

COMMENTARY

The opportunity to be misled in studies of sexual selectionM. D. JENNIONS*, H. KOKKO* & H. KLUG†¹

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Abstract

It is a challenge to measure sexual selection because both stochastic events (chance) and deterministic factors (selection) generate variation in individuals' reproductive success. Most researchers realize that random events ('noise') make it difficult to detect a relationship between a trait and mating success (i.e. the presence of sexual selection). There is, however, less appreciation of the dangers that arise if stochastic events vary systematically. Systematic variation makes variance-based approaches to measuring the role of selection problematic. This is why measuring the opportunity for sexual selection (I_s and I_{mates}) is so vulnerable to misinterpretation. Although I_s does not measure actual sexual selection (because it includes stochastic variation in mating/fertilization success) it is often implicitly assumed that it will be correlated with the actual strength of sexual selection. The hidden assumption is that random noise is randomly distributed across populations, species or the sexes. Here we present a simple numerical example showing why this practice is worrisome. Specifically, we show that chance variation in mating success is higher when there are fewer potential mates per individual of the focal sex [i.e. when the operational sex ratio (OSR), is more biased]. This will lead to the OSR covarying with I_s even when the strength of sexual selection is unaffected by the OSR. This can generate false confidence in identifying factors that determine variation in the strength of sexual selection. We emphasize that in nature, even when sexual selection is strong, chance variation in mating success is still inevitable because the number of mates per individual is a discrete number. We hope that our worked example will clarify a recent debate about how best to measure sexual selection.

Introduction

"Some people are lucky and other people aren't and not even a graduate of the Harvard Business School can say why." Kurt Vonnegut in *The Sirens of Titan*

"The meeting of preparation with opportunity generates the offspring we call luck." Life coach and motivational speaker Antony Robbins

One worldview is that success and failure are often attributable to stochastic events (as Vonnegut implies; see

also Kahneman, 2011). Another view is that success is almost inevitable for those with the necessary attributes (as Robbins implies). How prevalent are stochastic events in generating variation in reproductive success? And, can stochastic events vary in a predictable fashion? This may sound paradoxical, but chance can be more important in some contexts than others. Below, we illustrate how chance will often influence patterns of mating (or fertilization) success, even when individuals differ in the expression of traits that play a clear role in determining the likelihood that they mate (i.e. sexually-selected traits).

The role of chance will determine whether it is appropriate to estimate differences in the strength of sexual selection between the sexes, or among species or populations, using an approach based solely on variance in mating or reproductive success. Estimating the strength

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of sexual selection based on variance in mating success is common (review: Klug *et al.*, 2010a). In particular, the use of the opportunity for sexual selection, I_s , is often advocated to indicate general patterns in mating systems, as it measures the upper limit of sexual selection (reviews: Klug *et al.*, 2010a; Krakauer *et al.*, 2011). It is quantified as the square of the coefficient of variation in mating success for a given sex (Arnold & Wade, 1984; Shuster & Wade, 2003; for details of the relationship between I_s and I_{mates} and when they are equivalent see Shuster & Wade, 2003, p. 29).

We have previously examined the relationship between the opportunity for sexual selection, the strength of sexual selection and the operational sex ratio (OSR) (Klug *et al.*, 2010a). We found that:

- 1 The opportunity for sexual selection (I_s) is only accurately correlated with the actual strength of sexual selection under a restrictive set of circumstances. Specifically, the opportunity for sexual selection is affected by the OSR due to stochastic effects. Consequently, when the OSR varies, there is only a relationship between the opportunity for sexual selection and sexual selection on male traits when mating success is very strongly skewed towards males with the greatest expression of sexually selected traits (e.g. Fig. 3A–F of Klug *et al.*, 2010a). Extremely strong sexual selection will only occur when female mate sampling is so comprehensive, or male-male competition so severe, that it overrides the unavoidable increase in stochastic variation in male mating success that occurs when the OSR is more male-biased.
- 2 Unless mate monopolization due to sexual selection is incredibly strong, using I_s as a proxy for the actual strength of sexual selection can produce spurious results that lead to false inferences about the relative strength of sexual selection in different contexts (e.g. Fig. 3A,B,E & F of Klug *et al.*, 2010a).
- 3 I_s is not necessarily correlated with the strength of sexual selection even when sexual selection is operating and readily detectable by comparing sexually-selected traits in individuals that differ in their mating success (e.g. Fig. 3B,E,F of Klug *et al.*, 2010a).
- 4 The failure of I_s to correlate with the strength of sexual selection (i.e. covariation between mate monopolization and expression of sexually-selected traits) is not restricted to cases where stochasticity is high due to small population sizes (Klug *et al.*, 2010a; see below).

