REVIEW
# The mismeasurement of sexual selection

H. KLUG*, J. HEUSCHELE*, M. D. JENNIONS† & H. KOKKO*†

*Department of Biological and Environmental Science, University of Helsinki, Finland
†Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra, Australia

## Abstract

Sexual selection can explain major micro- and macro-evolutionary patterns. Much of current theory predicts that the strength of sexual selection (i) is driven by the relative abundance of males and females prepared to mate (i.e. the operational sex ratio, OSR) and (ii) can be generally estimated by calculating intra-sexual variation in mating success (e.g. the opportunity for sexual selection, $I_s$). Here, we demonstrate the problematic nature of these predictions. The OSR and $I_s$ only accurately predict sexual selection under a limited set of circumstances, and more specifically, only when mate monopolization is extremely strong. If mate monopolization is not strong, using OSR or $I_s$ as proxies or measures of sexual selection is expected to produce spurious results that lead to the false conclusion that sexual selection is strong when it is actually weak. These findings call into question the validity of empirical conclusions based on these measures of sexual selection.

## Introduction

'*It manifests itself in the shape of the lucky fool, defined as a person who benefited from a disproportionate share of luck but attributes his success to some other, generally very precise, reason'.*
Nassim Nicholas Taleb (author of *Fooled by Randomness*).

Over the last 25 years, sexual selection has been increasingly acknowledged as a major evolutionary force. It is invoked to explain widespread patterns in nature at scales that range from consistent differences between male and female longevity (Moore & Wilson, 2002), to variation in the rate of speciation and extinction among taxa (Seddon *et al.*, 2008) and to changing rates of molecular evolution (Dorus *et al.*, 2004). Current sexual selection theory makes two core predictions. First, that the relative numbers of males and females prepared to mate at a given time and place (i.e. the operational sex ratio, OSR) is a primary determinant of the strength of sexual selection (Emlen & Oring, 1977; Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjö, 1996; Reynolds, 1996; but see Shuster & Wade, 2003 and Shuster, 2009). Second, that the observed intra-sexual variation in mating success reflects, albeit imperfectly, the actual

*Correspondence:* Hope Klug, Department of Biological and Environmental Science, University of Helsinki, PO Box 65, 00014 Helsinki, Finland.
Tel.: +358 9 1915 7713; fax: +358 9 1915 7694;
e-mail: hope.klug@helsinki.fi

strength of sexual selection (Bateman, 1948; Wade, 1979; Arnold & Wade, 1984a; Shuster & Wade, 2003). These general predictions, which remain largely untested across a range of biological scenarios, have led to several measures to predict and quantify patterns of sexual selection (reviewed in Shuster & Wade, 2003; Mills *et al.*, 2007; Jones, 2009; Table 1).

The two most widely used measures are the operational sex ratio and the opportunity for sexual selection (see Box 1 and Fig. 1). Because of their disproportionate use (Box 1 and Fig. 1), we focus primarily on these two measures. The OSR is used to predict and explain patterns of mate competition, sexual selection and the type of mating system (Emlen & Oring, 1977; Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjö, 1996, 2002; Reynolds, 1996). Specifically, the strength of sexual selection on males and females is expected to increase as the OSR becomes more male- and female-biased, respectively (Emlen & Oring, 1977). The opportunity for sexual selection ($I_s$, quantified as the square of the coefficient of variation in mating success for a given sex; Arnold & Wade, 1984a) is a dimensionless measure of variation in mating success. The actual strength of sexual selection on a given sex is expected to increase as $I_s$ increases, which is based on the general evolutionary premise that 'the greater the variance in fitness, the stronger the force of selection'

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**Box 1: The measurement of sexual selection (2004–2008)**

Sexual selection has been quantified using numerous measures (Arnold and Wade, 1984a,b; Arnold & Duvall, 1994; Andersson, 1994; Ruzzante *et al.*, 1996; Kokko *et al.*, 1999; Mills *et al.*, 2007; Jones, 2009). We present and define six of the most frequently used measures in Table 1. Of these, the opportunity for sexual selection ($I_s$) is the most commonly used measure of sexual selection (Fig. 1a). During each of the past 5 years, $I_s$ accounted for $39.3 \pm 3.83\%$ (mean ± SE) of reported quantifications of sexual selection. The second most common measure, the selection gradient, accounted for $32.6 \pm 1.94\%$ of reported measures of sexual selection. Bateman gradients and selection differentials

accounted for $15.2 \pm 3.39\%$ and $9.58 \pm 2.90\%$ of reported measures, respectively, and Morisita's Index and the index of resource monopolization each accounted for $1.65 \pm 1.05\%$ of the reported measures of sexual selection.

Likewise, there are two quantitative proxies that are used to predict, explain and sometimes approximate the strength of sexual selection: the operational sex ratio (OSR) and potential reproductive rates (PRR) (Table 1). Of these, OSR was most frequently used or discussed in studies of sexual selection during the last 5 years (Fig. 1b). (See online Supporting information file for a list of the 59 studies that report at least one of the six measures of sexual selection listed in Table 1, and a list of the 79 studies that refer to operational sex ratio or potential reproductive rates during 2004–2008 (see also Fig. 1)).

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(Shuster & Wade, 2003, p. 19). This variation in fitness is known to be a necessary but not sufficient condition for sexual selection, and theoreticians regularly acknowledge that $I_s$ reflects the maximum, but not necessarily the realized, strength of sexual selection (Crow, 1958; Wade, 1979; Arnold & Wade, 1984a; Jones, 2009). Despite this, $I_s$ is promoted as an empirical measure of sexual selection (Arnold and Wade, 1984a,b; Shuster & Wade, 2003; Jones, 2009).

In practice, $I_s$ and the actual strength of sexual selection are regularly assumed to be strongly positively correlated and used interchangeably (Shuster & Wade, 2003; Bjork & Pitnick, 2006; Duval & Kempenaers, 2008; Vanpé *et al.*, 2008; Sword & Simpson, 2008; Box 2).

Given the importance of evaluating OSR and $I_s$ as predictors or measures of sexual selection, the number of studies to date that investigate their performance is

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**Box 2: Quotes illustrating current views and uses of the opportunity for sexual selection, $I_s$, and examples of how the 'opportunity for' and 'strength' or 'intensity' of sexual selection are used interchangeably**

Bateman (1948) asserts that: ''Variance in fertility is…a measure of the intensity of selection,'' where ''The fertility of an individual is here taken to mean its actual contribution to the next generation''.

Shuster & Wade (2003, p. 466) state: ''Quantification of the opportunity for selection…provides the only concrete method for identifying how and when sexual selection is a significant evolutionary force''.

Shuster & Wade (2003) argue that: ''the greater the variance in fitness, the stronger the force of selection'' (p. 19) and suggest that ''$I_{mates}$ measures the strength of selection arising from the variance among males in mate numbers'' (p. 41).

In describing a recent study, Sword & Simpson (2008) state that: ''To test [the hypothesis that the intensity of sexual selection is weaker in species exhibiting female-biased… dimorphism], the authors used a statistical measure of the strength of sexual selection known as the 'opportunity for sexual selection' ($I_{mates}$) … They found that the intensity of sexual selection on giant weta males was similar to that found in another co-occurring weta species…Thus, weta join other recent studies…suggesting that the intensity of sexual selection for female-biased dimorphism can equal that observed in male-biased species''.

Bjork & Pitnick (2006) state that ''The 'opportunity for sexual selection' is a standardized index…of sexual selection intensity on males and the sex difference in the strength of selection… $I_s$ estimates the overall intensity of sexual selection… High $I_s$ in *D. bifurca* and *D. lummei* exists despite there being no significant

difference between the male and female sexual selection gradients within these species. This bolsters the claims… that sperm gigantism in *Drosophila* is a product of intense sexual selection…The joint analysis of $I_s$ and sexual selection gradients provides a resolution to the paradox [regarding the predicted self-limiting nature of sexual selection for larger sperm].'' The authors additionally suggest that ''sperm length and relative investment in sperm production serve as additional indicators of the most widely accepted measures of sexual selection intensity. Thus, sperm size and spermatogenic investment may provide… accurate assays for comparative analyses of the strength of sexual selection… '' Note that conclusions in this paper regarding current sexual selection acting on *D. bifurca* and *D. lummei* were based on $I_s$ as the authors found no difference between the sexes in sexual selection (i.e. Bateman) gradients. Furthermore, there was no significant relationship between $I_s$ or $I_{male}$ and sperm investment across several species.

