Forum: Invited Review

Intrasexual competition in females: evidence for sexual selection?

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In spite of recent interest in sexual selection in females, debate exists over whether traits that influence female–female competition are sexually selected. This review uses female–female aggressive behavior as a model behavioral trait for understanding the evolutionary mechanisms promoting intrasexual competition, focusing especially on sexual selection. I employ a broad definition of sexual selection, whereby traits that influence competition for mates are sexually selected, whereas those that directly influence fecundity or offspring survival are naturally selected. Drawing examples from across animal taxa, including humans, I examine 4 predictions about female intrasexual competition based on the abundance of resources, the availability of males, and the direct or indirect benefits those males provide. These patterns reveal a key sex difference in sexual selection: Although females may compete for the number of mates, they appear to compete more so for access to high-quality mates that provide direct and indirect (genetic) benefits. As is the case in males, intrasexual selection in females also includes competition for essential resources required for access to mates. If mate quality affects the magnitude of mating success, then restricting sexual selection to competition for quantity of mates may ignore important components of fitness in females and underestimate the role of sexual selection in shaping female phenotype. In the future, understanding sex differences in sexual selection will require further exploration of the extent of mutual intrasexual competition and the incorporation of quality of mating success into the study of sexual selection in both sexes. *Key words:* aggression, female competition, intrasexual selection, mating success, sexual selection. *[Behav Ecol]*

INTRODUCTION

In recent years, behavioral ecologists have shown increased interest in sexual selection in females (Heinsohn et al. 2005; Lebas 2006; Clutton-Brock 2007, 2009; Watson and Simmons 2010), focusing especially on the phenotypic variation in and functional significance of female ornamentation (Amundsen 2000; Amundsen and Parn 2006; Kraaijeveld et al. 2007), vocalization (Langmore 1998), and weaponry (Estes 1991; Stankowich and Caro 2009). Although females appear to use these traits in same-sex competition, a consensus is lacking as to whether this competition constitutes sexual selection (Clutton-Brock 2007, 2009; Shuker 2010; Stockley and Bro-Jørgensen 2011).

In species with conventional sex roles, sexual selection is thought to act more strongly in males than in females due to the interplay between sexual selection, variance in mating success, and asymmetries in parental investment (Bateman 1948; Trivers 1972; Emlen and Oring 1977; Kokko and Jennions 2003; Wade and Shuster 2005, but see Drea 2005, Tang-Martinez and Ryder 2005). As a consequence, the frequency and intensity of exaggerated traits and behaviors tend to be greater in males than in females. When females exhibit versions of these traits, their evolutionary significance has proven to be enigmatic. Are these traits nonfunctional by-products of a genetic correlation with males (Lande 1980)? Are they primarily shaped by fecundity or survival selection (i.e., natural selection that excludes competition for mates)? Or do females use these exaggerated traits and behaviors to compete for mates in a context similar to sexually selected male–male competition? This third, more controversial possibility is the focus of this review.

More specifically, I explore the evolutionary mechanisms driving female–female competition, using intrasexual aggression as a model behavioral trait for drawing broad conclusions about sexual selection and competitive interactions among females. Though intrasexual competition frequently occurs without escalating to aggressive behavior (e.g., via threat displays, signals of aggressive intent, or other more subtle competitive interactions), direct or overt expressions of female–female aggression represent the culmination of competitive interactions (e.g., fighting, chasing, or attacking). These aggressive encounters therefore reveal the resources or individuals over which females compete and the benefited accrued by successful competitors. Moreover, female–female aggression has been widely studied in a range of natural and experimental conditions across the animal kingdom, but these data have not yet been synthesized to uncover the evolutionary mechanisms promoting competition among females. This review emphasizes female–female aggressive interactions in the context of mating competition, including examples that clearly fall within the purview of sexual selection as well as others that comprise the crux of the debate over sexual selection in females. I make predictions about patterns of female–female competition to discern how and why females compete. Based on the relative support for these predictions, I address how intrasexual competition may differ between the sexes, in function, outcome, and mechanism of selection, and I suggest clear directions for future research on the nature of intrasexual competition and sexual selection in both sexes.

What is sexual selection?