Given these problems, we previously urged caution in (i) the use of I_s as a surrogate for direct measurement of sexual selection and (ii) making predictions or drawing conclusions based on the assumption that I_s is correlated with the actual strength of sexual selection (Klug *et al.*, 2010a). All measures and proxies of sexual selection have strengths and weaknesses (Jennions & Kokko, 2010). We thus suggested that it is prudent to quantify multiple aspects of selection (Klug *et al.*, 2010a; see also Jones, 2009 and Jennions & Kokko, 2010 regarding utility of

alternative measures such as the Bateman gradient). We noted, however, that selection ultimately acts on specific sets of traits. As a result, it is necessary to quantify actual sexual selection on traits of interest if one aims to draw conclusions about sexual selection (Klug *et al.*, 2010a).

Here, we expand upon our concerns about drawing inferences about the strength of sexual selection based on the opportunity for sexual selection. Our aim is to make it clear that the heart of our disagreement with those who advocate using I_s to measure sexual selection (e.g. Shuster & Wade, 2003; Krakauer *et al.*, 2011) revolves around the relative importance of stochastic and deterministic processes in generating variation in reproductive success. If stochastic processes play no role, then variance-based approaches to the study of sexual selection are perfectly valid. What you see is what you get: males that mate more often and sire more offspring do so because they differ in their expression of sexually selected traits from males that are less reproductively successful. A more important point is that stochastic processes also remain relatively unproblematic if their expected magnitude does not vary systematically in ways that are likely to bias our conclusions or, more realistically, if the only systematic variation comes in forms that can be overcome by researchers sampling more extensively. As we will show, however, biologically realistic scenarios will often fail to fall into these relatively ‘safe’ categories.

Using a simple, biologically-realistic example in which strong sexual selection is operating, we show that the continued use of I_s as a proxy for actual sexual selection is problematic. The practice encourages interpreting a number derived from an observed *pattern* of reproductive success to infer causality. This interpretation is typically not accompanied by an attempt to calculate how much of the variation in reproductive success can be attributed to random events as opposed to causal or deterministic *processes* (i.e. selected traits that increase the likelihood of mating and gaining fertilizations).

Our worked example presents what most empiricists would consider an ideal system for the study of sexual selection. In brief, there are only two types of males: one type has a sexually selected trait that makes these males *twice* as likely to encounter and mate with females. We also assume that sample sizes are large. Thus, our illustrative example offers an unusually good opportunity for an empiricist to detect selection in action. We then show that even large sample sizes do not negate the fact that the number of females per male can be low. Chance plays an increasingly important role in generating variation in male mating success when matings are scarce. This greatly increases I_s when the OSR is male-biased, even if the selection differential does not change. This change in I_s is problematic because it tempts one to draw the erroneous conclusion that sexual selection is stronger when the sex ratio is more male biased.

Box 1: The thing about heroin (or why it's so damn hard to stop using I_s).

"The thing about heroin is... it's very morish, apparently." Harry Hill

Assuming I_s is correlated with actual sexual selection is valid if the proportion of variation in mating success due to random processes does not vary systematically with factors of interest. Our example, together with earlier work (Downhower *et al.*, 1987; Fairbairn & Wilby, 2001; Klug *et al.*, 2010a), shows that this is not the case for the OSR, which is a parameter of major interest to those studying sexual selection. Nor does I_s vary independently of other factors that contribute to the OSR (e.g. sex-specific re-mating interval, sex-specific mortality and birth and adult sex ratios; Sutherland, 1985, 1987).

