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REVIEWS AND SYNTHESIS

Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment

Hanna Kokko,[1]* Hope Klug[2] and Michael D. Jennions[1]

Abstract

What explains variation in the strength of sexual selection across species, populations or differences between the sexes? Here, we show that unifying two well-known lines of thinking provides the necessary conceptual framework to account for variation in sexual selection. The Bateman gradient and the operational sex ratio (OSR) are incomplete in complementary ways: the former describes the fitness gain per mating and the latter the potential difficulty of achieving it. We combine this insight with an analysis of the scope for sexually selected traits to spread despite naturally selected costs. We explain why the OSR sometimes does not affect the strength of sexual selection. An explanation of sexual selection becomes more logical when a long 'dry time' ('time out', recovery after mating due to e.g. parental care) is understood to reduce the expected time to the next mating when in the mating pool (i.e. available to mate again). This implies weaker selection to shorten the wait. An integrative view of sexual selection combines an understanding of the origin of OSR biases with how they are reflected in the Bateman gradient, and how this can produce selection for mate acquisition traits despite naturally selected costs.

Keywords

Bateman gradient, mate limitation, mate competition, operational sex ratio, scope for competitive investment, sexual selection, sex roles.

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INTRODUCTION

Sexual selection favours traits that increase the ability to gain access to a limited supply of opposite-sex gametes (Darwin 1871). However, what conditions favour the spread of such traits? Explaining variation in investment into such traits (among species or populations, or between the sexes) often makes use of one of two key concepts. First, mate limitation, an essential component of Darwin's definition, is typically quantified by the operational sex ratio (OSR), the average ratio of males to females who are ready to mate (forming the 'mating pool') at a given time and place (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996). Second, selection favouring an increased number of matings is quantified as the Bateman gradient ('sexual selection gradient': Arnold & Duvall 1994; 'Bateman gradient': Andersson & Iwasa 1996), that is, the slope of the relationship between reproductive success and mating success (Bateman 1948; Arnold 1994; Jones 2009).

Intriguingly, most explanations only emphasise one of these concepts (OSR: Emlen & Oring 1977; Clutton-Brock & Parker 1992; Clutton-Brock 2007; Bateman: Arnold 1994; Arnold & Duvall 1994; Jones 2009). The exact nature of the relationship between them is rarely commented upon. One exception is Jones *et al.* (2000) who stated that while the OSR is a potentially important determinant of sexual selection, it does so by influencing the Bateman gradient which ultimately captures the operation of sexual selection (see also Jones *et al.* 2002). Similarly, Kokko & Monaghan (2001) presented theoretical predictions about how the OSR influences sexual selection by deriving the relationship between mating rate and fitness (although they did not use the term 'Bateman gradient'). They predicted a generally steeper relationship with stronger OSR biases, but sex role reversal did not happen at 1:1 OSR.

It has been suggested that the Bateman gradient is not only a more accurate reflection of sexual selection but also easier to measure than the OSR (Jones *et al.* 2002). Of course, a choice between measures should not be based on practical convenience alone. Because no single measure captures all aspects of sexual selection (e.g. Jones *et al.* 2002; Klug *et al.* 2010), a more complete approach is to identify the conditions that lead to a high or low Bateman gradient in a given breeding system for each sex and in relation to the OSR. Our model below shows that the OSR influences the Bateman gradient, but its role is less straightforward than the simplistic expectation that a strongly biased OSR invariably generates stronger sexual selection (Jones *et al.* 2002; see Emlen & Oring 1977 for the origin of these predictions). The OSR as a predictor of sexual selection has strengths and limitations (Box 1).

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[1] *Centre of Excellence in Biological Interactions, Division of Ecology, Evolution & Genetics, Research School of Biology, Australian National University, Canberra, ACT 0200, Australia*

[2] *Department of Biological & Environmental Sciences, University of Tennessee Chattanooga, 215 Holt Hall, Dept 2653, 615 McCallie Aven, Chattanooga, TN, 37403, USA*

**Correspondence: E-mails: hanna.kokko@anu.edu.au; michael.jennions@anu.edu.au; Hope-Klug@utc.edu*

Box 1 A brief history of why the OSR was over-simplistically equated with sexual selection

The general assumption that sexual selection must be stronger on whichever sex the OSR is biased towards is so widely accepted that it is worth re-examining what Emlen & Oring (1977) wrote:

> '*The OSR provides an empirical measure of the degree of monopolizability of mates. The greater the degree of imbalance in the OSR, the greater the expected variance in reproductive success among members of the limited sex…*' (Emlen & Oring 1977)

The initial use of OSR as an empirical measure of the 'degree of monopolisability' of mates led Emlen & Oring (1977) to predict that a male-biased OSR leads to polygyny and a female-biased OSR to polyandry. This prediction seems well supported empirically as we usually associate polygyny with intense struggles among many males to acquire the best position on a lek or to acquire a harem. Unfortunately, this empirical association resulted in the widespread acceptance of the more general theoretical claim about the OSR, even though Emlen & Oring's statement was based on a very specific example: variation in the OSR due to changes in the synchrony of female arrival at a fixed number of males. At a proximate level, less synchronous female arrival (which makes the OSR more male biased) would seem to make it easier for more competitive males to sequentially acquire mates. This would appear to provide a general basis for linking the OSR to sexual selection via the ease of mate monopolisation.

The problem, however, is that it is easy to conceive of counter-examples where the reverse relationship holds. Specifically, because the OSR is a ratio, it can also become more biased due to an increase in the number of competitors. This leads to the implausible (although not impossible) prediction that it is easier to monopolise multiple mates when there are very many same-sex competitors trying to do exactly the same thing. It is likely to be harder for a single dominant male to monopolise every arriving female when competitors are added. A male bias can make monopolisation difficult (Klug *et al.* 2010), and there is also evidence that females find it more challenging to discriminate between male traits when they are faced with a greater number of signalling males (Hutchinson 2005). In addition, it is easy to generate biologically plausible scenarios where the OSR has no effect (Klug *et al.* 2010; Jennions *et al.* 2012) or a negative effect (Fitze & Galliard 2008, 2011) on sexual selection.

Regardless of the empirical evidence, the broader point is that there is no obvious theoretical basis to justify the general claim that a more-biased OSR leads to easier mate monopolisation (Klug *et al.* 2010). A more complete explanation for the link between the OSR and sexual selection must be sought not in the proximate effect of the OSR on mate monopolisation, but in the way the OSR is associated with conditions that make selection favour traits that reduce the time it takes to acquire another mating.

Bateman gradients ought to be measured under conditions determined by the degree of mate limitation each sex experiences (Arnold 1994; Jones & Ratterman 2009). This creates a link between the two measures, best illustrated by redrawing Bateman's most famous dataset (Fig. 1). The usual presentation shows two slopes, one for each sex. It ignores the fact that zero matings lead to zero fitness. Whether unmated individuals are included or excluded does not change the male slope much, but this is not true for females (Fig. 1). The unspoken assumption is that as females rarely experience mate limitation, real data sets are unlikely to include unmated females. Although this is demonstrably false in some systems (Calabrese *et al.* 2008; Rhainds 2010), the conceptual issue raised is important regardless of whether any females remain unmated in a given species: given a potentially non-linear graph, where do we quantify the slope between reproductive and mating success? The answer depends on the typical distribution of matings per individual.