Duval & Kempenaers (2008) claim that ''The potential for evolutionary change can more generally be quantified via the opportunity for selection, $I$, which is the variance in relative fitness… In polygynous mating systems, the opportunity for sexual selection is usually calculated as $I_{male}$… This measure quantifies the potential for selection to operate, separate from the evolutionary response to selective pressure and without requiring precise knowledge of the mechanism by which selection occurs…''

Vanpé *et al.* (2008) state that ''Measuring the opportunity for sexual selection is crucial for addressing many questions in behavioural ecology (such as the evolution of sexual size dimorphism, conspicuous male traits, alternative mating tactics, and sex-biased parental investment, Andersson, 1994) and population dynamics…''

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surprisingly low (Fairbairn & Wilby, 2001; Jones *et al.*, 2002; Mills *et al.*, 2007; Fitze & Le Galliard, 2008). Here, we use a simple model to critically evaluate the predictions that OSR and $I_s$ generally reflect the strength of sexual selection. In doing so, we highlight how easily these predictions can fail and draw attention to the danger of relying on OSR and $I_s$ as explanatory variables or measures of sexual selection.

## Why be suspicious of OSR and $I_s$?

### Issue 1: The OSR-mate monopolizability conundrum

Emlen & Oring (1977) argued that the intensity of sexual selection will depend on the potential for mate monopolization – that is, the extent to which certain individuals of a given sex can 'control' or dominate mating opportunities to the exclusion of other individuals of the same sex. Specifically, they suggested that the monopolization of mates by the more common sex will increase as the OSR becomes either more male- or female-biased, and that the strength of sexual selection will increase with greater mate monopolization (Emlen & Oring, 1977). In their words, 'the OSR provides an empirical measure of the degree of monopolizability of mates.... the greater the degree of
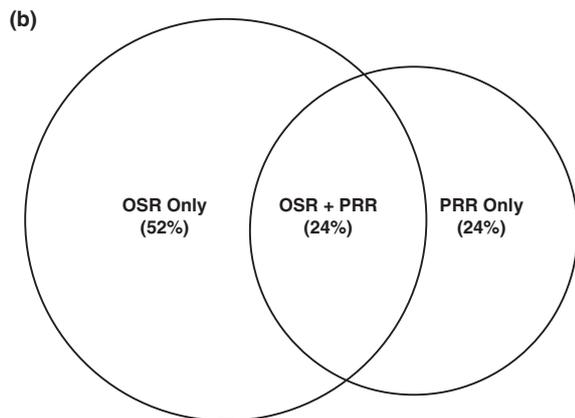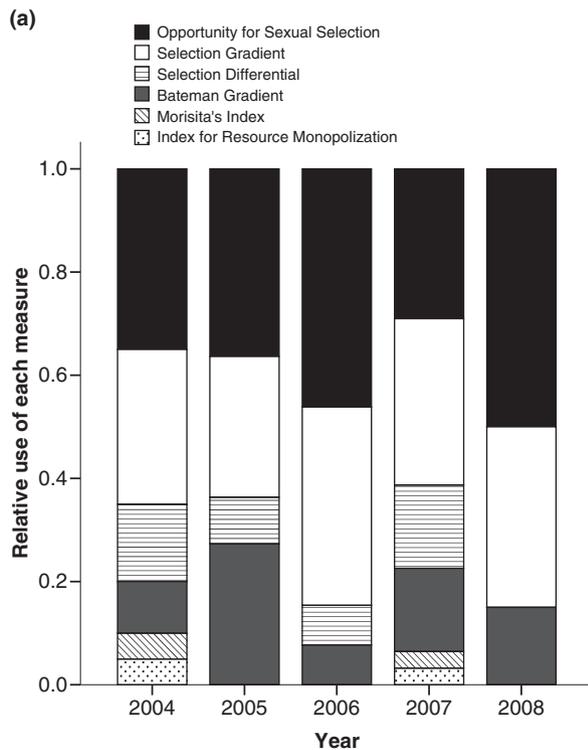
imbalance in the OSR, the greater the expected variance in reproductive success among members of the limited sex' (Emlen & Oring, 1977, p. 216). Despite some criticism of the use of OSR as a proxy for sexual selection (Arnold & Duvall, 1994; Shuster & Wade, 2003; Shuster, 2009), it is still regularly used to predict and explain patterns of sexual selection (Box 1 and Fig. 1b; Ahnesjö *et al.*, 2001; Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjö, 1996; Reynolds, 1996). Surprisingly, the actual relationship between OSR and mate monopolizability across various mating scenarios remains a mystery (see also Ims, 1988). The only guarantee as the OSR becomes more biased is that the mean mating success of the mate-limited sex will decrease. In contrast, the effect of OSR on mate monopolization, which relates to the variability in mating success for the mate-limited sex, depends on how mates are acquired. Variability in mating success can increase or decrease depending on the extent to which mate monopolization is possible across various OSRs (Arnold & Duvall, 1994; Shuster & Wade, 2003; Shuster, 2009; Fig. 2).

Here, we use simple examples to illustrate several possible relationships between mate monopolization and OSR (Fig. 2). For simplicity, we only consider sexual selection on males by assuming that females mate once

**Table 1** Measures used to quantify, predict and explain patterns of sexual selection.

| Measure | Brief description |
| --- | --- |
| The opportunity for sexual selection ($I_s$) | A standardized measure of intra-sexual variation in mating success; measured as the square of the coefficient of variation in mating success for a given sex. The upper limit to the strength of directional sexual selection (Wade, 1979; Arnold & Wade, 1984a; Shuster & Wade, 2003; Jones, 2009) |
| Bateman gradient ($\beta_{ss}$)[a] | The relationship between mating and reproductive success for a given sex, measured as the slope of the least-squares regression of reproductive success on mating success for the sex of interest. An estimate of the strength of selection acting on mating success (Arnold & Duvall, 1994; Jones, 2009) |
| Selection gradient ($\beta$)[a] | For the univariate case, the slope of the regression of relative fitness on the phenotypic value of the focal trait. If several traits are examined, the partial regression coefficient for each trait is equivalent to its selection gradient. When calculating the selection gradient with respect to sexual selection, the relative mating success of a given sex is used in place of relative fitness. Often referred to as the strength, intensity or force of selection on a given trait (Lande, 1979; Lande & Arnold, 1983; Arnold & Wade, 1984a; Arnold & Duvall, 1994; Andersson, 1994; Jones, 2009) |
| Selection differential ($s$) | The difference between the mean phenotypic trait value before and after one or multiple episodes of selection. Equivalent to the covariance between relative fitness and trait value. The selection differential with respect to sexual selection is equivalent to the covariance between relative mating success and trait value for a given sex (Lande, 1979; Lande & Arnold, 1983; Arnold and Wade, 1984a,b) |
| Morisita's index ($I_\delta$) | In studies of sexual selection, the observed variance in mating success corrected for by an estimate of the variance expected when all mate acquisition probabilities are equal (Morisita, 1962; Fairbairn & Wilby, 2001; Mills *et al.*, 2007) |
| Index of resource monopolization ($Q$) | In studies of sexual selection, the ratio of observed variance in mating success and the maximum possible variance in mating success, with both variances corrected for by an estimate of the variance expected when all mate acquisition probabilities are equal (Ruzzante *et al.*, 1996; Fairbairn & Wilby, 2001; Mills *et al.*, 2007) |
| Operational sex ratio (OSR) | The average ratio of males to females who are ready to mate at any given time in a given place (Emlen & Oring, 1977; Andersson, 1994; Kvarnemo et al, 1996) |
| Potential reproductive rate (PRR) | For a given sex, the number of independent, fledged offspring that parents can produce per unit time if they are unconstrained by mate availability (Clutton-Brock & Vincent, 1991; Clutton-Brock & Parker, 1992; Ahnesjö *et al.*, 2001) |

[a]The Bateman gradient is equivalent to the selection gradient of reproductive success on mating success. Both the Bateman gradient and selection gradients used to quantify the strength of sexual selection on traits other than mating success have been referred to as 'sexual selection gradients'. To avoid confusion between the two, the regression of reproductive success on mating success is now typically referred to as the Bateman gradient (see also Andersson & Iwasa, 1996 and Jones, 2009).

