

The measurement of sexual selection on females and males

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Abstract As in any field of research, the study of sexual selection is subject to ongoing debate over definitions and interpretations of the fundamental concepts involved. These arguments generally promote progress, as they highlight areas where current explanations are incomplete. Here we briefly review two ongoing discussions in the sexual selection literature. First, the definition of sexual selection has received renewed interest in light of increasing research effort into when and how it operates in females. Second, how best to measure sexual selection is an ongoing subject of debate; in practice, recognition that the appropriate measures depend on the focus of the specific study, and that multiple measures should be employed wherever possible, seems to provide the most informative approach. The wide scope of recent empirical work in these and related areas, with the application of new techniques and approaches, reflects that the field of sexual selection is being constantly expanded and enriched [*Current Zoology* 59 (4): 558–563, 2013].

Keywords Sexual selection, Mating system, Mating success, Reproductive success, Postcopulatory sexual selection, Sex roles

The 2012 ISBE symposium on ‘Recent developments in sexual selection research’ gave an eclectic taste of several current research avenues. Many speakers addressed longstanding debates over how to define, and use, some of the fundamental concepts in sexual selection theory. Here we attempt to give our perspective on two of these debates, which we see as closely interrelated but different in their focus. First, the last two decades have seen a gradual increase in research attention on whether, when and how sexual selection operates in females. The importance of these questions is by now well acknowledged (Clutton-Brock 2007, 2009; Rosvall 2011), though there is still only sparse information available on many aspects of female sexual selection. Investigating the differences in sexual selection and the interaction of selective processes between the sexes has already begun to improve our understanding of coevolution between the sexes, as well as the evolution and dynamics of mating systems. It has also led to some discussion over how sexual selection is defined. This links closely to a second problem: how should we measure sexual selection? Several measures are commonly used, but there is some argument over when these should be applied and how they are interpreted (e.g. Klug et al. 2010; Krakauer et al. 2011). Recent work has begun to distinguish the information captured using different measures, address how these relate to one another, and empirically test their utility (e.g. Fritzsche and Arnqvist,

2013). These studies further our ability to compare between studies and systems, and determine the generality of their results or identify previously unrecognized complexity in the processes of interest. Empirical tests are invaluable to the development of both these areas, and throughout our brief review we highlight some examples of recent empirical studies that are taking new directions, using innovative techniques, and bringing different perspectives to sexual selection research.

1 Sexual Selection in Females

Traits are sexually selected when they increase reproductive success by providing an advantage in competition for mates or fertilizations (Andersson, 1994; Shuker, 2010). Although proposed by Darwin (1859, 1871) as an explanation for the evolution of exaggerated weaponry and ornaments, traits that more often occur in males, the original definition of sexual selection was phrased in general terms that did not exclude females. Nevertheless, early research effort was concentrated on males. This focus has been changing, albeit slowly, since the 1990s with studies of “sex role-reversed” species demonstrating that sexual selection can act on females (e.g. Cumming, 1994; Berglund et al. 1997). Role-reversed systems have since been quite extensively investigated as they provide useful “exceptions to the rule” that males experience stronger selection to maximize mating rate, along with potentially illustrative dif-

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ferences in the nature of the constraints involved (Fitzpatrick et al., 1995). In general, however, studies of sexual selection in females are comparatively rare, and we still lack a thorough understanding of when and how sexual selection acts on females across other mating systems (Clutton-Brock, 2007, 2009; Stockley and Bro-Jørgensen, 2011). It is now clear that in most taxa individual females may mate with multiple males (Thornhill and Alcock, 1983; Pizzari and Parker, 2009) and that this polyandrous mating behaviour accrues direct and indirect benefits to females (Thornhill and Alcock, 1983; Arnqvist and Nilsson, 2000; Jennions and Petrie, 2000; Slatyer et al., 2011; Shuster et al., 2013). Tests of the expectation that polyandry enhances the possibility for sexual selection to act on females (Andersson, 1994) have increased with the recognition of the prevalence of polyandry. For example, sexual dimorphism is usually greater in polyandrous than monandrous species, suggesting that mating multiply strengthens sexual selection on both sexes (Andersson, 1994). Further examples are accumulating of both female competition for mates (Clutton-Brock, 2007, 2009; Rosvall, 2011), and the sexual selection of female ornamentation by male mate choice (Amundsen, 2000; Bonduriansky, 2001; Funk and Tallamy, 2000).

Estimates of the strength of sexual selection in females are particularly lacking, especially for species with “conventional” sex roles. Very few empirical studies have directly compared the strength of sexual selection in females and males (but see Lorch et al., 2008; Fitze and Le Galliard, 2011; Aronsen et al., 2013; Fritzsché and Arnqvist, 2013; Mobley and Jones, 2013). The results of this handful of studies, scattered across a variety of mating systems, range from stronger selection on males, to comparable selection on both sexes, to stronger selection on females; and follow patterns both consistent with and contrary to predictions from mating systems theory (Lorch et al., 2008). Despite the expectation that sexual selection acts differently on males and females, and a broad impression of the usual direction of these differences, we lack the direct comparisons essential for an explicit understanding of the parameters responsible. These are by no means easy data to collect, but as a starting point we suggest that wherever possible, studies estimating the strength of sexual selection in one sex should gather the same data for the other.