The likely number of mate encounters in any given time period is sex-specific and depends on the OSR (de Jong et al. in press). When more males than females are available to mate, each mating excludes a larger number of males than females, so males in the mating pool experience a longer wait (mate less often than females). In a male-biased situation, it is therefore often correct to follow the traditional approach of estimating the slopes with the assumption that mate finding is easy for females. Female-biased situations imply the reverse logic as it can then be difficult for females to find mates. For example, in a population where 50% of females remain unmated and 50% mate once, the female gradient should be measured near the origin where it is steepest for females (Fig. 1). Selection to increase the mating rate is now stronger on females than males (males under these conditions can mate multiply even if females do not; Fig. 1). The key message is that although one can quantify slopes for each sex by experimentally generating a wide distribution of mates per individual, in nature there are not equally many individuals in each mate number category (Arnold 1994; Jones & Ratterman 2009). This can change the biologically relevant Bateman gradients.

To obtain the shallow female slope in Bateman's most famous data set requires an implicit assumption about the OSR. It should therefore be clear that Bateman gradient estimates must be linked with an understanding of the natural origins of OSR biases. The OSR itself is an emergent property of sex differences in life-history traits. Factors influencing the OSR can be divided into factors that affect (1) the adult sex ratio, such as sex-biased mortality (Moore & Wilson 2002) and the primary sex ratio (West 2009), and (2) the sex-specific time that individuals spend outside the mating pool, for example, providing parental care (Trivers 1972; Kokko & Jennions 2008), replenishing gamete supplies or regaining body condition (Clutton-Brock & Parker 1992). Sometimes, changes in the OSR also occur very rapidly (e.g. due to sex-specific, temperature-dependent effects on breeding cycle duration, Kvarnemo 1994; or food availability affecting spermatophore production, Gwynne & Simmons 1990).

Our argument that integrating Bateman gradients and the OSR provides a more satisfying picture of sexual selection is not simply a case of two estimates being better than one. The extent to which either measure on its own can predict the actual strength of sexual selection is debatable. This is particularly obvious for the OSR where, despite its key theoretical role for over 35 years, there is mixed empirical support for how well it predicts various properties

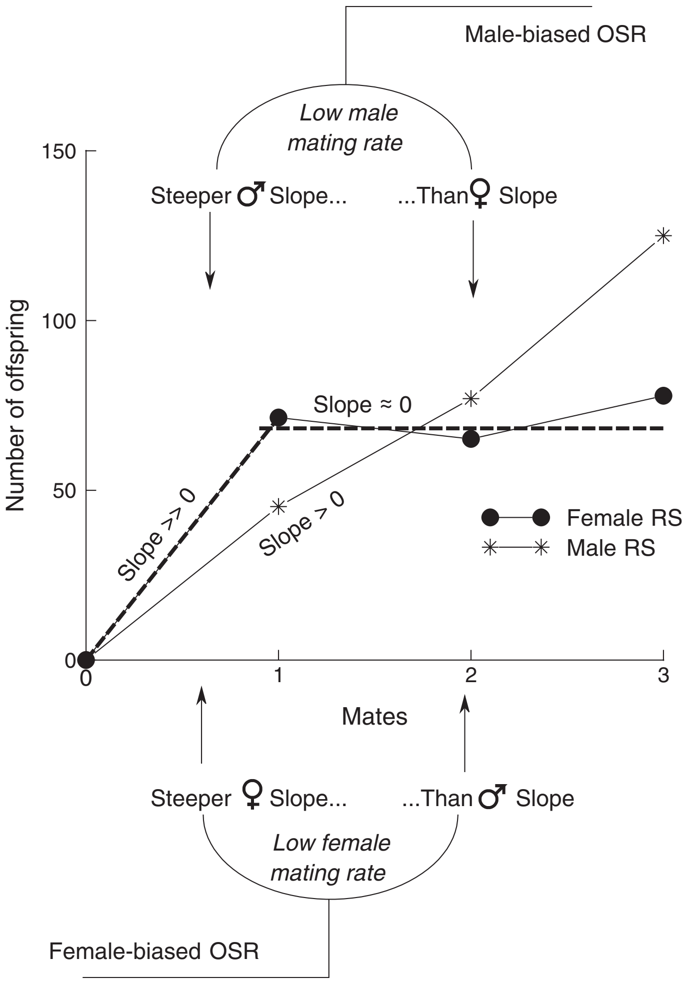

Figure 1 Bateman's (1948) *Drosophila* experiments yielded data on male and female fecundity for different numbers of mates (here, we depict his most well-known series 5 and 6). Whether the female slope is shallower than the male slope depends on the OSR. Two possible examples are shown: one with many more males than females (a typical male will mate less often than a typical female) and one with many more females than males (the reverse relationship: females do not mate often). If females often remain unmated and males rarely do so, the correct slope for females steepens. Note, however, that in reality the *y*-axis values can change with the general mating pattern: paternity can increase if females rarely mate multiply. Dashed lines are linear regressions.

of mating systems (Klug *et al.* 2010; Weir *et al.* 2011), including the Bateman gradient itself (Jones *et al.* 2004). Some studies find the expected positive relationship between OSR and mating competition, estimated via behavioural proxies or by measuring selection gradients on sexually selected traits (e.g. Berglund 1994; Vincent *et al.* 1994; Kvarnemo *et al.* 1995; Quinn *et al.* 1996; Jirotkul 1999; Kvarnemo & Simmons 1999; Grant & Foam 2002; Klug *et al.* 2008). Other studies report a positive relationship, but note that sex role reversal does not occur at a 1:1 OSR (Forsgren *et al.* 2004). Finally, some studies find no detectable relationship, or report unexpected results (e.g. Cleveland *et al.* 2002; Mills & Reynolds 2003; Denoël *et al.* 2005; Head & Brooks 2006; see de Jong *et al.* in press for insightful discussion).

Some readers might find it hard to understand why the OSR does not always predict the level of sexual selection. Surely, competition for mates is always stronger when the OSR is more biased? This misunderstanding might reflect ambiguity in usage of the term 'competition'. Competition sometimes refers to the active display of competitive behaviours and evolutionary investment in traits such as weapons (Weir *et al.* 2011). Competition can, however, also be used to describe the situation that individuals experience, regardless of their response. If competition is defined by the ratio of competitors to contested resources, the OSR is indeed synonymous with competition for mates. Tautologies (OSR equals competition in the latter sense) are, however, of no explanatory value. Mating system theory must therefore address the entire path from the competitive situation to the resultant sexually selected responses (i.e. investment into competitiveness). The main question then becomes: *Does being in a more competitive situation translate into stronger sexual selection?* If the answer is generally 'yes', then the OSR is a useful predictor of sexual selection. If the answer is 'no', the Bateman gradient can potentially help us understand why OSR does not predict sexual selection.

The widespread appeal of the OSR results from the intuitive notion that, all else being equal, investment into competitive traits is more necessary as competition intensifies. Here, we ask how well this intuition holds. We ignore other complicating factors such as post-copulatory sexual selection to address the core conceptual issues surrounding OSR as a determinant of sexual selection in those cases where it should in principle work well.

BATEMAN GRADIENT AND THE OSR, UNITE!

We can think of two potential answers for why more 'competition' (the situation) does not always lead to greater 'response to competition' (the presence and elaboration of competitive traits). First, the OSR might not fully characterise the situation. The OSR cannot be biased towards both sexes simultaneously, but both sexes can be mate limited (e.g. at very low density). We deal with this by including population-wide mate availability (parameter M) in the model below.