Many definitions of sexual selection exist, yet the specifics of the definition are critical to interpreting patterns of female–

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female competition. I advocate Shuker's recent "consensus definition" (2010), simply stated as "competition for mates," because this definition occupies a middle ground between broad (Huxley 1938; Selander 1972; Carranza 2009) and narrow (Wade and Arnold 1980; Andersson 1994). Under this view, if a trait influences competition for mates, then this trait is sexually selected. Therefore, sexual selection encompasses a rather broad array of processes, such as competition for the number or quality of mates as well as competition for resources that directly influence the probability of mating. Shuker's definition is therefore especially useful for addressing similarities and differences in intrasexual selection in the 2 sexes, while allowing for sex differences in the nature of this competition. I will address 2 points about this definition that are particularly relevant to sexual selection in females and leave the details of the current and historical debates over sexual selection to a handful of thoughtful reviews (Endler 1986; Andersson 1994; Kavanagh 2006; Roughgarden et al. 2006; Clutton-Brock 2009, 2010; Roughgarden and Akçay 2010; Shuker 2010).

The first point concerns the contrast between competition for mates and competition for resources. One focus of the current debate is whether or not sexual selection includes intrasexual competition for breeding opportunities instead of simply competition for mates (Clutton-Brock 2007, 2009, 2010; Roughgarden and Akçay 2010). Shuker's definition includes competition for resources that influence the quantity or quality of mates obtained (Lebas 2006; Stockley and Bro-Jørgensen 2011), but it excludes resource competition that only affects survival or fecundity, as this latter category does not differentiate sexual selection from fecundity or mortality selection (Wade and Arnold 1980; Endler 1986; Andersson 1994). Thus, sexual selection is maintained as a unique subset of natural selection, defined not only by the identity of competing parties (e.g., individuals of the same sex and species) but also by the component of fitness that is affected by competition, as described by Darwin (1859, 1871).

A second key point regarding the definition of sexual selection is whether it is sufficiently broad to include the myriad ways in which individuals compete for mates (Andersson and Iwasa 1996), without inherent sex biases. Theory suggests that females should not to compete for the quantity of mates because increasing mate number does not affect female reproductive success (Bateman 1948). If we then restrict sexual selection to competition for the "number" of mates or the ability to gain access to mates (Andersson 1994; Arnold 1994), we effectively bias its applicability to males, potentially missing clear conceptual parallels that may exist in females. By including all competition for mates within sexual selection, we thus bring in an array of evolutionary processes that are fundamentally similar to male–male competition for the number of mates, including cryptic female choice and sperm competition (Birkhead and Møller 1998; Andersson and Simmons 2006; Eberhard 2009; Jones and Ratterman 2009). Competition for mates may also involve competition over mate quality (or, competitive mate choice; Halliday 1983), an often ignored aspect of mating success that may be particularly relevant to females (Petrie 1983; Altmann 1997). In addition, sexual selection may include competition over entities that affect the probability of getting a mate or becoming a mate. For example, male satin bowerbirds (*Ptilonorhynchus violaceus*) compete with each other for bower adornments because more decorated bowers attract more mates (Borgia 1985a, 1985b). Same-sex competition for these bower adornments, like competition for territories, lekking positions, or nesting sites to attract mates, is typically considered sexual selection in males, even though males here compete to be qualified "as a mate," prior to any actual competition "to mate" (Ahnesjo et al. 2001; see Andersson 1994, Chapter 6).

WHY SHOULD FEMALES COMPETE?

Nonadaptive hypotheses

We might expect high levels of competition and aggression among females as a by-product of a genetic correlation with males: The sexes share the vast majority of their genome, and so, a behavior that is favored in one sex may exist in the other sex via correlational selection (Wallace 1891; Lande 1980). In spite of the historical argument that exaggerated female traits exist as nonadaptive by-products of selection on males, empirical tests demonstrate a range of intersexual genetic correlations (for an example with ornamentation, see Kraaijeveld et al. 2007). For same-sex aggression in females, high repeatability (e.g., Rosvall 2008; Sinn et al. 2008; While et al. 2010) and parent–offspring correlations (e.g., Maestripieri 2003) suggest a potential for high genetic variance and thus high heritability (Falconer 1989). More concrete support for correlational selection comes from a study in which female aggressiveness increased in lines of *Drosophila melanogaster* that were selected for high levels of male aggression (Edwards et al. 2006). High-throughput genomic analyses are beginning to identify genes that predict competitive ability (e.g., Renn et al. 2008; Zhou and Rao 2008), including some genes that differ between the sexes (Lee and Hall 2000). Collectively, these studies suggest that aggression in males and females may be mediated by some common mechanism, but they leave open the possibility that different genes or different mechanisms may be relevant in the 2 sexes.