Given these results, as well as frequent reminders by theoreticians (including proponents of I_s) that I_s does not measure actual selection but an opportunity (Crow, 1958; Wade, 1979; Arnold & Wade, 1984; Jones, 2009; Krakauer *et al.*, 2011), why do researchers often inadvertently use I_s as a measure of actual selection? Krakauer *et al.* (2011) suggest that we were overly harsh when stating that proponents of I_s fail, in practice, to make the distinction between opportunity and realized selection: '*statements from Shuster & Wade (2003) represent two quotations taken from a more than 500 page book*

describing many ways that calculation of I (and I_s) can be useful for understanding organismal ecology and evolution'. It is true that we highlighted phrases that most clearly conflated the potential and actual strength or intensity of sexual selection. In defence, the advice that the potential and actual should not be conflated has not been sufficiently clear to prevent conflation from occurring in practice (reviewed in Box 2 in Klug *et al.*, 2010a; for a recent example see Moorad *et al.*, 2011).

To be more forthright, we believe that these leaps in logic are not attributable to occasional imprecise wording or lapses in reasoning. We think that they expose an underlying belief that, despite its imperfections, I_s remains a useful first guide to the actual intensity of sexual selection. The ethos is to state that '*researchers must be careful not to interpret I_s as a measure of the actual strength of selection*' (Krakauer *et al.*, 2011) and simultaneously promote its general use, clearly including contexts where not much is known about underlying traits. It is similarly telling that our recent reminder that care is needed to distinguish between potential and actual selection (Klug *et al.*, 2010a) was met with an attempt to label it as a misunderstanding (Krakauer *et al.*, 2011). This unfortunately strengthens the impression that proponents of I_s want to have the cake, i.e. keep its meaning theoretically sound by reminding that it cannot be used to study actual selection, and eat it, i.e. encourage interpreting I_s as if it did measure actual selection.

(Obviously, selection *can be* stronger when the sex ratio is more male biased; however, if I_s increases irrespective of whether or not selection is stronger, we have a problem, as discussed in Klug *et al.*, 2010a).

Of course, erroneous conclusions will only be reached if I_s is treated as indicator of actual selection rather than the opportunity for selection. We therefore want to be explicit that the flaw we are pointing out does not lie in the mathematics of I_s *per se*, but rather in the common practice of assuming that there is a correlation between potential and actual selection (Box 1). In all that follows, unless otherwise stated, we are referring to the situation in which I_s is used as a cue to the actual level of sexual selection (Box 1; for further evidence see Box 2 of Klug *et al.*, 2010a; see also Krakauer *et al.*, 2011 for examples where this assumption is implicitly made and Moorad *et al.*, 2011 for a recent example of I_s being repeatedly referred to as the 'strength of sexual selection').

An illustrative example

In Klug *et al.* (2010a) we presented various scenarios using both small and relatively large populations (6–100 individuals) to show how I_s can covary with the OSR, while the relationship to the actual strength of sexual selection was less satisfactory. Here we reiterate that our disquiet with I_s as an estimate of selection does not depend on sampling error in small populations. Instead, an excess contribution of random events to variation in mating success is unavoidable when the number of females per male is relatively (but not unrealistically)

low. Crucially, this is true even in very large populations when mating decisions are based on fixed rules (e.g. mate with the best of N males) and there is strong sexual selection. Our current example is explicit as to why I_s will covary with the OSR in many biologically realistic situations.

Consider a study of mating success in a population with 1500 individuals. The species we describe is representative of any where males can mate again sooner than females (i.e. males have a far shorter 'time out' due to, say, female-only care). To make things computationally simple, we consider a species where females mate as soon as they encounter a male. The male fertilizes her eggs, and the female then leaves the mating pool to raise offspring. Males can, in principle, remate immediately after a short mating (i.e. the time taken to mate and replenish sperm is negligible). The breeding season ends when all females have mated once.