The more important answer is that even when the OSR measures how difficult it is to acquire a mating, it does not measure how much fitness increases (or decreases; e.g. Fig. 2 in Arnold 1994; Shuker *et al.* 2006) with each additional mating (Jennions & Kokko 2010; p. 354). How an individual's fitness changes with its mating rate is the focus of the Bateman gradient. The Bateman gradient and the OSR are incomplete in complementary ways: one describes the fitness gain per mating and the other the potential difficulty of achieving matings.

This leads to a major question: Is there a logical relationship between mate limitation (which increases with an OSR bias) and high fitness gains from additional matings (steep Bateman gradient; see Fig. 2 in Jones & Ratterman 2009)? This relationship, when positive, conspires against the success of individuals who form the OSR majority. The same individuals that experience stronger mate limitation (OSR bias) are also those who benefit more from additional matings (steeper Bateman gradient). In such cases, we expect selection to favour attempts to overcome mate limitation, even at the expense of a decline in other fitness components. There is also an intriguing paradox: a complete understanding of sexual selection clearly requires understanding why the OSR–Bateman relationship should often be positive. However, if this relationship predominates in nature, it is easy to discount the need to question it and instead to use either measure, ignoring the importance of the other. It is then deceptively easy for studies to appear to explain sexual selection fully even when only one of these measures has been considered.

Do not forget it is an investment

Although potentially common, a positive covariation between mate limitation and a steep Bateman gradient is not inevitable. Indeed, variation in this relationship explains cases where the majority sex in the OSR is under weaker sexual selection (Kokko & Monaghan 2001; Forsgren *et al.* 2004). The sex that experiences stronger competition does not invariably invest more in competitive traits, because more profitable routes to fitness than increased mating success can differ between the sexes. For example, should a paternally caring male desert his young to try to breed again? Strong mating competition can favour greater paternal investment, because mating investment brings meagre returns when the OSR is male biased (Kokko & Jennions 2008).

In general, investment in sexually selected traits is expected to trade-off with other fitness components (e.g. immunocompetence, parenting ability, survival). The more important these other components are for net fitness, the stronger the trade-off selecting against further investment into sexual competitiveness. Any evolutionary analysis of investment into sexually selected traits must consider the associated costs and not just the Bateman gradient and OSR. This should be obvious because, in the absence of costs, even a minute benefit of multiple mating would select for infinitely elaborated sexually selected traits, rendering quantitative differences in Bateman and OSR irrelevant to predicting the strength of sexual selection.

Below, we present a model that explicitly adds investment costs to existing theory. Our model is also inspired by questions that have arisen in a related debate about the use of I_{mates} and OSR as proxies for sexual selection (Klug *et al.* 2010; Krakauer *et al.* 2011; Jennions *et al.* 2012): these papers describe situations in which sexual selection appears unchanged across a range of OSR values, despite variance in male mating success, and variance-related measures (e.g. I_{mates}) responding to the OSR.

A MODEL TO INTEGRATE OSR, BATEMAN AND INVESTMENT PRINCIPLES

The 'time-in, time-out' framework has proven a useful tool in mating system theory (e.g. Clutton-Brock & Parker 1992; Parker & Simmons 1996; Kokko & Monaghan 2001; Kokko & Ots 2006; Kokko & Jennions 2008), although the somewhat clumsy terminology is better expressed as time spent in the mating pool and its opposite, which we call 'dry time'. Individuals wait (and potentially compete) for another mating to happen while in the pool. Each mating is followed by a 'dry' state, the length of which, the 'dry time', was originally called 'time out'. An individual is 'dry' as long as parental care, sperm replenishment, foraging to regain energy to breed and similar 'renewal' activities preclude an immediate return to the mating pool.

Kokko & Jennions (2008) derived the OSR from first principles assuming that the sex ratio at maturation is r, that males and females can differ in their 'dry time' (T) and mortality rates, and that mortality can also differ between individuals in the pool (μ_{p}, originally μ_{I}) and those in the dry state (μ_{d}, originally μ_{O}). The fitness of an individual (see Appendix) then becomes

$$w = \frac{a e^{\mu_{\mathrm{d}} T}}{e^{\mu_{\mathrm{d}} T}(a + \mu_{\mathrm{p}}) - a} \tag{1}$$

where a is the mating rate (the inverse of the average waiting time) for individuals in the pool. The link between the OSR and eqn (1) arises because the OSR affects a. Each mating removes one male and one female from the mating pool for a sex-specific dry time period. The mating rate of a focal individual is $a = M\sqrt{OSR}$ for females and $\tilde{a} = \frac{M}{\sqrt{OSR}}$ for males, where M is the population-wide mate-encounter rate (see Kokko & Jennions 2008, including the 'sperm-like' notation ~ to denote male-specific values). Neither sex mates fast when M is low (e.g. low density or inefficient locomotion). At any value of M, mating rates are lower for the sex that forms the OSR majority. At OSR = 1 : 1, both sexes mate at a rate M. The OSR is an emergent property of the dry time, pool time, sex-specific mortalities and the sex ratio at maturation (Appendix).

Our goal is to predict how individuals of a given sex respond to mate competition. Answers to such questions are probabilistic (Box 2) because an evolutionary innovation that improves mating rates might not arise, but several established principles outline a likely answer. A trait will not spread unless selected for (except under fortuitous drift), and stronger selection makes it more likely that a beneficial trait becomes established (Barrett *et al.* 2006; Patwa & Wahl 2008). So, assuming that the relevant trait exists, selection theory predicts the evolutionary response to be proportional to the Bateman gradient. However, proportionality only applies if other fitness component are unaffected by investment into the sexually selected trait. This is unlikely, so we must specify how selection operates in the presence of trade-offs with other fitness components.

To start, we derive the Bateman gradient (expressed as a fitness differential) to investigate how the importance of overcoming mate limitation covaries with the limitation itself (i.e. the OSR). Thereafter, we derive the expected scope for investment into competitive traits given an evolutionary trade-off.

The Bateman differential

Definitions of the Bateman gradient are problematic because theoretical studies rarely define the time frame over which matings should be measured. In empirical studies, conventions vary widely (3–4 days in Bateman's original study; > 60 days in Jones *et al.* 2004). To overcome any ambiguity, we define the 'Bateman differential' as the derivative of fitness with respect to the mating rate for an individual currently in the mating pool. The value of this quantity, $\frac{\partial w}{\partial a}$, answers the key question 'How much fitter are individuals that mate faster?' The goal is to understand under what conditions large values of $\frac{\partial w}{\partial a}$ (indicating strong benefits from a high mating rate) tend to co-occur with a biased OSR (which pushes a towards low values, indicating mate limitation).

Differentiating eqn 1, we obtain, for females,

$$\frac{\partial w}{\partial a} = \frac{\mu_{\mathrm{p}} e^{2\mu_{\mathrm{d}} T}}{\left(e^{\mu_{\mathrm{d}} T}(a + \mu_{\mathrm{p}}) - a\right)^2} \tag{2}$$

The corresponding male equation is obtained by marking each variable with ~ .

It is worth noticing that $\lim_{a\to\infty} \frac{\partial w}{\partial a} = 0$. This means that if an individual's mating rate is already very high, selection does not favour additional effort to increase it further. The discussion includes a graphical model that explains why reducing the waiting time to the next mating is then not selected for; this evokes the classical scenario where mate availability does not constrain female reproduction.

Box 2 A hypothetical example to drive home why competition does not equal selection

Intuitively, competition is stronger if more individuals compete for the same number of resource items or, equivalently, if the same number of individuals compete for fewer items. So why contest the statement that the OSR predicts the level of competition and selection for mate acquisition? One problem (which we resolve in our model) is that if one wrongly assumed that being a member of the majority sex in the OSR is required for mate acquisition effort to be selected for, one could not easily explain situations where both sexes are simultaneously selected to search for mates, as the OSR can only be biased towards one sex at a time.