While we are just beginning to understand the genetics of aggression, more is known about the hormonal mechanisms mediating aggressive behavior, especially in vertebrates. Much research has focused on the relationship between aggression and testosterone (T), although the list of hormones and neuropeptides that mediate aggression continues to grow (Stribley and Carter 1999; Adkins-Regan 2005; Nelson and Trainor 2007; Soma et al. 2008; Kabelik et al. 2010). Notably, evidence is mixed as to whether T influences aggression in females in the same way that it does in males (Desjardins et al. 2006; Zysling et al. 2006; Gill et al. 2007; Sandell 2007, but see Elekonich and Wingfield 2000; De Ridder et al. 2002; Jawor et al. 2006; While et al. 2010). Furthermore, sex and seasonal differences in neuroendocrine mechanisms of aggression question the assumption that behavioral mechanisms are fixed within a species (Soma 2006; Canoine et al. 2007; Voigt and Goymann 2007; Sperry et al. 2010), thus challenging the notion that female aggressive behavior exists simply as a nonadaptive by-product of male aggression.

Female competition and natural selection

A review of the naturally selected functions of female–female competition is vital to placing this behavior's possible sexually selected functions into context; however, because female–female competition for nonmating resources is widely accepted, I will only briefly summarize competition that directly influences fecundity, survival, or offspring survival.

Several lines of evidence suggest that females compete for food access. For example, when food is rare or difficult to obtain, female–female aggression increases in frequency (Ueda and Kidokoro 2002; Baird and Sloan 2003). Because maternal investment is linked with high energetic demands, same-sex competition for food may be especially common when females heavily invest in parental care. Not surprisingly, much of the support for this hypothesis comes from mammalian species, with female aggression peaking during pregnancy and lactation (Boness et al. 1982; McDonough 1994; Wolff and Peterson 1998; Rodel et al. 2008, but see Derix et al. 1993), although this temporal pattern is also consistent with protecting offspring from infanticide. Female–female competition and

associated aggression also tend to be more frequent at higher densities (Cassini 2000; Klatt et al. 2004; Robinson and Kruuk 2007) and larger group sizes (Snowdon and Pickhard 1999). Aggressive interactions that determine long-term rank relationships may likewise affect competition for food. For example, higher ranking female chimpanzees (*Pan troglodytes*), gain access to higher quality foraging areas (Murray et al. 2006, 2007; Kahlenberg et al. 2008), and ultimately, they produce more surviving offspring and daughters that mature more quickly (Pusey et al. 1997).

Although some evidence points to food as a source of female–female competition, other work advocates an offspring protection hypothesis (Maestripieri 1992; Wolff and Peterson 1998). Females often defend eggs or offspring, especially those with a protracted dependent phase during which they are at risk of injury or death from infanticidal rivals (Hrdy 1979; Ebensperger 1998). For example, female northern elephant seals (*Mirounga angustirostris*) that initiate more frequent aggressive interactions are more effective at preventing other females from biting their offspring, and these offspring are more likely to survive to weaning (Christenson and Leboeuf 1978). Similarly, nonmammalian females respond aggressively in defense of eggs from infanticidal females, as may be the case in some frogs (Summers 1989), reptiles (Sinn et al. 2008), and birds (Gowaty 1981; Chek and Robertson 1991; Alworth and Scheiber 1999; Veiga 2004). Finally, females may compete to maximize their own survival, with more aggressive or dominant females obtain safer, more central positions in groups and reducing their own risk of predation (Ron et al. 1996; Ost et al. 2007).