Our scenario does not include mate choice because we opt for a very simple way to implement sexual selection: some males have an enhanced ability to detect the olfactory cues provided by virgin females. All males are in principle able to locate unmated females, but some males achieve a higher encounter rate by virtue of possessing a superior trait favored by sexual selection (we denote trait values by 0 and 1, with 10% of males having the superior trait with a value of 1).

We contrast two population scenarios: either a female-biased sex ratio with 500 males competing to fertilize the eggs of 1000 females (population F); or a male-biased sex ratio with 1000 males competing to fertilize the eggs of

500 females (population M). In each scenario we wish to quantify sexual selection on the male trait. We assume that the mate encounter rate of the 10% of superior males is k -fold compared to the 'non-superior' males. For the worked example we use $k = 2$.

First, consider a deterministic approach to calculating the composition of the population of sires. In population F we must solve the following equation: each of the 50 superior males (10% of 500) fertilize k times as many females as the other 450 males. Given there are 1000 females, and denoting the number of females per regular ('non-superior') male as x , we find:

$$50kx + 450x = 1000$$

$$\text{Hence } x = \frac{20}{9+k}$$

For example, if $k = 2$ (males with superior olfactory talents are twice as good at locating females), then I_s is computed for 50 males with 3.64 mates each, and 450 males with 1.82 mates each. Hence the opportunity for sexual selection, I_s , is 0.0744 (Table 1).

In population M there are 500 females, 100 males with superior olfactory talents, and 900 regular males, so we have to solve $100kx + 900x = 500$. This gives $x = \frac{5}{9+k}$ so that the number of females per non-superior male, x , is approximately 0.45 when $k = 2$.

Again, I_s is 0.0744, now computed with 100 superior males with 0.91 mates each, and 900 males with 0.45 mates each. In this deterministic world I_s is an attractive measure because it remains unchanged when the same subset of males have their mating success elevated to the same degree. In addition, the opportunity for selection agrees perfectly with actual selection on the male trait. The selection differential is the mean of all sires *minus* the mean of an average male (divided by 1/2 to account for the fact that female mating success is equal regardless of their trait value). The mean trait value of all sires, denoting the trait value as 1 for males with superior olfactory talents and 0 for the other males, is the same in both populations F and M $[(50k \times 20/(9+k))/1000 = (100k \times 5/(9+k))/500 = k/(9+k)]$; the other compo-

nent of the selection differential is unchanged. For example, when $k = 2$, the mean sire value is 0.1818 (Table 1).

Given these results, why are we so pessimistic about I_s being a reliable correlate of sexual selection? The above scenario is biologically naïve for one basic reason. No matter what the population size, the number of mates for a given male is always an integer (0, 1, 2 ...N): no male can ever have 0.91, 0.45, 3.64 or 1.82 mates. This real world constraint does not significantly affect the strength of selection (i.e. the selection differential remains stable in all reasonable sized populations, see below), but the effect on I_s is profound.

To illustrate the problem we simulated 10 000 replicates of breeding in populations M and F respectively. In each replicate, exactly 10% of males had the superior trait. Given the reality that a mating either does or does not occur, we now interpret k as the ratio of the relative *propensity* for a superior male to sire a female's eggs compared with a non-superior male. (Thus the propensity is $P = 1$ for regular males with trait value 0, and $P = k$ for superior males with trait value 1; the probability that a focal male with propensity P_i is the sire when a female mates is $P_i / \sum_{i=1}^n P_i$ where n is the number of males). Each female was assigned a mate this way, and each male remained available as mates for all subsequent females regardless of whether or not he had previously mated.

The situation is identical to the deterministic situation in all respects, except for the unavoidable stochasticity that arises because the number of mates per male is an integer. The distribution of mates per male was then used to calculate I_s and the mean trait value of sires.

The mean trait value for sires remained near $k/(9+k) = 0.1818$ in both populations M and F (means of 0.1821 and 0.1820 respectively; Fig. 1a and Table 1). A mild effect of drift is visible in that population M, i.e. the population with fewer females, exhibits larger variation around this mean value across simulated populations (Fig. 1a). However, this slight variability aside, the selection differential is the same in both populations, is unaffected by the OSR, and is the same as that for the deterministic scenario.