**(a)**

Legend:
- ■ Opportunity for Sexual Selection
- □ Selection Gradient
- ▤ Selection Differential
- ▦ Bateman Gradient
- ▧ Morisita's Index
- ⬚ Index for Resource Monopolization



**(b)**



OSR Only (52%) | OSR + PRR (24%) | PRR Only (24%)

Fig. 1 (a) The relative use of the six most common measures of sexual selection during 2004–2008. These data are based on a literature review of all manuscripts reported in a Web of Knowledge search for six standard measures of sexual selection: the opportunity for sexual selection, the Bateman gradient, sexual selection gradients and differentials, the Morisita index, and the index for resource monopolization (Web of Knowledge topic key word: 'opportunit* for sexual selection' or ('selection gradient*' and 'sexual selection') or ('selection differential*' and 'sexual selection') or 'bateman* gradient*' or ('morisita* index' and 'sexual selection') or ('index for resource monopolization' and 'sexual selection'); search performed on 5 June 2009). During 2004–2008, 59 studies (10 in 2004, 8 in 2005, 9 in 2006, 16 in 2007 and 16 in 2008) reported at least one of these measures. Here, we report the relative frequency with which each of the six measures was used to quantify sexual selection. A full list of the studies that reported at least one of these measures is provided in the Online Supporting Information file. (b) The relative use of the operational sex ratio (OSR) and potential reproductive rate (PRR) in studies of sexual selection during the last 5 years (2004–2008). Here, we show the percentage of citation counts resulting from a Web of Knowledge search for operational sex ratio and/or potential reproductive rates. (Topic keywords: 'sexual selection' and [('potential reproductive rate*' or 'potential rate* of reproduction') or 'operational sex ratio*')] results in 79 citations; 'sexual selection' and [('potential reproductive rate*' or 'potential rate* of reproduction') NOT 'operational sex ratio*') results in 19 citations; 'sexual selection' and ('operational sex ratio*' NOT 'potential reproductive rate*' NOT 'potential rate* of reproduction') results in 41 citations; searches performed on 5 June 2009].

and male fitness is mate-limited. We first assume an unbiased OSR consisting of three males and three females in which there is a moderate degree of monopolization (Fig. 2a). If a new male is added to the system, the OSR becomes male-biased (Fig. 2b–c). According to Emlen & Oring (1977, p. 216), monopolization is expected to increase with OSR, in which case a single male now monopolizes all females despite the additional male competitor (Fig. 2b). This scenario – that is, the case in which unsuccessful males are added to the system – is often used as a textbook example of how sexual selection will operate as the OSR changes (Andersson, 1994; Hardy, 2002). On the other hand, the additional male competitor might make maintaining a monopoly more

difficult such that no male can now monopolize more than one female (Fig. 2c; see discussion of monogamy in Emlen & Oring, 1977; Wiegmann & Nguyen, 2006).

In the previous examples (Fig. 2a–c), absolute density increases as OSR becomes skewed. Alternatively, OSR can change independently of density (Kokko & Rankin, 2006). For example, an unbiased OSR of three males and three females (Fig. 2d) can become male-biased if a single female leaves the system and an additional male competitor enters. Again, it is possible that a single male will monopolize both females (Fig. 2e); alternatively, monopolization might decrease, such that mating success is as equitable as possible (Fig. 2f). It is not intuitively obvious why one of these scenarios (Fig. 2b vs. c or e vs. f) should be expected *a priori*. In fact, no biological process preordains that new males will be unsuccessful, and it is often more plausible that mate monopolization will become more difficult as the number of potential male rivals increases (e.g. as reported in several lekking species; Kokko *et al.*, 1998; ch. 11 of Shuster & Wade, 2003; Fitze & Le Galliard, 2008). In short, it is impossible to make general predictions about the relationship between the OSR and sexual selection in the absence of additional knowledge about the mating system and the proximate processes that determine the degree of mate monopolization (see also Shuster & Wade, 2003; Shuster, 2009).
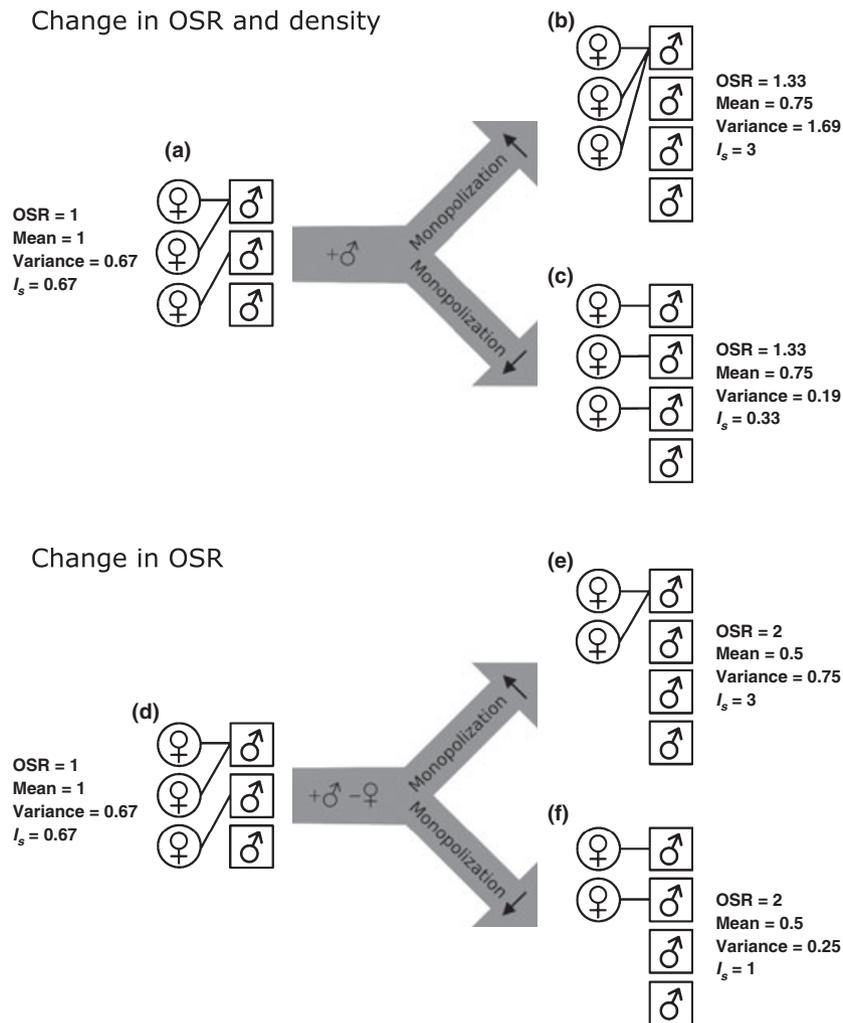
## Change in OSR and density



## Change in OSR

**Fig. 2** The OSR-Monopolizability Conundrum: Alternative relationships between operational sex ratio (OSR), the mean and variance in male mating success, and the opportunity for sexual selection ($I_s$). Males are mate-limited and females mate with one male. We first assume an unbiased OSR with some mate monopolization (a). A new male is then added to the system, causing the OSR to become male-biased (b–c). If OSR increases monopolization of females, $I_s$ increases as OSR increases (b). In contrast, if the additional male competitor makes maintaining a monopoly more difficult and no single male can now monopolize more than one female, $I_s$ will decrease as OSR increases (c). In this example (a–c), absolute density increases as OSR became skewed. Alternatively, OSR can change independently of density. For example, an unbiased OSR (d) can become male-biased if a single female leaves the system and an additional male competitor enters. One can again assume increases (e) or decreases (f) in monopolization, but $I_s$ is now bound to increase in either case. This fails to capture the fact that (f) exhibits the most egalitarian mating success possible at this OSR – such a pattern could be caused by random mating or selection, and it is impossible to distinguish between the two. Using $I_s$ as a proxy for actual selection is therefore problematic.

