Review

The effect of operational sex ratio on the opportunity for sexual selection: a meta-analysis

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The proportion of sexually receptive males in relation to females (operational sex ratio, OSR) is often invoked as an important determinant of the potential for sexual selection. Although the opportunity for sexual selection metric (I_s) is frequently used to estimate such potential, recent doubts have been cast about its capacity to disentangle the relative effect of sexual competition from that of random matings with increasing bias in OSR. To address this, we performed a meta-analysis to evaluate whether the potential for sexual selection in males increases as OSR becomes more male biased and to estimate the relative effects of random matings and sexual competition on this relationship. We performed the analyses using two data sets (one with I_s values and one with I_{dif} values, which estimate how far mate monopolization deviates from the minimum possible for each population). We found that the relationship between OSR and I_s varied from positive to neutral, while I_{dif} was unrelated to OSR variation. This indicates that variation in reproductive success among individuals due to random matings or sexual competition is not influenced by OSR. However, when the correlation between OSR and I_s was positive, random matings appeared to be important in I_s estimations. Perhaps the responses of males and females differ from species to species as OSR becomes more male biased, disrupting the relationship between OSR and I_s when species are pooled.
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Selection may be defined as a nonrandom difference in survivorship or reproduction of phenotypically different individuals during one or more generations (Futuyma 2005). Sexual selection, in particular, occurs when this difference is associated with variation in traits that affect access to mating partners or individual mating success (Darwin 1871; Cornwallis & Uller 2009). It is responsible for the evolution of dimorphisms in secondary sexual characteristics, such as sounds and chemical signals, ornaments and weapons (Anderson 1994).

Variation among individuals in attributes that contribute to fertilization success is necessary for the occurrence of sexual selection (Ridley 2004; Freeman & Herron 2009). Greater variation in reproductive success associated with specific attributes presumably allows for greater change in mean attribute values among individuals between generations (Brodie et al. 1995; Shuster & Wade 2003). Consequently, it is expected that the greater the variation in reproductive success among individuals the greater the potential for selection to occur (Shuster & Wade 2003; Klug et al. 2010). Although different metrics have been used to quantify such potential, one of the most currently used measures is the opportunity for sexual selection (I_s) (Wade 1979; Brodie et al. 1995; Shuster & Wade 2003; Klug et al. 2010). I_s is calculated as the variance in fitness among individuals in a population divided by the square of the average fitness $\overline{W}$ (also called I_{mates}: Shuster & Wade 2003). I_s is a dimensionless metric, allowing variance in mating success to be compared across species (Shuster & Wade 2003; but see Klug et al. 2010).

Particularly for sexual selection, the number of sexually receptive males in relation to females (operational sex ratio, OSR: Emlen & Oring 1977) is frequently used as an important determinant of the variation in reproductive success among individuals of each sex. Variation in reproductive success is expected to occur in populations with highly skewed OSRs (often male biased), because only competitively superior individuals of the more abundant sex should be able to secure a mate and reproduce, leaving the great majority of individuals without descendants (Clutton-Brock 2007; Emlen & Oring 1977; Anderson & Simmons 2006). Consequently, populations with a strong bias in OSR should present greater variance in mating success among individuals of the more abundant sex, leading to higher values of I_s (Shuster & Wade 2003; Shuster 2009).

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Despite the benefits of using I_s to represent the maximum potential for selection (Krakauer et al. 2011), there is growing concern about its use when OSR varies. This concern stems from the fact that it is possible to find a positive correlation between I_s and OSR when there is sexual selection, but also high values of I_s when OSR becomes male biased, even if mate monopolization does not increase (Klug et al. 2010; Jennions et al. 2012). In this situation, it may be difficult to disentangle the real effect of sexual competition for mates from that of random matings on the opportunity for sexual selection among populations with different OSR values or even within populations when OSR changes through time. However, because the basic problem is that I_s values increase as the OSR becomes more biased towards one sex, if one is able to calculate the I_s value that should be obtained if matings were evenly distributed among individuals of the more abundant sex (base I_s), it should be possible to calculate how much the actual I_s values differ from the base I_s (we call this difference between the base I_s and the actual I_s, I_{dif}). Such a difference necessarily implies greater mate monopolization, and although it is still possible that I_s is affected by random matings, increases in mate monopolization are less likely to be predominantly affected by random chance.