Another problem is that actual sexual selection on specific traits does not automatically follow from being in a competitive situation. To make a convincing case, we present a thought experiment that should dispel the illusion that the two phenomena are inexorably linked; thereafter, the nature of the real link (if any) can be reassessed. Consider a hypothetical species where females live underground in burrows where they tend their young, while males are sessile and live aboveground. Females emerge to feed aboveground using multiple burrow exits, but foraging does not make them available as mates. They can only mate immediately after moulting, which happens once every breeding cycle. Females mate with the first male that they encounter. As a newly moulted female can emerge from any one of her many burrow entrances, it is difficult for males to predict where to settle to maximise mating encounters. Consequently, males space themselves to minimise competition for food, and this spacing pattern also happens to minimise interference competition with other males when a mating opportunity arises. Beyond adopting this settlement pattern, there is no way for a male to improve his mating rate: no trait is under sexual selection even if there are always many males ready to mate with each receptive female (male-biased OSR).

Of course, one can argue against this very artificial example. In reality, some male trait is likely to be favoured by selection (e.g. greater production of olfactory cues if females locate males using scent, or a major evolutionary innovation such as the ability to move and enter burrows). In the absence of traits that increase access to mates there would be no need for sexual selection theory. Any theory, therefore, has to answer two questions raised by this hypothetical example. First, can theory comment on the likelihood that a trait currently exists that increases the ability of individuals of a given sex to compete for mates, despite there being no guarantee that this is the case? Second, if competitive traits exist, does the OSR predict the likely extent to which individuals of each sex will invest in such traits? The model we present shows that the answers come with some important caveats (Box 3).

Close inspection of the equation also reveals that $\lim_{a \to 0} \frac{\partial w}{\partial a} = 1/\mu_{\mathrm{P}}$. For example, if an individual's mortality while in the mating pool is 0.1, then the Bateman differential cannot exceed the value 10. This offers technical rather than biological insight: it is inappropriate to compare absolute Bateman differential values across different life-history scenarios. Whether a value is high or low has to be judged in relation to the expected lifespan. What counts as 'fast mating' for a long-lived male marine turtle is very slow for a short-lived mite. Even if sexual selection was equally strong in turtles and mites, the answers to 'How much does fitness increase if a male turtle gains one extra mating per day?' and 'How much does fitness increase if a male mite gains one extra mating per day?' will differ because one extra mating per day represents a vastly greater improvement of mating success for a turtle that normally mates very rarely, compared with a mite for which many daily matings are the norm.

The scope for competitive investment (SCI)

We will now consider investment decisions with an approach that readily handles life-history differences (see above): making fitness trade-offs explicit puts each value of the Bateman differential in the appropriate context. We ask whether a trait that increases mating rate but trades off with some other fitness component can spread. We define SCI as the *scope for competitive investment*. SCI quantifies the 'weight' that an individual puts on elevating mating success relative to investing into other fitness components. SCI is trait-independent in the sense that it can be computed for a hypothetical mating-rate improving trait. This is worthwhile because in the absence of actual evidence for sexual selection, we often want to know if this is because the relevant traits are not selected for, or whether an appropriate trait simply has not yet arisen.

We follow a long tradition in sexual selection theory by deriving our examples using survival as the 'other' fitness component (Andersson 1994). Future models could, of course, consider other fitness trade-offs. SCI = 1, in our case, implies that sexual selection can favour investment into mate acquisition up to equivalently high costs of reduced survivorship. For example, a trait that doubles mating success is favoured as long as it does not increase the individual's mortality more than twofold (i.e. halve expected lifespan). When SCI < 1, smaller survival costs suffice to prevent trait evolution, and SCI = 0 predicts that there will be no investment in traits that improve mate acquisition. Our approach is similar in gist to measuring the likely magnitude of female mating preferences as the maximum cost females are prepared to pay to express them (e.g. Fig. 2b in Kokko *et al.* 2002).

The reasons why SCI is generally likely to be a good predictor of variation in investment into sexually selected traits operate at two scales: initiation and elaboration. Consider variation in investment among species. The initial spread of newly arisen beneficial traits is more likely if net selection favouring them is strong (Patwa & Wahl 2008). The costs of a trait can vary among species. High SCI implies net selection favours the trait whether it imposes low or high costs. For example, mate searching could be riskier for some species than others. If SCI is high, mate searching is favoured even if there is high predation risk. If the appropriate traits arise, the SCI also measures the expected investment made before further elaboration is halted (at the current OSR). Low SCI indicates sensitivity to costs that affect other fitness components, identifying that trait elaboration will be halted sooner than when the SCI is high. Consequently, life histories strongly shaped by sexual selection, such as those where signalling or mate searching seriously compromises lifespan, are only expected to evolve when the SCI is substantial.

We will now derive the SCI for our scenario. We denote the sexually selected trait by x. The fitness of an individual is a function of the trait x,

$$w(x) = \frac{a(x)e^{\mu_\mathrm{d}(x)T}}{e^{\mu_\mathrm{d}(x)T}(a(x)+\mu_\mathrm{p}(x)) - a(x)} \tag{3}$$

The relevant fitness differential is now taken with respect to x:

$$\frac{\partial w(x)}{\partial x} = \frac{e^{T\mu_\mathrm{d}(x)}\left[e^{T\mu_\mathrm{d}(x)}\mu_\mathrm{p}(x)a'(x) - a(x)\left(e^{T\mu_\mathrm{d}(x)}\mu'_\mathrm{p}(x) + Ta(x)\mu'_\mathrm{d}(x)\right)\right]}{\left(\left(e^{T\mu_\mathrm{d}(x)}-1\right)a(x) + e^{T\mu_\mathrm{d}(x)}\mu_\mathrm{p}(x)\right)^2} \tag{4}$$

Here, $\mu'_\mathrm{p}(x) = \frac{\partial \mu_\mathrm{p}(x)}{\partial x}$ is the increase in 'pool time' mortality caused by the trait x, $\mu'_\mathrm{d}(x) = \frac{\partial \mu_\mathrm{p}(x)}{\partial x}$ is the increase in 'dry time' mortality caused by the trait x, and $a'(x) = \frac{\partial a(x)}{\partial x}$ is the increase in mating success caused by trait x. To derive the SCI, we ask how high $a'(x)$ must be to compensate for a given increase in mortality.

Selection favours an increase in the trait x if $\frac{\partial w(x)}{\partial x} > 0$, which yields

$$\frac{a'(x)}{a(x)} > \frac{\mu'_\mathrm{p}(x) + \mu'_\mathrm{d}(x)Ta(x)e^{-T\mu_\mathrm{d}(x)}}{\mu_\mathrm{p}(x)} \tag{5}$$

Equation 5 is general in the sense that mortalities can be sex-specific and differ between the dry and pool times. In our examples, however, we assume that the proportional increase in mortality applies equally strongly in either state ($\mu'_\mathrm{p}/\mu_\mathrm{p} = \mu'_\mathrm{d}/\mu_\mathrm{d}$, denoted below as μ'/μ). This is appropriate when, say, bright plumage makes an individual visible to predators regardless of whether it is currently seeking mates, or when large-bodied individuals must forage more to avoid starvation. Other types of cost that are only paid while actively seeking mates can be analysed by returning to eqn 5 rather than following our approach below.