## Issue 2: the opportunity-outcome conundrum

The observed intra-sexual variation in mating success is generally assumed to reflect the actual strength of evolutionary change stemming from sexual selection (Bateman, 1948; Wade, 1979; Arnold and Wade, 1984a,b; Shuster & Wade, 2003). We call this the 'opportunity-outcome conundrum' to reflect the widespread assumption that the opportunity for sexual selection ($I_s$) is a good predictor of the strength of sexual selection, despite the lack of knowledge of the relation-ship between $I_s$ and the actual strength of sexual selection. $I_s$ is the most widely advocated index used to quantify sexual selection empirically because it is unitless (hence ideal for comparative analyses) and directly linked to formal selection theory (Crow, 1958; Wade, 1979; Arnold & Wade, 1984a; Shuster & Wade, 2003; Jones, 2009; see also Arnold & Duvall, 1994 and Jones, 2009 for discussion of other measures). The use of $I_s$ has been criticized for unreliability stemming from sampling issues (Downhower et al., 1987), variability in measures of fitness (Downhower et al., 1987), the lack of reference

values (Downhower *et al.*, 1987; but see Shuster & Wade, 2003 for refutations of such criticisms), the nonindependence of mean and variance in relation to the use of $I_s$ in comparative analyses (Ruzzante *et al.*, 1996; Fairbairn & Wilby, 2001), and the absence of a direct link to traits of interest (Koenig & Albano, 1986; Grafen, 1987, 1988; Andersson, 1994; Ruzzante *et al.*, 1996; Fairbairn & Wilby, 2001; Ferguson & Fairbairn, 2001). Despite such criticisms, $I_s$ remains the most commonly used measure of sexual selection (Box 1; Fig. 1a).

Regardless of whether one agrees with the previous criticisms, it is surprising that the most fundamental concern – the general relationship between the opportunity for and actual strength of sexual selection – has been largely overlooked. Although there are examples of within-species studies on relationships between $I_s$ and the strength of sexual selection on particular traits (Jones *et al.*, 2002, 2004; Mills *et al.*, 2007), the general scenarios under which $I_s$ serves as a reliable proxy for the strength of sexual selection remain unknown.

Our simple example of Fig. 2 highlights one danger of straightforwardly assuming that $I_s$ will predict the strength of sexual selection across a range of scenarios. In Fig. 2, we intentionally provide no information on male traits. Such a scenario (i.e. one in which researchers have no information regarding phenotypic traits under selection) is likely to be a case in which researchers are particularly tempted to use $I_s$ to draw conclusions about sexual selection. Here, $I_s$ behaves as predicted in some cases – in the first scenario, $I_s$ increases as mate monopolization increases (Fig. 2a → b) and decreases as mate monopolization decreases (Fig. 2a → c). This is precisely the pattern we would expect if selection is operating. Also as predicted, $I_s$ increases when more males remain unmated in our second scenario (Fig. 2d → e), but $I_s$ also increases when mating success becomes as egalitarian as possible (Fig. 2d → f). If one assumes that $I_s$ reflects actual sexual selection, the conclusion is that selection is stronger in Fig. 2f in comparison with Fig. 2d. This might be true if selection is operating; however, there is no *a priori* reason to assume that sexual selection is the cause of unequal mating success among males in 2 F. In this case (Fig. 2f), $I_s$ can never be lower than 1. The mating scenario depicted in Fig. 2f will always result in a greater $I_s$ than that of Fig. 2d, even if mating in Fig. 2f is entirely random. This is true regardless of the number of males and females sampled (see Appendix for a large-sample version of Fig. 2) and the level of replication. Even if the scenarios in Fig 2d–f were replicated many times, $I_s$ values would still always be higher in E and F than in D even if mating was random with respect to male traits. It will therefore never be possible to use $I_s$ to distinguish between selection and random mating for such a case. In other words, $I_s$ confounds the potential evolutionary change associated with selection and chance or sampling error (i.e. drift). This is in stark contrast to the case in which it is possible to calculate selection directly on phenotypic traits. If we had information on male traits and sufficiently replicated the scenarios in Fig. 2d–f, the mean selection gradient and differential would equal zero if mating were random (see also Fig. 3). Thus, using $I_s$ as a proxy for the actual strength of sexual selection across scenarios (or species) is inherently precarious.

It is worthwhile asking why we so readily assume that selection differs between the scenarios in Fig 2. If we ask colleagues to rank these scenarios for the strength of sexual selection, most will happily attempt to do so. This seems to arise from a cognitive bias: humans like to attribute causality if they see a pattern (Hood, 2009). This becomes apparent if the lines connecting females to males are drawn differently in, say, Fig 2f (e.g. if females mate with the two males at the bottom of the 'hierarchy', or with the top and bottom male). This will not change the $I_s$ value but it does alter the viewer's perception. The belief that selection must be operating to produce Fig. 2f is extremely hard to shake whenever figures or tables rank males according to their mating success. The *post hoc* identification of successful males creates an illusory 'hierarchy' with top males more successful than bottom males that we then feel compelled to attribute to inherent properties of these males. (In an analogous context, the recent popular book *Fooled by Randomness* (Taleb, 2007) provides amusing accounts of the tendency to seek out behavioural features that distinguish successful from unsuccessful stock market investors when chance alone will generate millionaires and paupers.)

In Fig. 2f, assuming that each female mates only once, there is no way to connect females to males that can produce a value of $I_s$ lower than that obtained under the illusory hierarchy with two 'top' males having one female each. It is therefore simply wrong to *a priori* assume that selection is stronger in Fig. 2f than in Fig. 2d. Distinguishing between selection and drift is fruitless based on such data. At a minimum, we need a null model to determine whether there is greater variance in male success than expected by chance (e.g. Sutherland, 1985).

