-x(t)) + 2fmx(t)}{2(1-(1-f)x(t))(1-(1-m)x(t))}. \quad (\text{A } 1)$$

In the current model, we let population size follow  $N(t+1) = N(t)(1-N(t)/K)F[x(t)f + (1-x(t))]$ , where  $K$  is the carrying capacity of the environment. We also modify the original model (Kokko & Brooks 2003) by letting  $m$  depend on density,

$$m(t) = 1 + (m_{\max} - 1)(1 - e^{-kN(t)}). \quad (\text{A } 2)$$

This function implies that  $m$  increases from the value 1 (no relative advantage in low-density populations) asymptotically towards the maximum value  $m_{\max}$  as population density increases. Assuming ‘fast-slow dynamics’ (i.e. evolutionary dynamics occurs over slower timescales than ecological dynamics), an allelic frequency  $x(t)$  predicts an equilibrium population size

$$N(t) = K \left( 1 - \frac{1}{F(1-x(t)(1-f))} \right). \quad (\text{A } 3)$$

The direction of evolution (increasing or decreasing frequency  $x(t)$ ) is obtained by taking the value of  $N(t)$ , calculating  $m(t)$  using equation (A 2), and then  $x(t+1)$  using equation (A 1). From equation (A 3) it also follows that the population goes extinct if  $x(t) > (F-1)/(F(1-f))$ .

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