Equation 5 together with $\mu'_\mathrm{p}/\mu_\mathrm{p} = \mu'_\mathrm{d}/\mu_\mathrm{d} = \mu'/\mu$ can be written in the form $Ca'/a > \mu'/\mu$. Here, C indicates how much mating gains must compensate for increased mortality, to still generate net selection for x. The concept of the scope for competitive investment (SCI) is therefore expressed as the value of C. Whenever $C > 0$ a trait can, in principle, spread due to sexual selection. However, if C is low the trait only spreads if it greatly elevates mating success at little cost. If C is high, far more costly traits can still spread. If $C = 0$, the trait is never favoured by sexual selection. This coincides with a zero Bateman gradient, but the SCI is a broader concept because it offers a general measure of the range of costs of a trait that can be 'tolerated' and the trait will still spread. This integration of gains (via matings) and losses (via other life-history components) means that the SCI provides a more robust expectation of whether sexually selected traits will actually evolve than the OSR, Bateman gradient or any other measure on its own.

The actual value of C is solved as

$$C = \left(1 + a(x)Te^{-T\mu_\mathrm{d}(x)}\frac{\mu_\mathrm{d}(x)}{\mu_\mathrm{p}(x)}\right)^{-1} \tag{6}$$

The value is low (rendering competitive trait evolution and/or elaboration unlikely) if individuals are not mate limited (a is already high) and if matings are followed by a substantial dry time T. Strictly speaking, an exceedingly long dry time again increases the scope for competitive investment (via the term $e^{-T\mu_\mathrm{d}(x)}$), but this is only relevant when the dry time is so long compared with the expected lifespan that individuals usually die before completing their first breeding cycle. Realistic values of T should fall below the inverse of the mortality rates, and here, the scope for competitive investment declines with a longer dry time.

WHEN DOES THE OSR PREDICT THE DIRECTION AND LIKELY STRENGTH OF SEXUAL SELECTION?

Equation 6 provides an analytical solution for the scope for competitive investment evolving in a given sex and setting. To return to our main question, we must ask whether the OSR and the Bateman differential are always positively related to the value of the SCI (i.e. the degree to which competitive traits are expected to be observed). Whenever a discrepancy is found, we need to determine whether this reflects negative (rather than positive) covariation between the OSR and selection for increased mating success (i.e. the Bateman gradient).

It is important to note that the OSR is not a population parameter that can be assigned arbitrary values. It is inexorably linked to the dynamics of matings and deaths. By varying the relevant underlying parameters (M, μ_p and μ_d for each sex), we can derive the OSR together with the simultaneously occurring values of the Bateman differential and the SCI. We cannot generate arbitrarily large or small OSR values if these are not achievable given the underlying parameters specifying the mating dynamics. This is why, in our examples, the OSR values are limited to a realistic range.

Likewise, the OSR and the mating rate a (or $\tilde{a}$) cannot vary independently. For males $\tilde{a} = \frac{M}{\sqrt{OSR}}$, for females $a = M\sqrt{OSR}$, thus an OSR bias towards either sex lowers the mating rate for that sex, which then (eqn 6) increases the relevant sex-specific SCI. It is nevertheless overly simplistic to assume that the OSR straightforwardly drives mating investment. Instead, inspection of model outcomes yields the following general conclusions.

> **Conclusion 1.** *If individuals of a given sex have a very short dry time, then the scope for competitive investment becomes large – irrespective of the OSR.*

This follows from eqn 6 because when $T = 0$ then $C = 1$ regardless of other parameter values. Notably, it applies whether mate availability is high or low (the value of a is irrelevant).

A short male dry time not only makes the male SCI high, but also has the causal effect of making the OSR male biased (Clutton-Brock & Parker 1992). One might therefore assume that whenever males experience high SCI, the OSR will be male biased. This is only a useful rule of thumb, however, as male SCI remains high under a short male dry time regardless of whether their brief dry time also results in a male-biased OSR. Put differently, even if the OSR is female biased (due to other factors) when male dry time remains brief, an abundance of females does not remove selection on males to invest in competitive traits.

We illustrate this with a situation where a large range of female dry time lengths – from as short as those of males to much longer – occur together with a female-biased sex ratio at maturation. Female-biased maturation sex ratios can arise due to high male juvenile mortality (e.g. mammals, Moore & Wilson 2002), or a biased primary sex ratio (e.g. *Wolbachia* and selfish male-killing elements in many insects, Werren *et al.* 2008). The OSR now varies from female biased to strongly male biased as female dry time increases (Fig. 2). Females are under strong selection to improve their mating rate (high female SCI) only at female-biased OSRs. For males, however, whose dry time is brief, there is strong scope for sexual selection (high male SCI) across the entire OSR range (Fig. 2). This finding is in line with the scenario in Jennions *et al.* (2012), where males were immediately available to re-mate (i.e. male dry time was brief) while females permanently exited the mating pool after mating. The selection differential on a hypothetical male trait did not depend on the number of females per male (i.e. OSR).

How to explain this result? In general, if paternal care or other routes to increase fitness are absent, then a male's fitness is solely determined by his mating rate. The competitive environment (or the OSR as its proxy) then becomes irrelevant for how much weight a male should put on increasing his mating rate compared with investing into other traits. Regardless of whether there are many or few competitors (or females), a male's sole task is to balance self-maintenance and mating success per unit time to maximise his expected lifetime mating success. The level of competition scales this expectation upwards or downwards, but it is erroneous to assume that gaining the maximum possible share of a population of a few females is less important than gaining the maximum possible share of many females. In hindsight, this simple insight makes our current finding (Fig. 2), and that of Jennions *et al.* (2012), obvious.

> **Conclusion 2.** *When the dry time of one sex varies from short to long, we expect a positive relationship between the OSR and the SCI in this sex.*

From eqn 6, it follows that the scope for the evolution of competitive traits is reduced by a long dry time T (mathematically: high T implies low C for realistic values of T), and intensified by greater mate limitation (low a implies high C), *except* if T is already very short in which case a has no effect (see Conclusion 1 above). If the dry time of the focal sex varies across situations (e.g. populations, species or over time), then a will be positively related to T for the focal sex. Simultaneously, the OSR is more heavily biased towards the focal sex when T is shorter. In combination, we have identified the conditions where intense competition (highly biased OSR) leads to a stronger response to mating competition (high SCI) in the manner described in many textbooks.

We illustrate this with a situation where $\tilde{T}$, the dry time of males, varies from very short to far longer than that of females (e.g. due to more male care), and female dry time T is moderately long in all situations (Fig. 3). For each sex, the OSR, the Bateman differential and the SCI all covary positively. The system switches from stronger competition among females to stronger competition among males at OSR = 1 : 1, where the dry time of both sexes is equally long.

Here, the scope for the evolution of female competitive traits is high at female-biased OSR. This is *not* because of the direct effect that T has on C (eqn 6) as female dry time does not vary (Fig. 3). Instead, females experience an indirect effect: when male dry time $\tilde{T}$ increases, there are fewer males in the mating pool, which decreases the female mating rate a and increases the scope for competitive investment. Competition among females intensifies when the balance of T and $\tilde{T}$ shifts towards a longer male dry time, even if female dry time remains unchanged. Here, the OSR is a good predictor of the likelihood of sexual selection because its shifting values determine whether mate limitation has a major influence on the reproductive success of individuals of a given sex.