Figure 2 draws attention to the need to specify the process underlying the depicted unequal mating success. If we know the processes involved we can directly assess how well the OSR and $I_s$ do in identifying cases of actual versus apparent selection. Below, we use a series of simple simulations to specify biological processes of interest. By creating scenarios in which the actual strength of sexual selection is known, we can test how well OSR or $I_s$ perform as proxies of sexual selection. This allows us to critically evaluate the predictions that (i) a more biased OSR leads to a greater $I_s$, and (ii) $I_s$ predicts the strength of sexual selection. We thereby identify scenarios in which the OSR and/or $I_s$ fail to predict the strength of or sexual selection.
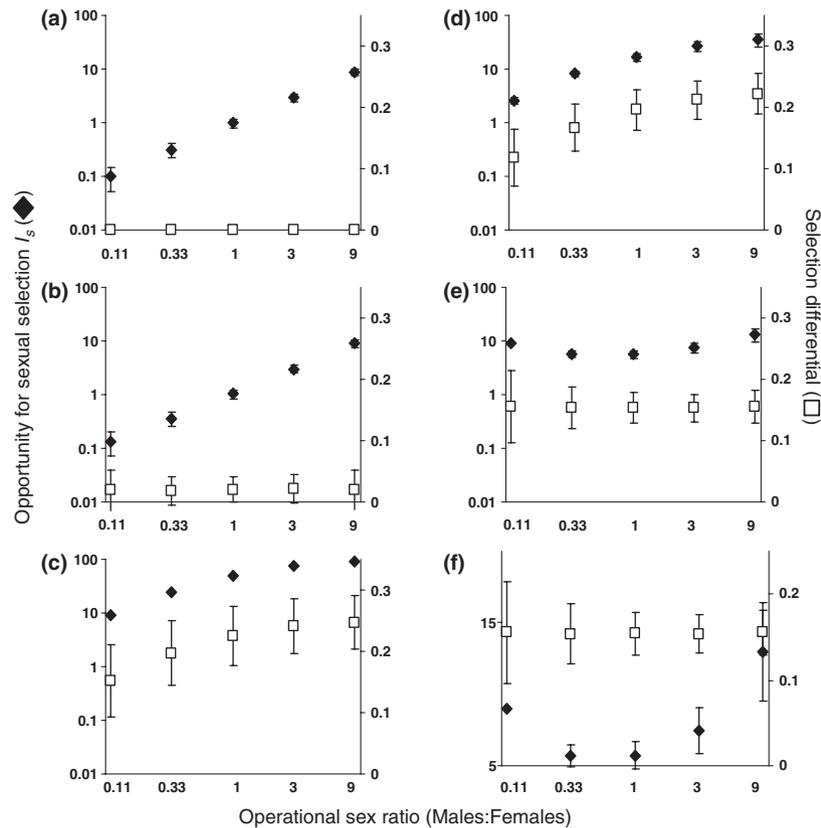
**Fig. 3** The Opportunity-Outcome Conundrum: The relationship between the operational sex ratio, the opportunity for sexual selection $I_s$ (filled diamonds) and the selection differential (i.e. the difference between mean trait value for the population and mean trait value of males that sire offspring, which will predict the response to selection given a constant level of additive genetic variation in the direction of selection; open squares) when (a) mating is random and no variation exists in the trait of interest, (b) there is a positive relationship between a male's trait value and his propensity to mate, (c) females sample and mate with the best male (i.e. male with the highest trait value) of all males present, (d) females sample and mate with the best of half of all males present, and (e, f) females sample and mate with the best of 10 males present. To allow for easy comparisons across cases, the figure axes are identical in panels A–D. However, the range of $I_s$ values makes it difficult to visually discern the relationship between OSR, $I_s$ and the selection differential when $I_s$ is plotted on a log scale in panel E. Thus, for the case in which females sample and mate with the best of 10 males, we also present a close-up view of these data in panel F. Note that the data presented in E and F are identical. Male traits are drawn from the same distribution in all our scenarios (SD = 0.1) except Case 0; thus, the selection differentials, $s$, can be converted into a standardized selection differential by multiplying by 10 (1/SD). We present means ± SD based on 1000 simulations in all cases.

# A thought-provoking example

## The model

In all examples, we study a population with 100 individuals that occurs at five different OSRs: two female-biased (10 males, 90 females, OSR = 0.11; 25 males, 75 females, OSR = 0.33), one unbiased (50 males, 50 females, OSR = 1), and two male-biased (75 males, 25 females, OSR = 3; 90 males, 10 females, OSR = 9). Except in a null scenario (Case 0 described later), males have a genotypic value of a sexually selected trait that is sampled independently for each from a normal distribution with a mean 0.5 and a standard deviation of 0.1. In each reproductive bout,

females mate with only one male and produce one offspring, whereas males can mate multiply such that their fitness is mate-limited.

Our examples explore the relationship between OSR and $I_s$ (Arnold & Wade, 1984a; Jones, 2009) and a measure of the strength of sexual selection, the selection differential ($s$) of a male trait of interest (i.e. the difference in mean trait value between all males and sires; Arnold and Wade, 1984a,b; Lynch & Walsh, 1998; Jones, 2009). Selection theory identifies this selection differential to be directly proportional to the phenotypic outcome of selection (i.e. evolutionary change in a trait from one generation to the next), given a constant level of additive genetic variation in the direction of selection.

As mentioned earlier, the opportunity for sexual selection for a given sex, $I_s$, is calculated as the square of the coefficient of variation in mating success for that sex (Arnold & Wade, 1984a; Shuster & Wade, 2003; Jones, 2009). Mean male mating success, $M$, and variance in male mating success, $V_m$, are calculated as

$$M = \sum_{i=1}^{n} (k_i m_i) / \sum_{i=1}^{n} m_i \qquad (1)$$

and

$$V_m = \sum_{i=1}^{n} (k_i^2 m_i) / \sum_{i=1}^{n} m_i - \left[ \sum_{i=1}^{n} (k_i m_i) / \sum_{i=1}^{n} m_i \right]^2 \qquad (2)$$

where $k_i$ and $m_i$ are the number of mated females and the number of males in the $i$th mating class, respectively (following Shuster & Wade, 2003, p. 25). In our examples, this is equivalent to the measure $I_{mates}$ proposed by Shuster & Wade (2003), eqns. 1.21 b–c).

We consider three general relationships between the male trait of interest and mating success: Case 0: random mating in which all males have the same genotype (trait value = 0.5); Case 1: a positive, linear relationship between a male's trait value and likelihood of mating (for simplicity, we assume that mating success is directly proportional to the value of the trait; thus, the probability that a male mates with a given female equals his trait value divided by the sum of all male trait values); Case 2: a 'Best-of-N' scenario in which females mate with the male with the highest trait value that they encounter in a sample of N males, and the sample is drawn independently for each female. This 'Best-of-N' scenario could stem from female choice (where females sample and choose a mate) or male–male competition (where males monopolize females and prevent rivals from mating). For this scenario, we considered three sampling regimes: females mate with the best of (i) all males present, (ii) a fixed proportion of the males present (half of the males in our example), or (iii) a fixed number of males (10 males in our example). As mentioned earlier, females can mate only once and males can mate multiply. Because males can mate multiply, our scenarios do not impose any covariation between OSR and male trait distribution.

## Results and interpretations

*Case 0: The perfect null model: all males are equal and mating is random*
As the OSR becomes more male-biased, the mean and variance in male reproductive success decreases because the proportion of unmated males during a given reproductive bout increases. The net effect is a greater $I_s$ at male-biased OSRs (Fig. 3a), which is consistent with previous theory (Emlen & Oring, 1977; Clutton-Brock & Parker, 1992; Ahnesjö *et al.*, 2001). However, because mating is random, selection is not operating (Fig. 3a). The OSR and $I_s$ are therefore unrelated to the strength of

sexual selection (Fig. 3a). Although the lack of sexual selection is unsurprising for this case (e.g. Sutherland, 1985; Shuster & Wade, 2003), it is noteworthy that $I_s$ changes systematically with the OSR in a way that, to a naïve interpreter of this dataset, would suggest systematically stronger sexual selection at a more highly biased OSR. Under entirely random mating, both OSR and $I_s$ fail to represent the true strength of sexual selection. Thus, neither measure evaluates whether or not sexual selection operates or distinguishes random from nonrandom mating patterns.

*Case 1: Nonrandom mating because of a positive relationship between a male trait and mating success*
As with Case 0, $I_s$ increases as the OSR becomes more male-biased. Here, however, there is sexual selection on the male trait: the trait value of sires is, on average, 0.02 units greater than mean population value of 0.5 (Fig. 3b), thus given the requisite additive genetic variation, evolutionary change will occur. Even so, there is no relationship between either $I_s$ or OSR and the strength of sexual selection (Fig. 3b). Based on previous statements on the suitability of OSR and $I_s$ as measures of sexual selection (e.g. '[The opportunity for sexual selection] measures the strength of sexual selection…' (Shuster & Wade, 2003, p. 41); 'To understand the intensity of sexual selection it is…the operational sex ratio (OSR) [that is of importance]', Emlen & Oring, 1977, p. 216), and given that we have specified a very simple mating system where sexual selection clearly operates, we suspect that many researchers will find this result counter-intuitive. In hindsight though, it is unsurprising that OSR and $I_s$ fail to predict the strength of sexual selection. Selection remains unchanged because females are sampling male traits from an identical distribution. OSR and male trait distribution do not covary. Thus, the only difference the OSR makes is that it alters the sample size that generates the distribution of the traits of sires. The distribution of male traits is sampled 10, 25, 50, 75 or 90 times (once by each reproducing female), and the results form the trait distribution of males who sire the next generation. Whereas there will be less sampling error when the sample size is large (more male-biased OSR), the mean of the distribution of sires increases from that of all males by 0.02 across all sample sizes.