Increasing emphasis on the fact that both sexes are subject to sexual selection is generating interest in how selection on one sex affects selection on the other (Bonduriansky, 2009; Clutton-Brock, 2009; Rosvall,

2011; Kvarnemo and Simmons, 2013). For example, the strength of postcopulatory sexual selection on males, through cryptic female choice or sperm competition, will affect male investment in ejaculate (Parker et al., 1997; Engqvist and Reinhold, 2007). The cost of ejaculate should influence how beneficial it is for males to be choosy about their mates, thus affecting intra-female competition (Lorch, 2002; Kvarnemo and Simmons, 2013).

While sexual selection evidently can occur in females, reproductive success is subject to different selective pressures and trade-offs in each sex (Fitzpatrick et al., 1995; Parker, 2006). Frequently, competition for mates is not the most important factor influencing variation in reproductive success among females. For example, females commonly compete for breeding resources, such as territories, that are nonetheless vital for reproduction (Rosvall, 2011; Stockley and Bro-Jørgensen, 2011). Even when females compete for mates, the benefit is often access to resources provided by males, rather than sperm. Some authors have argued for a broader definition of sexual selection to encompass all intrasexual reproductive competition (Clutton-Brock, 2009) or any sex-specific selection (Carranza, 2009; see Stockley and Bro-Jørgensen 2011 for an overview). Discussion of when female-female competition constitutes sexual selection highlights that some traits are not easily categorized as being mainly naturally or sexually selected. “Social selection”, that is, selection arising from *intra- or inter-sexual* competition for any resource increasing reproductive success (West-Eberhard, 1983), has been suggested as an alternative framework (Lyon and Montgomerie, 2012; Rubenstein, 2012; Berglund, 2013 this issue). Generally, distinguishing sexual from natural selection provides a useful and productive conceptual tool in the study of trait evolution, and defining the boundaries of social selection appears, if anything, to be less straightforward than defining sexual selection. The current framework of sexual and natural selection is able to incorporate environmental, including social, effects. Rather than moving the definitional boundaries, it seems more helpful to accept that any terminology has limitations and to be aware of them.

2 How should Sexual Selection be Measured?

Over the last decades several approaches to quantify the strength of sexual selection have been proposed (Bateman, 1948; Arnold and Duvall, 1994; Shuster and Wade, 2003; Jones, 2009; Collet et al. 2012; McDonald

et al., 2013). There is no consensus on which measure most accurately reflects the strength of sexual selection operating in a given species or population (Klug et al., 2010; Krakauer et al., 2011, Jennions et al., 2012). Ideally, studies should aim to gather as holistic and comprehensive a dataset as possible, for which several measures of sexual selection for females and males can be calculated simultaneously and compared (Kvarnemo and Simmons, 2013; Fritzsche and Arnqvist, 2013). These data should be generated with an experimental design that includes the two key selective episodes: (i) precopulatory sexual selection, including intrasexual competition and intersexual mate choice and (ii) postcopulatory sexual selection including cryptic female choice, cryptic male choice and sperm competition. Furthermore, to get realistic estimates of sexual selection, its strength should be measured throughout the entire reproductive period and preferably on a population level (Rodriguez-Munoz et al., 2010, McDonald et al., 2013). Such comprehensive data sets are difficult to obtain and the most appropriate method and set of measures will depend heavily on both the model system and the specific research question. However, the suggestion that researchers take advantage of the complementary information provided by different measures is not just a recommendation to double-check measurements, but vital to ensure a complete picture of selection. It has been pointed out by authors on all sides of the measurement debate that the different approaches measure different components of the selective process, and that no one measure will suffice for a truly accurate picture of sexual selection (e.g. Jones, 2009; Fitze and Le Galliard, 2011; Kokko et al., 2012).

Besides deciding which measures to use for estimating the strength of sexual selection, another important consideration is how to derive the parameters necessary to calculate those estimates. How mating success and reproductive success are defined, which traits are chosen for study, and consequently what is directly measured, all affect estimates of selection. Estimating the strength of sexual selection on a phenotypic trait can be difficult and should be subject to careful interpretation. First, choosing an appropriate focal trait can be problematic, particularly if the aim is to compare the strength of selection across sexes or species. Even when comparable traits can be identified, phenotypic variability can differ between species and limit the usefulness of such comparisons. Further, traits that are or have been under strong directional or stabilizing sexual selection show reduced phenotypic variability (Reinhold, 2011).

This means that trait-based measures will often underestimate sexual selection because strong selection has already depleted phenotypic variance.