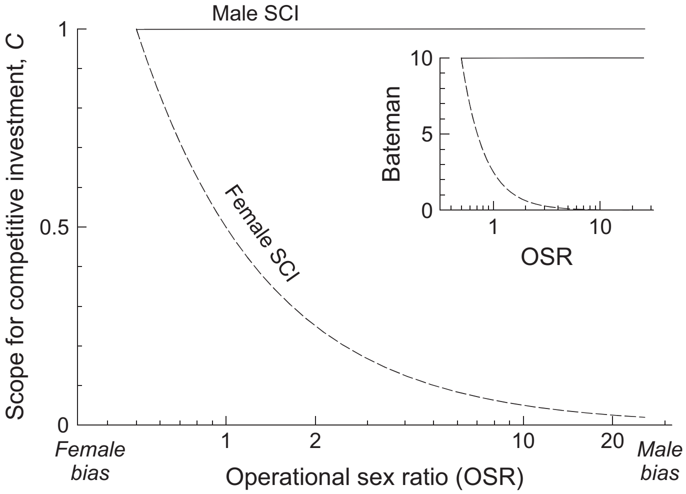

Figure 2 The scope for competitive investment (SCI, main figure) and the Bateman differential (insert) for males (solid lines) and females (dashed lines), when female dry time T varies between 10^{-6} and 1, and male dry time is always brief (though never below the smallest female value) at $\tilde{T} = 10^{-5}$. The OSR then varies between 0.499 (when $T = 10^{-6}$) and 26 (when $T = 1$). Other parameter values: sex ratio at maturation $r = 0.5$, mate-encounter rate $M = 100$, $\mu_d = \mu_p = \tilde{\mu}_d = \tilde{\mu}_p = 0.1$. The Bateman differential is always high for males regardless of the OSR, as is the scope for competitive investment.

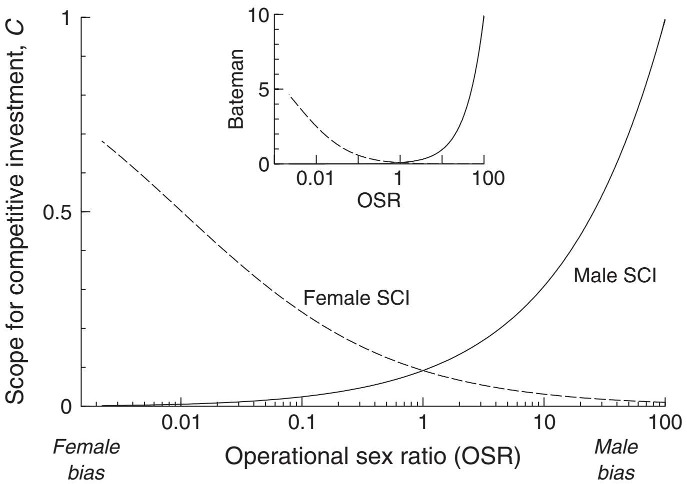

Figure 3 The scope for competitive investment (SCI, main figure) and the Bateman differential (insert) for males (solid lines) and females (dashed lines), when female dry time is always $T = 0.1$, and that of males varies between $\tilde{T} = 10^{-6}$ and $\tilde{T} = 10^{-0.5}$. Other parameters as in Fig. 2 except that the sex ratio at maturation is now even ($r = 1$). These assumptions yield OSR values ranging between 0.0022 and 101. In this example, the sex that shows greater scope for competitive investment is always the majority sex in the OSR. Stronger biases predict larger sex differences in competitive investment.

Conclusion 3. *If other life-history aspects vary, it is difficult to make simple predictions about investment in competitive traits based solely on the OSR.*

For simplicity, we present this section from a male perspective. In the scenarios summarised in Fig. 2, we had a female-biased sex ratio at maturation, while in Fig. 3 it was even. What happens when the sex ratio at maturation *and* the overall mate-encounter rate M vary among study populations or species? The effects are relatively straightforward. Anything that biases the adult sex ratio shifts mating rates up or down for a given sex, making it less (if up) or more (if down) valuable to increase the current mating rate. The effects of M and r differ only in that the effect of M operates in the same direction for both sexes (though the magnitude of this effect can differ between the sexes, see eqns 5–6 recalling that a depends on M). This explains why, in scenarios where variation in the OSR is partly due to differences in the sex ratio at maturation, SCI is strongest when the OSR is biased towards the focal sex and/or when the overall mate-encounter rate M is low (Fig. 4). Here, the relationships between the OSR, Bateman differential and SCI are all positive.

These results fit the general expectation that the scope for the evolution of competitive traits will intensify with a more biased OSR. Even so, this relationship can readily be reversed if data come from study systems where variation in underlying life history and population characteristics occurs in specific combinations. If two species differ for more than one variable that affect the OSR and the SCI, then the difference in competitive trait expression between the species might not be captured by predictions that assume that 'all else is equal'.

For example, if species B tends to have populations with a more male-biased OSR than A, this factor, when operating alone, predicts greater competitive investment by males in B than in A (assuming that male dry time is not extremely short; see Conclusion 1). Reflecting this, SCI always increases with the OSR along each curve (Fig. 4). But what if species B also occurs at higher densities so that the mate-encounter rate M is higher than in A? It is then possible that A follows the uppermost curve of Fig. 4, while B follows the lowest curve. The consequence? Even though B has a more male-biased OSR, males of species B are expected to invest less into competitive traits than those of species A (Fig. 4), despite both species having the same dry time parameters and adult mortalities.

Depending on the relationships between parameters that affect the OSR and SCI respectively, very different inferences about how the OSR relates to competition for mates can be drawn. As is often the case in evolutionary ecology, it is relatively easy to derive 'all else being equal' predictions by varying a single parameter. This approach is dangerous, however, if in nature key parameters covary in ways that obscure the predicted bivariate pattern.

The worst case scenario

By investigating all possible patterns of covariation between parameters, one could become quite sceptical about the notion that the OSR can yield general predictions. To provide something akin to a 'worst case' scenario, consider a set of species where mortality and mate-encounter rates M are negatively related. This pattern of covariation is biologically plausible if high mortality lowers the population density, thereby reducing M. If mortality is also sex-specific, and there is greater variation in male than female mortality across species, the OSR and SCI show a surprising relationship (Fig. 5). In stark contrast to the traditional view, the SCI declines *for both sexes* when the OSR increases from female biased to male biased. Why?

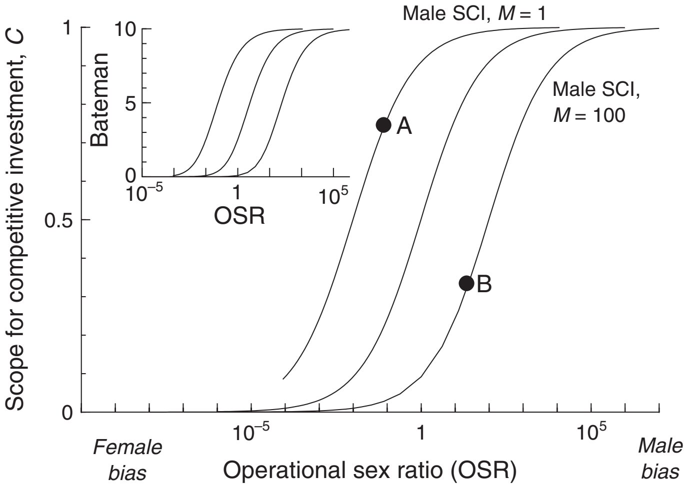

Figure 4 The scope for competitive investment (SCI, main figure) and the Bateman differential (insert) for males under three different mate-encounter scenarios: low (M = 1, leftmost curve), medium (M = 10, middle curve) and high (M = 100, rightmost curve). In each scenario, sex ratio at maturation, r, varies from 10^{-3} to 10^{3}, yielding a large range of OSR values. Within each scenario, a more male-biased OSR predicts greater scope for investment in competitive traits by males. However, this prediction can be broken if different species follow different curves because, for example, they live at different densities (exemplified by A and B). Other parameter values: $\tilde{T} = T = \mu_p = \mu_d = \tilde{\mu}_p = \tilde{\mu}_d = 0.1$.