*Case 2: Nonrandom mating and mate monopolization*
When a single male can completely monopolize all possible mates, or when females mate with the best of a relatively large proportion of all males, OSR and $I_s$ are positively related to the strength of sexual selection (Fig. 3c,d). This is consistent with Emlen and Oring's statement (Emlen & Oring, 1977; p. 222) that 'the greater the potential for individuals to monopolize resources or mates, the greater the intensity of sexual selection…'. However, when females mate with the best of some fixed

number of males (ten males, in our example) – perhaps the most biologically realistic scenario – then OSR and $I_s$ are not related to one another in a straightforward manner, and neither predicts the strength of sexual selection (Fig. 3e). This lack of a clear relationship is difficult to visualize when $I_s$ is plotted on a log scale (Fig. 3e), but it becomes obvious if we take a closer look at the data by focusing more specifically on the range of observed $I_s$ values (see Fig. 3f).

The OSR and $I_s$ only accurately predict sexual selection when the degree of mate monopolization remains high across all OSR values (as in Fig. 3c,d) and when a more biased OSR increases the extent to which mates are monopolized by individuals with the highest trait values (Fig. 2). Emlen & Oring (1977) revealed a fundamental truth when they argued that the ability to monopolize mates determines the strength of sexual selection. However, our examples illustrate that their associated but separate claim, that the OSR is an index of the degree of mate monopolization, is less generally true (Figs 2 and 3). This makes the OSR a poor predictor of sexual selection (e.g. Figs 2 and 3a,b,e,f) under many biologically relevant scenarios.

Obviously, sexual selection could be more predictable than in our scenarios if the relationship between male traits and mating success changes systematically with OSR. For example, OSR and the distribution of male traits in the mating pool might be related if mated males cannot re-mate for an extended period of time and new males rarely enter the mating pool (e.g. in a territorial breeding-resource defence system with male care). Here, the OSR would become less male-biased with each successive male mating. If there is a positive relationship between male trait value and propensity to mate, males with the highest trait value would leave the mating pool first (i.e. at the most male-biased OSR). This, in turn, might lead to a systematic change between male trait distribution and mating success at varying OSRs. We assumed no such systematic change in Fig. 3 because it is not *a priori* clear in what direction such covariation should occur. This is because of the first problem we identified, i.e. the OSR-mate monopolizability conundrum: this relationship depends on the biological details of mate acquisition (Fig. 2). There is therefore no generic solution to the potential failure of OSR and $I_s$ to accurately predict sexual selection.

## What does all this mean?

### The bottom line(s)

In general, OSR and $I_s$ are correlated (Fig. 3a–d), although this is not always the case (Figs 2 and 3e,f). It is, however, seriously misleading to assume that either OSR or $I_s$ will accurately reflect the strength of sexual selection because this is only true under remarkably restrictive conditions. We rarely find a systematic and

clear relationship between the OSR and the selection differential (the difference between the mean of the trait value of sires vs. all males). In our examples, this happens only when the degree of mate monopolization attributable to sexually selected traits remains relatively high across all OSR values. One can ask, though, what use are measures that only work consistently when the measured effects are at their strongest? The available evidence (Kokko *et al.*, 1998; Preston *et al.*, 2001; Fitze & Le Galliard, 2008) suggests that mate monopolizability is rarely uniformly strong, so this cannot simply be assumed for the sake of convenience. In general, OSR and $I_s$ values, by themselves, do not function as reliable indicators of strong monopolization, and thus, they do not reliably predict the strength of selection.

Our models are an explicit reminder that $I_s$ captures nonrandom and random variance in mating success and can reach high values without selection (Sutherland, 1985; Westneat, 2006) (Figs 2 and 3a). Although some empirical studies conclude that the use of $I_s$ works well within a species (Jones *et al.*, 2002), our results suggest that even this claim should be treated cautiously (e.g. ability to monopolize mates is potentially affected by absolute density; Kokko & Rankin, 2006; Fig. 2). When sexual selection is absent or weak, the use of OSR and $I_s$ can easily lead to false positives, i.e. the conclusion that sexual selection is intense (Figs 2 and 3).

## Why is this important?

The use of $I_s$ and OSR should be reconsidered. Our models do not merely reiterate earlier complaints. We have used straightforward scenarios to show that neither $I_s$ nor OSR is expected to consistently and accurately quantify or predict sexual selection.

Current theory recognizes that OSR is not the only factor influencing competition for mates (Kvarnemo & Ahnesjö, 1996, 2002; Reynolds, 1996; Kokko & Monaghan, 2001; Kokko & Jennions, 2003; Shuster & Wade, 2003; Shuster, 2009). Recent work has highlighted the role of other factors such as mate quality (Johnstone *et al.*, 1996), mortality patterns (Okuda, 1999), breeding costs (Kokko & Monaghan, 2001) and density (Kokko & Rankin, 2006) in determining the strength of sexual selection. Thus, our results for OSR are, perhaps, not wholly unexpected, although they do highlight that the concept of 'monopolizability' (Emlen & Oring, 1977) has survived in the literature for a long time without having ever been given a very precise definition or indeed a precise reason why a biased OSR scenario with many competitors should make it easier for individuals to monopolize many mates.

The failure of $I_s$, however, is likely more surprising. $I_s$ reflects the maximum possible strength of selection (Crow, 1958; Wade, 1979; Arnold & Wade, 1984a; Jones, 2009). However, using $I_s$ as an empirical measure of sexual selection assumes implicitly that this maximum (or

a consistent proportion of it) is reached. This is a very strong assumption that will often be violated in nature (as it is in our hypothetical examples). Our results indicate that any inferences based on $I_s$ will be entirely spurious if the maximum strength of selection is not realized (Fig. 3a,b,e,f) and that it is not scientifically sound to make inferences as if the difference between actual and maximum strength of selection was analogous to a randomly distributed (and thus uninteresting) noise term when fitting models to data. This is disconcerting given that $I_s$ has been used to characterize mating systems (Krakauer, 2008; Vanpé *et al.*, 2008), 'solve' the big-sperm paradox (Bjork & Pitnick, 2006), assess the relative effect of extra-pair or parasitic copulations on the strength of sexual selection (Albrecht *et al.*, 2006; Kleven *et al.*, 2006; Singer *et al.*, 2006; Dolan *et al.*, 2007) and draw conclusions regarding the effects of temporal variability (Weatherhead, 2005; Reichard *et al.*, 2008), human-induced environmental change (Järvenpää & Lindström, 2004; Perlut *et al.*, 2008) and local climatic variability (Twiss *et al.*, 2007) on the strength of sexual selection. Unfortunately, it is impossible to know if and when $I_s$ has led to spurious results and unfounded conclusions.

This problem is exacerbated by many studies reporting $I_s$ but not quantifying selection on phenotypic traits (Table 2). A number of studies do report selection gradients with respect to traits of interest (Box 1; Fig. 1a). However, of the 36 studies that quantified $I_s$ during 2004–2008, only 13 report selection gradients with respect to a phenotypic trait (Table 2). In some cases, this might be because selection gradients are not essential for the study's research goals; however, in other cases, it appears that $I_s$ is simply viewed as a comprehensive measure of sexual selection (Box 2; Table 2). When studies do report selection gradients with respect to a trait (or traits) of interest, any incongruence between $I_s$ and measures of phenotypic selection is difficult to interpret. Of the thirteen studies that reported both $I_s$ and selection gradients during 2004–2008, nearly half found conflicting results between $I_s$ and selection gradients (Table 2). Currently though, conflicting results are often attributed to changes in behaviour with OSR/density or experimental limitations rather than the possibility that the indices simply do not work as intended (Mills *et al.*, 2007; Head *et al.*, 2008; but see also Kelly, 2008 for discussion of limitations of $I_s$ as an empirical measure).