In stark contrast, in population F the values of I_s greatly exceed the deterministic version of 0.0744 (Fig. 1b and Table 1). The mean value is now 0.57, and all the values exceed 0.44 (Fig. 1b). In population M the values of I_s are even greater. The mean value is 2.07, and all the values exceed 1.75 (Fig. 1b).

Table 1 The key similarities and differences in outcome for a male-biased and female-biased population when a deterministic and stochastic approach to assigning mates is applied (see text for details). Note that while the mean number of females per male type remains the same, the variance around the mean differs. There is no variation in the deterministic case. For an example of variation in the stochastic case see Fig. 2.

	Deterministic		Stochastic	
	Female biased	Male biased	Female biased	Male biased
Mean female mates per 'superior' male	3.64	0.91	3.64	0.91
Mean female mates per 'non-superior' male	1.82	0.45	1.82	0.45
Selection differential	0.18	0.18	0.18	0.18
Opportunity for sexual selection	0.074	0.074	0.57	2.07

Lessons

There are three lessons from our simple example. First, plausible and biologically reasonable scenarios exist in which the difference in sexual trait expression between mating and non-mating males is independent of the sex ratio. Krakauer *et al.* (2011) suggested that the examples

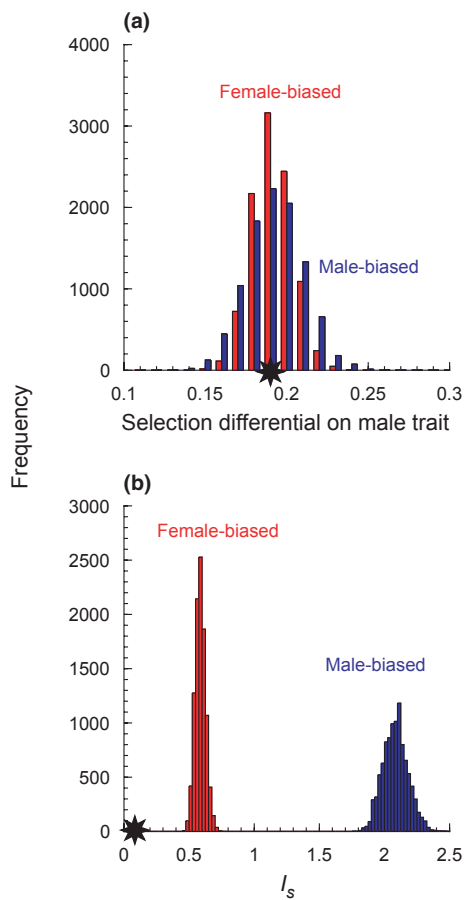


Fig. 1 (a) Values of the selection differential obtained from 10 000 simulation runs for population F (1000 females and 500 males, red histogram) and M (1000 males and 500 females, blue histogram). The star indicates the deterministic value of 0.1818, derived assuming there is no stochasticity. (b) Values of I_s obtained from the same set of simulation runs (red and blue), and the deterministic value of I_s that assumes no stochasticity (stars). The populations differ in I_s values but not in selection for the male trait.

of Klug *et al.* (2010a) intentionally made the difference between mating and non-mating males independent of the sex ratio. This statement is misleading because the relationships reported in Klug *et al.* (2010a) emerged from the female mate sampling tactics. Indeed, selection differentials did increase with the sex ratio in some of the scenarios modeled by Klug *et al.* (2010a). In our current example, some males have a trait that improves their mate encounter rates. This is a biologically plausible and simple process that results in superior males maintaining a higher mating rate regardless of the sex ratio.