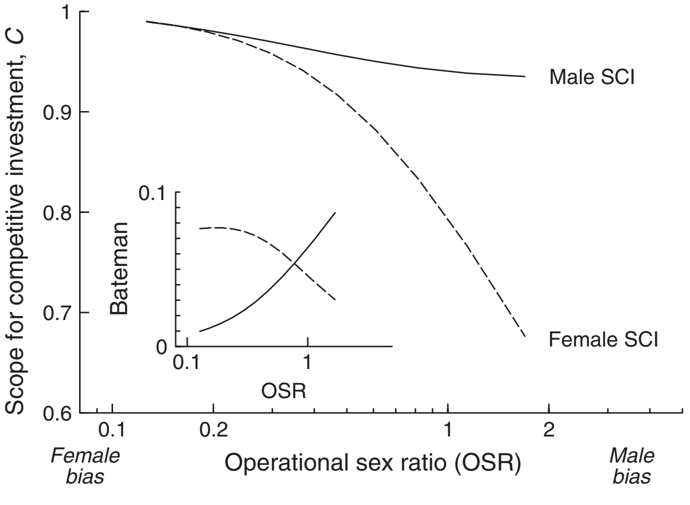

Figure 5 Scope for competitive investment (main figure) and Bateman differential (insert) for males (solid lines) and females (dashed lines), when higher OSR values are associated with three concurrent changes: from left to right, $\mu_p = \mu_d$ changes from $10^{1.1}$ to 10^{1} (the exponent takes 11 equally spaced values 1.1, 1.09, …, 1.0), $\tilde{\mu}_p = \tilde{\mu}_d$ changes from 10^{2} to 10^{1} (the exponent takes 11 equally spaced values 2, 1.9, …, 1.0), and M changes from 1 to 10 (11 equally spaced values 1.0, 1.26, …, 10). The OSR ranges between 0.126 and 1.7. While at male-biased OSR males are more likely to show competitive investment than females, males here (right side) have a lower competitive scope than they do when the OSR is female biased (left side).

Box 3 Take-home messages

(1) *OSR and the Bateman gradient should not be considered alternative approaches to predict sexual selection.* They provide complementary information. The model presented formally describes causal links between the two measures.

(2) *Ease of mate monopolisation is not necessarily greater if the OSR is more biased.* Emlen & Oring (1977) illustrated the effect of the OSR with an example where a more male-biased OSR (due to less synchronous female arrival) led to greater monopolisation of females. This relationship is not inevitable. This is readily apparent when recalling that the OSR (being a ratio) can become more male biased due to an increase in the number of competitors. It is hard to conceive of a widespread proximate mechanism that would lead to more competitors increasing mate monopolisation (Klug *et al.* 2010).

(3) *The terms 'competition' and 'competitive' are used ambiguously.* It is important to discriminate between the competitive situation that an individual encounters, and the observed response in terms of investment into sexually selected traits. The OSR is always related to the former, only sometimes to the latter (e.g. Fig. 2).

(4) *A competitive situation does not always generate strong net selection for competitive traits.* Alternative routes to fitness matter and these can lower the SCI even when the OSR suggests strong competition for mates.

(5) *Causal explanations are more complete when considering why dry time, and its sex differences, affect how strongly an individual benefits by mating more frequently than when simply assuming that OSR drives competitive responses.* Individuals with very short dry time should always be selected to mate frequently (Fig. 2), and individuals with long dry time are often not selected to reduce the time it takes them to mate if achieving this task reduces other fitness components (e.g. survival).

(6) *Bateman gradient interpretations require considering the origin of OSR biases.* An understanding of sexual selection based on observed Bateman gradients is not complete, unless we also investigate what creates mate limitation that determines the distribution of observed matings at which the gradient is appropriately measured.

(7) *Despite complexities, there are general rules.* We can identify situations where traits that improve mating rates are (1) likely to be absent, (2) likely to be present (and more strongly so if the OSR is suitably biased) or (3) likely to be present in a manner that does not depend on the OSR. These correspond to (1) SCI = 0 (when dry time T is long and the waiting time in the mating pool is short in the focal sex; note that these often co-occur because $T > 0$ tends to shorten the wait via its effect on the OSR), (2) SCI > 0 combining with $T > 0$ and (3) SCI > 0 because dry time $T \approx 0$ for the focal sex.

Moving from left to right (Fig. 5), female mortality declines from 1.1 to 1, male mortality from 2 to 1 and M increases from 1 to 10. A low mate-encounter rate, M, increases the SCI because it more beneficial to increase the mating rate when mates are encountered rarely. Improved mate-locating ability is therefore selected for *in both sexes* in populations near the left of the figure. Here, the OSR also happens to be female biased, because male mortality greatly exceeds female mortality. In contrast, mate location is far easier for populations near the right-hand side of the figure where M is higher. Here, the OSR re-establishes its importance in the limited sense that males, being the more numerous sex, display greater scope for the evolution of competitive traits than do females. This limited sense success of the OSR is also reflected in the Bateman differential, which is highest for males at strongly male-biased OSRs. The SCI makes it clear, however, that males are still expected to invest most heavily in mate acquisition traits when the OSR is female biased (left end of Fig. 5). Here, selection has switched to an emphasis on mate location ahead of competitors when females are numerous relative to males but still scarce in absolute terms (low density). This type of competition (caused by low M) can select for investment into sexual traits than reduce survival, but is not captured by the OSR.

DISCUSSION

> 'To understand the intensity of sexual selection it is not the overall population ratio of males to female that is of importance, but rather … the operational sex ratio…' *Emlen & Oring 1977*

> 'Among other factors, parental investment, the operational sex ratio and potential reproductive rates are certainly important to the process of sexual selection, but perhaps they should be seen as affecting sexual selection through their impact on the realized relationship between mating success and fertility, Bateman's true cause of sexual selection.' *Jones et al. 2000*

How does the OSR translate into sexual selection? We have shown that the OSR will often covary with the scope for competitive investment into traits that improve mate acquisition. The problem, however, is that a description of nature (an observed pattern of covariation) can provide a 'rule of thumb' without constituting an explanation. This is most noticeable when dealing with exceptions to a rule (e.g. our Conclusion 1). A valid explanation must identify the causal mechanisms underlying a relationship.

When defining the OSR, Emlen & Oring (1977) attempted to do so by equating it with the ease with which individuals of one sex monopolised access to the other (Box 1). Although this is conceivable true in some cases (e.g. when considering the temporal 'clumping' of females arriving on a lek), it does not follow from first principles. The weakness in their argument is readily apparent when one considers that the OSR is a ratio that can be altered by changes in the numbers of either sex. Monopolisation is not necessarily easier when the OSR is more biased if the bias indicates that there are now more competitors trying to gain access to the same number of potential mates (Klug *et al.* 2010).