Some readers will correctly point out that the opportunity for sexual selection is just that (an 'opportunity') (Fisher, 1930; Arnold & Wade, 1984a; Jones, 2009) and reporting a metric while acknowledging its limitations cannot be considered incorrect. In practice though, both empiricists and theoreticians show a consistent tendency to interpret opportunities as if they reflect actual sexual selection (Shuster & Wade, 2003; Bjork & Pitnick, 2006; Sword & Simpson, 2008; Duval & Kempenaers, 2008; Vanpé *et al.*, 2008; Box 2). Merely acknowledging the limitations of a metric does not justify its continued usage.

Furthermore, others might argue that in some cases it is impossible to measure selection directly and that the information $I_s$ provides is better than no information at all. The mentality that if we cannot fix it, we should just continue to use it (regardless of any shortcomings) is dangerous. The information $I_s$ provides can be actively misleading if one is trying to draw conclusions about sexual selection (see, e.g. Figs 2d–f and 3a,b,e,f). Limitations in the measures one can obtain for a given system do not justify unfounded conclusions. Thus, authors who measure only the opportunity for sexual selection (whether by choice or because it is the only measure they can acquire) should recognize the limitations of $I_s$ and be cautious in their conclusions regarding sexual selection. Given the results of our model, we are left wondering what empirical conclusions, if any, should be based on $I_s$.

## What now?

We urge caution in (i) the use of the OSR or $I_s$ as surrogates for direct measures of sexual selection and (ii) making predictions or drawing conclusions (be they in the real world or in theoretical models) on the assumption that OSR and $I_s$ reflect the actual strength of sexual selection. It is important to reiterate that our results suggest that reliance on $I_s$ and OSR as proxies for the strength of sexual selection is likely to lead to spurious results and false conclusions in cases that closely resemble several widely studied types of mating systems (Fig. 3a,b,e). The use of single proxies is ideal when they are reliable, but shortcuts that consistently fail have to be abandoned.

Drawing general conclusions about sexual selection requires the ability to accurately quantify its strength and make comparisons across varying contexts. The development of measures of sexual selection that allow for such comparisons remains an important task. However, it is essential to recognize that no single measure encompasses all aspects of sexual selection. Importantly, this applies not only to the opportunity for sexual selection and the OSR, but also to selection gradients and differentials with respect to traits of interest and the Bateman gradient (Emlen & Oring, 1977; Arnold & Wade, 1984a; Arnold & Duvall, 1994; Shuster & Wade, 2003; Jones, 2009). Many of our conclusions above could be repeated for other proxies of sexual selection. For example, the Bateman gradient quantifies the relationship between mating and reproductive success (Arnold & Duvall, 1994; Jones, 2009; Table 1). In our hypothetical examples, the Bateman gradient for each sex differs (positive for males and zero for females), but this difference remains the same across all scenarios (as the relationship between mating and reproducing does not vary across scenarios for each sex). Thus, the Bateman gradient cannot, even in principle, predict differences in the outcome of sexual selection across the scenarios presented (Fig. 3). Further-

**Table 2** Studies reporting the opportunity for sexual selection ($I_s$) during 2004–2008. We note whether selection gradients with respect to a phenotypic trait were calculated and whether there was congruence between the patterns suggested by $I_s$ and the selection gradient(s). We also provide additional relevant comments, and note whether Bateman gradients (which are a particular type of selection gradient, see Table 1) are reported in the final column. For full list of references, please see Online Supporting Information file.

| Study | Selection gradient calculated with respect to a phenotypic trait? | Agreement between selection gradient and opportunity for sexual selection calculations? | Some relevant comments |
|---|---|---|---|
| 1. Duval & Kempenaers (2008) | No | N/A | Selection gradients were not calculated, but there was a relationship between male status and reproductive success |
| 2. Kelly et al. (2008) | Yes | Yes | Variance in mating success was related to phenotypic traits that covary with mobility |
| 3. Krakauer (2008) | No | N/A | Bateman gradients were calculated: both the opportunity for sexual selection and Bateman gradients suggest the potential for stronger sexual selection on males than females |
| 4. Lorenzi & Sella (2008) | No | N/A | |
| 5. Vanpé et al. (2008) | No | N/A | |
| 6. Lee et al. (2008) | No | N/A | |
| 7. Perlut et al. (2008) | No | N/A | |
| 8. Kelly (2008) | Yes | No | The opportunity for sexual selection was not related to the strength of selection on male body size, and was NEGATIVELY correlated with the strength of selection on male head size |
| 9. Reichard et al. (2008) | No | N/A | Selection gradients were not calculated, but the authors did find a relationship between male body size (i.e. small, medium or large) and number of offspring sired |
| 10. Head et al. (2008) | Yes | Yes | Neither density nor OSR affected $I_s$ or selection on male traits |
| 11. Gopurenko et al. (2007) | No | N/A | Bateman gradients were calculated. Reproductive success was positively correlated with mating success in both males and females, and the slopes of the two regressions did not differ significantly. However, the opportunity for sexual selection on females was twice the opportunity for sexual selection on males |
| 12. Dolan et al. (2007) | Yes | Yes | In separate analyses, the authors examine the relationship between male traits and male mating success that stems from both within- and extra-pair paternity. There are significant correlations between some male traits and within- and extra-pair success |
| 13. Klemme et al. (2007) | Yes | No | $I_s$ was significantly greater at male-biased OSR treatments. In contrast, the directional selection gradient on male body size was positive, relatively large, and significant at highly female-biased and intermediate OSRs, but it was nonsignificant and relatively small at male-biased OSRs |
| 14. Webster et al. (2007) | No | N/A | Bateman gradients were calculated, and there was a significant and positive correlation between male reproductive and mating success |
| 15. Mobley & Jones (2007) | No | N/A | Estimates of the opportunity for sexual selection and Bateman gradient were higher among males in a Florida population in comparison with a Virginia population of Syngnathus floridae. Mean mating success was positively correlated with male length in both populations, although the directional selection gradients were not presented |
| 16. Albrecht et al. (2007) | No | N/A | |
| 17. Twiss et al. (2007) | No | N/A | |
| 18. Kvarnemo et al. (2007) | Yes | Yes | The opportunity for sexual selection was greater for females than males, and selection gradients suggest directional selection acting on female head size |
| 19. Mills et al. (2007) | Yes | No | The opportunity for sexual selection for males was greatest at moderate and highly male-biased OSRs; selection gradients on male testosterone levels were marginally significant and positive at moderately, but not highly, male-biased OSRs. Bateman gradients were also reported, and there was no effect of OSR on the Bateman gradients calculated for males |
| 20. Spence et al. (2006) | No | N/A | |
| 21. Singer et al. (2006) | No | N/A | |
| 22. Rossiter et al. (2006) | No | N/A | |
| 23. Westneat (2006) | Yes | No | Despite a strong opportunity for sexual selection, there was no evidence of current sexual selection on several morphological traits |