Second, our example highlights that problems of interpreting I_s are not confined to situations with extreme biases in the OSR. In Klug *et al.* (2010a), we demonstrated that I_s can fail to correlate with the strength of sexual selection when the sex ratio covers a wide range (1:9–9:1) (see Krakauer *et al.*, 2011 for a

criticism of this approach). Importantly, our current example shows that there is a severe problem even with OSR values that are only moderately biased (2 : 1 and 1 : 2). Further, the OSR can exhibit strong biases in nature. Even the adult sex ratio, which usually varies less than the OSR, has been reported to be male-biased 6 : 1 in Kentish plovers (Kosztolányi *et al.*, 2011), while female-biased values exceeding 2 : 1 (females : males) are common in, for example, Poeciliid fish (e.g. Jennions & Kelly, 2002) and sexually dimorphic antelopes (Fig. 7 in Owen-Smith, 1993).

Third, the direct effect of the OSR on I_s arose even though the OSR did not alter the selection differential (i.e. strength of sexual selection) on the male trait. This is worrisome because, given the intuition that a more male-biased OSR tends to increase competition for females (e.g. Emlen & Oring, 1977), it is tempting to assume that observed differences in I_s provide independent evidence that sexual selection is stronger when the OSR is more male-biased. The variance based approach is particularly problematic as Krakauer *et al.* (2011) explicitly recommend using the difference between the sexes, $I_{\text{males}} - I_{\text{females}}$, to identify the direction and degree to which sexual dimorphism is expected to evolve. Symmetry dictates that the number of mates per individual of the focal sex must be large for one sex when it is small for the other. Consequently, sex differences in I_s cannot yield any other answer than spuriously supporting preconceived ideas. In other words, I_s will never be small for the sex that is very mate-limited, so its use automatically provides unwarranted support that sexual selection underlies phenotypic differences between the sexes without actually testing its true role.

It is, of course, possible to remain on theoretically sound ground by stating that I_s should never be used as a cue for actual selection (Krakauer *et al.*, 2011; for acknowledgement of the fact that I_s measures the maximum, but not necessarily the realized, strength of selection see also Crow, 1958; Wade, 1979; Arnold & Wade, 1984; Jones, 2009). However, this caveat then raises the question: what precisely should motivate us to measure I_s ? Also, guidance on the restricted use of I_s is often contradicted by its actual deployment (Box 1; Klug *et al.* 2010a; for a recently published example see Fig. 3 of Moorad *et al.*, 2011 where the terms ‘opportunity for sexual selection’ and ‘strength of sexual selection’ are used interchangeably).

Why large sample sizes did not come to the rescue

Why does stochasticity matter so much, even in large populations where strong sexual selection is operating? The crux of the problem is that even with hundreds of males and females, the expected number of females per male remains low (in our examples, ranging between 0.45 and 3.64). Even if natural populations are large, this

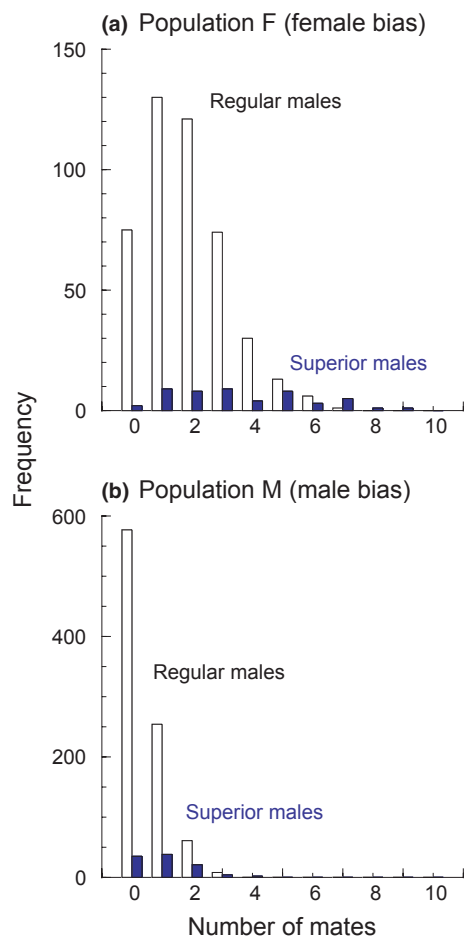


Fig. 2 An example of male mating success distributions in (a) female-biased and (b) male-biased populations. The example graphs data from the last of the 10 000 simulation runs summarized in Fig. 1. In both cases, males favoured by selection (blue histograms) have distributions that are shifted to the right compared with regular males. This predicts a positive selection differential (Fig. 1). However, in both cases there are males with superior traits that do not mate. The number as well as proportion of these males whose failure is due to luck alone is higher when the population is male-biased than when it is female-biased.