The definition and measurement of mating success is another important consideration. Is it enough to observe apparently successful execution of mating behaviour (mounting, intromission) or should mating success only include pairings that are confirmed to result in sperm transfer? In practice, several methods are used, from counting “the number of mates acquired or matings achieved during some relatively long interval of time such as a day (for an insect), season (for a vertebrate), or lifetime” (Koenig and Albano, 1986; see also Arnold and Wade, 1984), to the number of genetic mates (with whom at least one offspring is produced, e.g. Topping and Millar, 1998; Barreto and Avise, 2010). While they are variably explicit about what constitutes success, these definitions do not allow a detailed breakdown of how selection acts across the mating process. This is important to understand, as a large body of work predicts that postcopulatory processes play a significant role in sexual selection, and may augment, diminish, or act on entirely different traits than precopulatory selection (Kvarnemo and Simmons, 2013). Jones (2009) suggested a method to estimate the contribution of postcopulatory sexual selection using the residuals from calculating the Bateman gradient; Fritzsche and Arnqvist (2013) showed that this residual selection can be a sizeable component of total selection. A rare attempt to measure the separate contributions of precopulatory mating success (the number of females a male mated with) and fertilization success (the mean proportion of offspring sired across those females) to total male mating success found that their effects were approximately equal in strength (Pischedda and Rice, 2012). However, studies examining postcopulatory processes in isolation have yielded results ranging from strong effects of postcopulatory selection to no evidence for its occurrence, even in related species with similar mating systems (e.g. in pipefish *Syngnathus spp.*, Partridge et al., 2009; Paczolt and Jones, 2010). Although it is difficult to empirically disentangle the pre- and postcopulatory components of mating success, recent innovative work has allowed postcopulatory processes to be observed directly. In *Drosophila melanogaster*, Manier et al. (2010) labelled sperm from different males with coloured fluorescent proteins to observe sperm competition in the female reproductive tract. Male fertilization success depended on both ejaculate-female and ejaculate-ejaculate interactions, as well as complex sperm

behaviour. Another exciting development seeks to use labelled sperm in combination with transparent study organisms (such as *Macrostomum* and *Caenorhabditis*), allowing postcopulatory mechanisms to be measured directly and non-invasively in live individuals (Lukas Schärer, personal communication, October 2012). Similarly the transparent squid, *Sepiadarium austrinum*, in which spermatophore usage has been directly observed in females (Wegener et al., 2013), are another promising system allowing the detailed study of both pre- and postcopulatory processes at once.

Defining and measuring reproductive success is equally important and no less problematic. If reproductive success is to reflect an individual's fitness, the necessary measure is the number of offspring that contribute to the next generation (Westneat and Fox, 2010). This is often difficult to achieve, and the number of eggs laid, offspring hatched/born, or offspring that survive to adulthood can be useful approximations (e.g. Howard, 1979; Pelissie et al., 2012; Fritzsche and Arnqvist, 2013), although their limitations should be kept in mind when interpreting results. Random stochastic events, as well as other sources of selection, mean that offspring survival might have little to do with the focal trait under selection and are likely to affect the measure of reproductive success. As these additional influences can occur throughout development, measures taken at different stages will yield different estimates of the strength of selection on the focal trait. In order to isolate the contribution of sexual selection and estimate its potential it is important to generate these measures in controlled laboratory experiments that limit or make uniform such external forces. The use of experimental evolution designs in laboratory populations provides a powerful way to examine selection. For example, this approach has been very successful in illuminating how sexual conflict can shape coevolution between the sexes. Several studies show that females pay elevated costs under enhanced sexual conflict. Female *Drosophila melanogaster* evolving under low mating frequency conditions lose resistance to male harm (Holland and Rice, 1999; Wigby and Chapman, 2004), while monogamously housed males become more benign in their effects on female fitness (Crudgington et al. 2005; Holland and Rice, 1999). Similar findings were made in the bulb mite *Rhizoglyphus robini* (Tilszer et al., 2006), in *Sepsis cynipsea* (Martin and Hosken, 2003), and the seed beetle *Acanthoscelides obtectus* (Maklakov et al., 2005). By varying single key parameters predicted to alter the strength of sexual selection (e.g. mate availability) experimental

evolution designs could additionally provide a valuable platform for the comparison of different measures of selection.

3 Conclusion

Sexual selection is a huge field, expanding rapidly in many directions. The current framework and definition of sexual selection are broad enough to account for sexual selection occurring in females as well as males. Yet, there are considerable gaps in the study of sexual selection in females and future research needs to concentrate on these, especially the comparison of measures of sexual selection of females of different mating systems. Comprehensive measurement of the strength of sexual selection in both sexes across taxa, as well as determining the relationships between measures targeting different components of the selective process, are critical to a thorough understanding of sexual selection. A better resolution of the main parameters involved in sexual selection – mating success and reproductive success – will be another fruitful challenge in the development of informative measurement approaches. We are well on the way to a thorough understanding of sexual selection, especially if we continue to critically question, test and revise its underlying assumptions.

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