Today, our understanding of why the OSR is likely to be associated with the observed level of investment into sexually selected traits (explaining sex roles and across species variation in sexual selection) is more nuanced. The OSR is strongly influenced by the times individuals spend in and out of the mating pool (Appendix). Our model shows that these two parameters, in turn, have a direct effect on the extent to which an individual of a given sex benefits from improving its mating rate (i.e. its Bateman differential).

The OSR is an emergent property of the life history of the two sexes. It does not contain any information about the extent to which an individual will benefit from additional matings. Our approach, however, makes it possible to investigate whether the factors that create OSR biases simultaneously tend to create conditions where individuals of a given sex will benefit from greater investment into mate acquisition traits, even at the expense of lower survival or a decline in other important fitness components. This is the core of our method for calculating the SCI.

Unfortunately, the SCI is far less readily measured than counting individuals that are ready to mate (the OSR). This is a natural consequence of its inclusiveness: benefits must be contrasted against costs, to predict whether a trait causing a higher mating rate can spread. An additional complication is that the current competitive environment might differ from the ancestral one. Evolving traits are expected to change sex-specific mortalities, with feedback effects on the OSR itself (see Kokko & Jennions 2008 or Lehtonen & Kokko 2012 for how this could be taken into account in future models).

Although rarely discussed, there is also a major issue when empirically measuring Bateman gradients: choosing the duration over which matings occur. In principle, a faster mating rate will translate into more matings acquired (e.g. in an experiment of a fixed duration). However, there is little discussion in the literature that explicitly confronts the issue that analysis of mating rates might have to be quantified differently in systems where 'dry time' commences as soon as a mating happens (as in our model, allowing us to concentrate on mating rates of individuals in the pool) vs. those where several matings can contribute to one 'dry time' cycle. In many cases, an additional mating enhances fitness more after the previous one has been completely dealt with than if the opportunity arises too soon. This argues against measuring the Bateman gradient without thinking about the relevant timescales for a given species. For example, matings that occur within a day or over several months might have very different effects on the reproductive output of a female lizard that produces clutches every few weeks.

Despite such complications, we believe that the SCI, by encouraging empiricists to ask how strongly an individual is selected to shorten its waiting time in the mating pool (Box 3), has heuristic value that can inform empirical studies. The essential gist of the SCI can be expressed in a toy model (Fig. 6). We consider three scenarios that could be interpreted as a male in a weakly male-biased OSR scenario, a male in a very male-biased OSR scenario and a female of a species with conventional sex roles (or a male performing extensive paternal care). In each case, we ask the same question: if a novel trait arises that shortens the time taken to acquire a mate by 2/3 (i.e. mating rate triples), but at a cost of 30% shorter lifespan, will it spread? The SCI approach predicts that the trait benefits individuals with $C = 1$ (whose dry time is very short) even if it shortened their lifespan up to 66%, while individuals with lower C (longer dry time) will not benefit. Indeed, if the trait appears in individuals whose dry time is short (A and B in Fig. 1), the spread begins: a 30% shortening of lifespan is amply compensated for by participating in many more mating events before dying. Although a more biased OSR creates a far longer wait time for individuals in B, the trait benefits A and B individuals alike, simply because the dry time is short for both (Conclusion 1: short dry time, hence the OSR does not matter).

By contrast, the same trait, if it appears in individual C, will be selected against. Strong mate acquisition effort shortens the waiting time, but if the long dry time and biased OSR conspired to make any wait short to begin with, the benefit of faster commencement of each (still lengthy) breeding cycle remains so meagre that it fails to compensate for a shorter lifespan (Fig. 6). We believe that an emphasis on whether it pays to invest in shortening the average

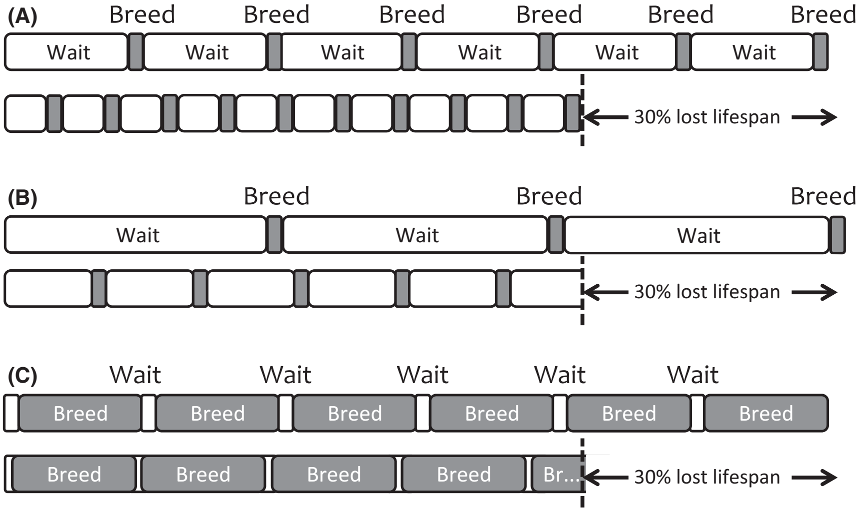

Figure 6 A hypothetical trait triples the mating rate (2/3 reduction in waiting time before mating compared with the population average) but decreases expected lifespan by 30%. Will it spread, and is this related to dry time (dark bars)? Expected reproductive success is the lifetime number of completed breeding events. In A and B, short-lived individuals with the trait (lower rows) achieve higher reproductive success than longer lived individuals without the trait, regardless of the OSR value (inferred from the population average expected waiting times, i.e. less biased OSR in A than B). However, if dry time is long relative to pool time (case C), the trait's effect on waiting time is insufficient to compensate for its detrimental effect on lifespan.

waiting time to acquire a new mate steers clear of pitfalls inherent in many current verbal explanations of sexual selection. For example, any explanation purely based on the supposed intensity of competition at different OSRs, in our experience, leaves many students puzzled as to why this is not the case in the very simple example of Jennions *et al.* (2012). Likewise, statements about the direction of sexual selection based on sex differences in parental investment become clearer once they are explicitly framed in terms of the length of the dry time and the corresponding wait time in the mating pool rather than the greater 'value' of acquiring a mate when the opposite sex invests more heavily into parental care. An astute student could ask why, if breeding requires a sexual partner for both sexes, investment in parenting should predict mate seeking by only one sex (Hammerstein & Parker 1987). This becomes much more understandable once the meagre benefit of reducing the waiting time on the heavily investing sex is highlighted.

The SCI is a measure of whether a costly trait that improves mating rates can, in principle, be expected to evolve at a given OSR. Whether a single, specific trait is able to improve mating rates equally well across a variety of scenarios (OSRs and population densities) is a separate question. The answer depends on biological and mechanistic detail. For example, weaponry might become relatively useless at low density and be replaced by selection for efficient mate searching (locomotion). It is therefore appropriate to conceive of trait x in our model as a suite of traits that together affect mating success. The SCI indicates the total investment into these traits, while the distribution of this investment among traits might change with the OSR or with density.

Despite these challenges, we encourage researchers to test whether high SCI situations do indeed reliably produce evolutionary responses with greater investment into traits that enhance mating rates. Ultimately, progress is not made by approaches that produce unwarranted support for their claims merely by matching empirical results to theoretical predictions if the underlying reasoning is problematic (Klug *et al.* 2010; Jennions *et al.* 2012). We hope that our model has provided a logical analysis of the causal factors that affect the strength of sexual selection and, more specifically, that it has clarified potential reasons for different relationships between Bateman gradients, the OSR and sexual selection.

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AUTHORSHIP

HK wrote the equations and all authors contributed to writing.

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