number can often remain small (precisely because sex ratio variations are not usually extreme). By chance, some males will not mate even if they have a trait that should give them a mating advantage, while other males that lack the trait will mate. In our example there is thus significant overlap in the distribution of the number of mates per male for males with and without the superior trait (Fig. 2).

If we succumb to the temptation to use I_s as a cue to the likely strength of selection, we will downplay the extent to which chance generated differences in individual's mating success. Not every male who mated did so because he had the superior trait, and likewise

there is no cause behind every failure. Kahneman (2011) appears to take the middle ground position between the worldviews of Vonnegut and Robbins, by stating

*“success = talent + luck
great success = a little more talent + a lot of luck.”*

To apply these ‘equations’ to mating success, one must add that what counts as a lot of luck depends on the OSR. While some mating failures are inevitable, they become more common when the number of females per male is low. This helps explain why I_s depends so strongly on the OSR. Fairbairn & Wilby (2001) made the same point, albeit from a purely mathematical perspective, noting that when mating is random and the distribution of mates per male has a Poisson distribution, then I_s must decrease with the mean mating success (see also Downhower *et al.*, 1987) and must increase with the number of individuals competing for mates. In our example the Poisson distribution is also a good approximation: the number of mates per males is approximately Poisson-distributed for both male types in both populations (Fig. 2). The approximation has its limitations (e.g. the Poisson does not preclude acquiring very large numbers of mates with very low probability, whereas it is impossible for a male to mate with more females than exist in a finite population), so we prefer to present our results based on the observed distributions rather than their Poisson approximations. Either way, I_s automatically guides one's thinking away from the possibility that mating might be influenced by chance when potential mates are scarce. This is because the value of I_s is never low in situations where many males must go unmated due to a strongly male-biased sex ratio.

Several empirical studies show that I_s is greater when the OSR is more male-biased (e.g. Fairbairn & Wilby, 2001; Jones *et al.*, 2004, 2005; Mills *et al.*, 2007; Croshaw, 2010; Fitze & Le Galliard, 2011; Pérez-González & Carranza, 2011). This could be because sexual selection on male traits that affect mating success is indeed stronger when the OSR is more male-biased (e.g. Jones *et al.*, 2005; but see Fitze & Le Galliard, 2011). Unfortunately, however, an approach based on I_s without the use of an appropriate null model only leaves us with uncertainty as to whether chance alone leads to mating variance covarying with a factor of theoretical interest, such as the OSR (as shown here) or sex (Sutherland, 1985, 1987). The use of I_s to infer the likely range of selection is susceptible to misinterpretation.

Ultimately, phenotypic evolution depends on selection for heritable units (i.e. traits). It seems a more profitable use of resources to measure a range of traits and test whether they are correlated with an individual's mating success (i.e. calculate selection gradients). There is, of course, the problem that it is far more work to do this than to measure I_s , and one might often fail to identify the relevant traits. We thus fully sympathize with

Krakauer *et al.* (2011) when they state 'If, for example, the researcher has failed to measure the trait that is the target of selection...then the conclusion would be that selection is acting weakly on the traits that were measured, but selection on any unmeasured traits would go undetected despite being potentially strong... In contrast, I_s would indicate the potential strength of selection in the population: whether or not a high potential for selection is typically matched by actual selection on phenotypic traits is an important empirical question that remains to be answered.' On closer examination, however, we are puzzled as to the value added by measuring I_s . The only way to answer the question posed (rather than opting out with the quintessential undergraduate essay conclusion that 'much still remains unknown') is to measure selection on traits that are putative targets of selection. Put differently, it is more informative to know that there is not selection on specific traits than to know that there might or might not be selection on unknown traits (ignoring the extreme case of $I_s = 0$, which in practice is never reached).