**Table 2** (*Continued*)

| Study | Selection gradient calculated with respect to a phenotypic trait? | Agreement between selection gradient and opportunity for sexual selection calculations? | Some relevant comments |
|---|---|---|---|
| 24. Bjork & Pitnick (2006) | No | N/A | $I_s$ was relatively high in *Drosophila bifurca* and *D. lummei*; however, the authors found no difference between the sexes in Bateman gradients. Across species, there is no significant relationship between $I_s$ and sperm investment |
| 25. Kleven *et al.* (2006) | Yes | Yes | Extra-pair paternity affected the opportunity for sexual selection, and the likelihood of obtaining extra-pair fertilizations increased as male tail streamer length increased |
| 26. Rios-Cardenas (2005) | Yes | No | When all males were considered, the opportunity for sexual selection was greater for males than females and suggests that sexual selection is potentially operating on males. Likewise, when all males were considered, the Bateman gradient was significantly positive. In contrast, there was no evidence of sexual selection acting on the male traits measured (i.e. body size and parental behaviour) |
| 27. Weatherhead (2005) | No | N/A | |
| 28. Prohl (2005) | No | N/A | |
| 29. Freeman-Gallant *et al.* (2006) | No | N/A | |
| 30. Järvenpää & Lindström (2004) | No | N/A | The opportunity for sexual selection was lower in turbid tanks in comparison to clear tanks; while selection gradients were not calculated, mating success was less skewed towards larger males in turbid tanks |
| 31. Jones *et al.* (2004) | Yes | Yes | Sexual selection tended to favour taller tails in males. There was no evidence of sexual selection on female phenotypic traits. Likewise, the opportunity for sexual selection was greater for males than females. Bateman gradients were also positive for males but not females |
| 32. Vieites *et al.* (2004) | No | N/A | |
| 33. Byers *et al.* (2004) | No | N/A | |
| 34. Emlen & Wrege (2004) | Yes | Yes | The opportunity for sexual selection was greater for females than males, and there was a significant, positive relationship between female tarsus length and mating success |
| 35. Schulte-Hostedde *et al.* (2004) | Yes | No | The opportunity for sexual selection was higher for males than females. Additionally, the Bateman gradient for males was significantly greater than zero, and also sleeper than the Bateman gradient for females. However, there was no evidence of directional selection on male body size |
| 36. Andersson (2004) | No | N/A | |

more, it does not quantify the difficulty of actually achieving matings for the average male, or indeed for males with specific traits, nor does it evaluate the costs of developing traits required to elevate mating success. Therefore, this measure should also not be assumed *a priori* to predict the actual strength of sexual selection (Jennions & Kokko, in press).

When measuring sexual selection, quantifying selection in relation to phenotypic traits could be considered ideal, although the study of species-specific traits has the obvious downside of making across-species comparisons harder. Of course, this approach is not without its own challenges; it is often difficult to know which traits are under selection or to gather such data in some species. Even the use of multivariate selection techniques to identify selection on constellations of traits is limited by the way in which traits are identified and whether these capture a sufficient amount of the total phenotypic variation in characters that affect fitness.

Measuring sexual selection is not analogous to reading a temperature off of a scale. Each of the aforementioned proxies of sexual selection has various strengths and weaknesses and quantifies a particular component of sexual selection (reviewed in Jones, 2009; Jennions and Kokko, in press; Table 1). Thirty-six of the 59 studies that quantified at least one of the six common measures of sexual selection during 2004–2008 reported only one of those measures. Quantifying single measures might allow researchers to answer very specific questions, but over-reliance on any single measure can lead to erroneous conclusions.

We suggest that future studies of sexual selection should focus on quantifying multiple aspects of selection and in particular focus on quantifying selection in relation to phenotypic traits. A more comprehensive approach to quantifying sexual selection has been advocated previously. Jones and colleagues (2002, 2004) note that it is important to quantify multiple measures of

mating systems, including the opportunity for selection, the opportunity for sexual selection and the Bateman gradient. We agree that it is critical to quantify multiple components of selection. Many experimental and observational studies of sexual selection yield data that can be used to quantify multiple measures of sexual selection (for examples of such studies, see Jones *et al.*, 2004; Rios-Cardenas, 2005; Kvarnemo *et al.*, 2007; Mills *et al.*, 2007). In contrast to previous authors (e.g. Jones *et al.*, 2004), we argue that much less emphasis should be placed on indirect measures of selection (i.e. opportunities for selection and the Bateman gradient). Indirect measures can provide insight into whether selection might be operating, and this might help researchers decide what questions to ask in a given system. However, indirect measures do not provide information on whether selection is operating or how strong it might be. To answer any broad questions about sexual selection, you need to actually measure selection on phenotypic traits (see also, e.g. Koenig & Albano, 1986; Grafen, 1987, 1988; Andersson, 1994).

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Data S1.** The 59 studies in which at least one of the first six measures of sexual selection listed in Table 1 was calculated and reported (see also Box 1 and Fig. 1a).

**Data S2.** The 79 citations (see Box 1 and Fig. 1b) resulting from a Web of Knowledge search for operational sex ratio and/or potential reproductive rates.

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## Appendix

In Fig. A1, we present a large-sample version of Fig. 2. Specifically, we maintain the same mating distribution as in Fig. 2 and repeat the example when male and female numbers are multiplied by ten. The patterns are qualitatively (and in some cases quantitatively) identical to those in Fig. 2. Fig. A1 illustrates that using $I_s$ as a proxy for the strength of sexual selection will be problematic even when sample sizes are relatively large.
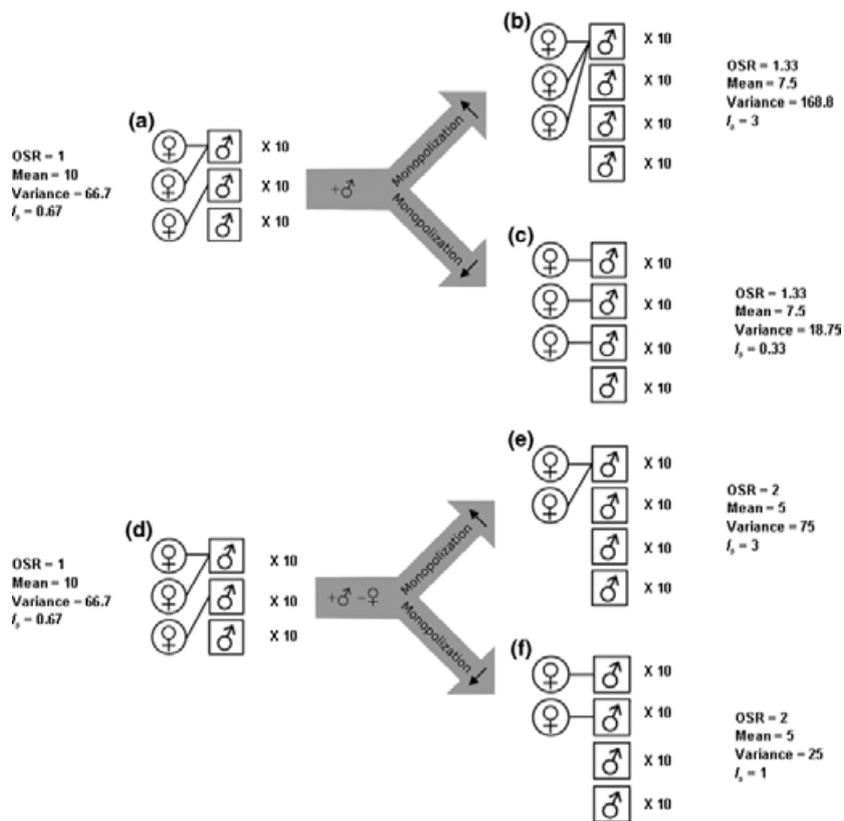


**Fig. A1** The OSR-Monopolizability Conundrum: Large-Sample Version. Alternative relationships between operational sex ratio (OSR), the mean and variance in male mating success, and the opportunity for sexual selection ($I_s$). Males are mate-limited and females mate with one male. We first assume an unbiased OSR with some mate monopolization (a). Ten new males are then added to the system, causing the OSR to become male-biased (b–c). If OSR increases monopolization of females, $I_s$ increases as OSR increases (b). In contrast, if the additional male competitors make maintaining a monopoly more difficult and no single male can now monopolize more than one female, $I_s$ will decrease as OSR increases (c). In this example (a–c), absolute density increases as OSR became skewed. Alternatively, OSR can change independently of density. For example, an unbiased OSR (d) can become male-biased if ten females leave the system and an additional ten male competitors enters. One can again assume increases (e) or decreases (f) in monopolization, but $I_s$ is now bound to increase in either case. This fails to capture the fact that (f) exhibits the most egalitarian mating success possible at this OSR – such a pattern could be caused by random mating or selection, and it is impossible to distinguish between the two. Using $I_s$ as a proxy for actual selection is therefore problematic.