In addition to using I_{dif} to tease apart the mathematical link between I_s and OSR, note that, if there is greater competition for matings among individuals of the more abundant sex when OSR becomes more biased, the costs of mate monopolization should also increase (Emlen & Oring 1977). Such an increase may reach a threshold value from which any increase in OSR should be followed by a reduction in mate competition (and consequently in I_s) due to exacerbated monopolization costs (e.g. Weir et al. 2011). However, if I_s is mainly affected by random matings, there should be no a priori reason to expect such a pattern. In fact, simulation models based on this possibility predict a linear increase in I_s with greater OSR bias or, in more biologically realistic situations (as pointed in Klug et al. 2010), an initial decrease followed by an increase in I_s with increasing bias in OSR. In this sense, although both random matings and mate monopolization probably influence the potential for sexual selection, by evaluating the relationships between I_s and OSR and I_{dif} and OSR in empirical studies, we may be able to infer how much the OSR contributes to the intensity of intrasexual competition among individuals in the more abundant sex. To achieve this goal, we conducted a meta-analysis to evaluate how variation in OSR affects the potential for sexual selection. If the relation between OSR and I_s is mainly due to the increasing effect of random matings, we would expect either a linear positive relationship, or an initial decrease in I_s with a subsequent increase with increasing OSR, but no relationship between OSR and I_{dif} for each population. On the other hand, if the relation between OSR and I_s is mainly determined by mate competition in the more abundant sex, we would expect a hump-shaped relationship between I_s and OSR and a positive or curvilinear relationship between I_{dif} and OSR.

METHODS

Selection of Articles

We selected articles from the Web of Science database (www.isiknowledge.com) between February and March 2012 and April and May 2013. To perform the search, we used the following keyword combinations: 'sex*ratio' and 'opportunity for selection', 'sex*ratio' and 'mat*success' and 'sex*ratio' and 'copulation'. We also selected articles from Google Scholar (scholar.google.com) using the keywords 'sex ratio' and 'opportunity for selection'. However, we found no studies containing the measures of interest after the 100th result, so we opted to search for suitable studies in the first 500 articles. Because of the small sample size obtained

from these searches, we also searched for articles that cited Wade (1979). Furthermore, when a study obtained by our searches mentioned other studies containing the aforementioned keywords that were not previously included, we also included them in our selection.

After the first selection, we used a three-step classification process to include the articles in the final analyses. In the first step, we considered only studies that presented the words 'sex ratio', 'OSR', 'opportunity for selection', 'mating success' or 'reproductive success' in the title or summary. In the second step, we analysed the methods and results of the studies selected in the first step and included only those that evaluated OSR, opportunity for selection and mating success. In the final step, we included only studies that estimated or provided conditions to calculate I_s and OSR from one or more populations. The final selection provided 60 studies comprising 55 species and a total of 189 different estimates of I_s and OSR values (Table 1). We used only studies that calculated I_s as the variance in fitness among males in a population divided by the square of the average male fitness (or allowed its calculation) and calculated OSR as the number of sexually receptive males per receptive female.

When the studies provided data through figures, we used the software GIMP 2.6.11 (www.gimp.org) to estimate the exact values of I_s. To do so, we calculated the number of pixels from the origin to a known value of I_s on the Y axis of each figure. This allowed us to estimate the exact value of I_s for each point by converting the pixels associated with a specific point into I_s units for each OSR value on the X axis.

To calculate I_{dif}, we used only a subset of 57 samples from which we could obtain information about the total number of observed mates. We estimated the base I_s by equally distributing the number of mates among all males reported in each study. Afterwards, we subtracted the reported I_s from our estimate of the base I_s to obtain I_{dif}.

Statistical Analysis

Because I_s is a standardized, dimensionless metric, it can be used as an index of effect size in a meta-analysis. However, since only 16 studies provided a measure of variance associated with I_s (and in general it was calculated when there were values of I_s for more than one population), we opted to use sample size as the weight in our analyses (e.g. Kraaijeveld et al. 2011).

There was variation between studies in how mating success was estimated. While some authors observed mating events to estimate mating success, others used genetic approaches to measure reproductive success. In addition, there was pseudoreplication associated with more than one I_s value for the same species among different studies (Hulbert 1984). In this sense, we used two approaches to analyse the data. In the first approach, we used the complete data set with 189 samples to perform general mixed effects models. We considered I_s and I_{dif} as the response variables and OSR and the type of measurement of male success (mating or reproductive) as predictor variables. Since there was more than one measure for the same species and also measures from different species belonging to the different phylogenetic groups, we used species nested in large phylogenetic groups as a random factor. To obtain the phylogenetic groups, we followed information from the Tree of Life Project (http://www.tolweb.org) and nested each species into amphibians, birds, crustaceans, fishes, insects, lizards, mammals, sea spiders or worms (Annelida). In these analyses, we log transformed I_s and I_{dif} to meet test assumptions (generalized linear models did not improve model fit after looking at the Pearson residuals; Crawley 2007). To test for both linear and nonlinear relationships between I_s or I_{dif} and OSR, we fitted models with linear