Discussion

We hope that our simple examples have convinced the reader of the problems that arise when I_s is used in the real world as an index of the relative importance of sexual selection in different species, populations or sexes. Additional scenarios to the one here and those in Klug *et al.* (2010a) can be generated to illustrate that comparable problems will arise when species with different biological details are considered; we have intentionally kept our example minimalistic to show precisely why I_s can vary so much when selection does not.

Much of the debate around I_s arises because fitness and reproductive success are conflated. Fitness is usually defined with respect to a specific genotype or phenotype and refers to a propensity of producing a certain number of descendants (in our example, the propensity to encounter mates varies as a function of olfactory sensitivity). Fitness can be empirically estimated by calculating the reproductive success of specific genotypes or phenotypes. Maynard Smith (1989) noted that: 'Fitness is a property, not of an individual, but of a class of individuals – for example homozygous for allele A at a particular locus. Thus the phrase 'expected number of offspring' means the average number, not the number produced by some one individual. If the first human infant with a gene for levitation were struck by lightning in its pram, this would not prove the new genotype to have low fitness, but only that the particular child was unlucky.'

Shuster & Wade (2003) appear to assume that because fitness is empirically measured as reproductive success, theoretical statements about variation in fitness can equally readily be applied to statements about reproductive success. Specifically, the valid theoretical claim derived from Fisher's fundamental theorem that 'the greater the variance in fitness the stronger the force of

selection' (Shuster & Wade, 2003, p. 19) then takes the form of ' I_{mates} provides a standardized measure of the intensity of sexual selection on males and the sex difference in strength of selection (Wade, 1979, 1995; Wade & Arnold, 1980)' (Shuster & Wade, 2003, p. 29). The problem with this extrapolation is that it ignores the fine print. Fisher's fundamental theorem states that: 'the rate of increase in the mean fitness of any organism at any time ascribable to natural selection acting through changes in gene frequencies is exactly equal to its genetic variance in fitness at that time' (from Edwards, 1994). The estimation of the relevant genetic variance requires, however, that there are known genotypes to which fitness can be assigned in a quantitative genetic study. Indeed, the genetic variation is what remains once random variation is removed from the total phenotypic variation.

Although we want to warn against simplistic interpretations of I_s , it is important for us to stress that we are not attacking selection theory. We simply caution against overly optimistic use and interpretation of one measurable parameter. Selection theory as a whole provides a logical structure which we have endorsed elsewhere (Kokko *et al.*, 2006; Anthes *et al.*, 2010; Klug *et al.*, 2010b). Krakauer *et al.* (2011) appear to see this endorsement as inconsistent with our criticisms of I_s , despite Anthes *et al.* (2010) explicitly pointing out that it would be better to shift the focus away from I_s and towards more informative measures, and Klug *et al.* (2010b) likewise reminding that 'it is possible that the potential for selection (unequal male mating success) is simply not realized with respect to male size in this system'. Perhaps the simplest way to summarize the entire debate is to note that it is possible to use a variance-based approach to estimate the importance of selection if one can first identify how much variation is likely to be attributable to chance. This can be achieved by designing appropriate null models, of the type that are now standard in many areas in ecology (Gotelli & Graves, 1996).

While preparing this reply we again read a short paper by William Sutherland, now written a quarter of a century ago (Sutherland, 1987). It was disconcerting to be reminded that he recites almost exactly the same list of concerns that we have raised about the merits of measuring variance in mating (or reproductive) success rather than pursuing other approaches. Although he emphasized the need for formal null models to predict how much variation we can expect due to chance alone, his underlying scepticism of the exercise is revealed when he slyly enumerates the many factors that could contribute to differences in variance in mating success due to chance that are unrelated to sexual selection that includes 'mating time, mortality, local sex ratio, male dispersion and female dispersion' and, with a sense of bathos, concludes with an example pointing out that how sunny it was affected variance in mating success in some damselflies (Sutherland, 1987).

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