Female–female competition for mates

Within the broad context of competition for mates, I review the evidence for several possible functions of female–female competition, emphasizing taxonomic patterns and differences between the sexes whenever possible. I make several predictions about the nature of intrasexual competition in females based on the availability of mates or mating resources and the potential direct and indirect benefits to be obtained via competition for mates. I describe select examples in support of or opposition to each prediction.

To determine whether sexual selection shapes the patterns described under each prediction, the issue at hand is which component of fitness is affected by this competition: If the selection differential (or, covariance between competitive ability and reproductive success) is directly affected by variance in fecundity or survival, then, intrasexual competition is shaped by natural selection. If the selection differential is influenced by competition for mates (as described in the INTRODUCTION above), then sexual selection applies. Thus, for each prediction, I distinguish between natural and sexual selection whenever possible, although this task may be difficult in some cases, especially when natural and sexual selection work in the same direction (Darwin 1871; Clutton-Brock 2004; Carranza 2009). Each prediction therefore serves as a starting point for exploring patterns of female competition, with the aims of clarifying recent debates and highlighting key next steps in the study of intrasexual selection.

Competition for access to mates

Prediction 1: as the operational sex ratio becomes more female biased, females should compete for access to males. If the operational sex ratio (OSR) determines which sex will compete for access to the other sex (Emlen and Oring 1977; Kvarnemo and Ahnesjo 1996), we should expect frequent female–female competition in populations where males are limiting, such as sex-role reversed systems where the OSR is female biased (Eens and Pinxten, 2000). In the sex-role reversed tidewater goby

(*Eucyclogobius newberryi*), for example, females compete for access to territorial males and their associated burrows (Swenson 1997). Strong same-sex competition in role-reversed species has long been seen as supporting classical sexual selection theory (Darwin 1871; Trivers 1972), but whether systems with conventional sex roles show similar patterns is less clear.

In populations with dynamic OSRs, we should expect increased female–female competition as the OSR becomes more female biased. Both experimental and observational evidence supports this prediction, with more frequent competitive interactions among females when there are fewer available males or more ready-to-mate females (e.g., Kvarnemo et al. 1995; Forsgren et al. 2004). In one fish species, the sand goby (*Pomatoschistus minutus*), OSR, not density, predicts the frequency of female–female competitive interactions, just as it does with males (Kvarnemo et al. 1995). The observation that higher densities do not increase female competition also suggests that female sand gobies do not compete primarily for density-dependent resources, such as food. Instead, they appear to compete for access to males themselves or for male-held nest sites. Similar patterns of female aggression are also found in species where males do not care for offspring (Weckerly et al. 2001; Hohmann and Fruth 2003; Bebie and McElligott 2006; Razzoli and Valsecchi 2006). Pairs of captive female house mice (*Mus musculus*), for example, are more aggressive toward each other when presented with one male than when presented with 3 males (Rusu and Krackow 2004), again suggesting that females vie for access to males themselves. Humans are also thought to show increased levels of female–female competition in populations with a scarcity of available males (typically associated with political or war-time demographic shifts, Schuster 1983; Campbell 1995), although more rigorous cross-cultural tests are warranted.

In the sand goby case described above, female competition changed as the OSR became more female biased, but all females were able to find a mate regardless of OSR (Kvarnemo et al. 1995). When the OSR was male biased, however, some males were excluded from breeding altogether. This sexual disparity in the impact of OSR on mating success draws into focus a key question: If the outcome of female–female competition does not predict the number of mates, why should females compete? In other words, if males are not limiting, why do females bother to compete at all? One solution to this question is that females do not compete for the number of mates, but instead, they compete for the direct and indirect benefits those males provide.

Competition for high quality mates

Prediction 2: females should compete for access to males that provide direct benefits. In many systems, females receive a variety of direct benefits from their mates (e.g., nutrients, space, parental care, etc.). Patterns of competition and aggression suggest that females may compete for these direct benefits or the high-quality males that are best able to provide these benefits. For example, female–female aggressive interactions are common in many insect species where males provide nutrient rich spermatophores to their mates (e.g., Gwynne and Bailey 1999; Lewis et al. 2004). If the outcome of these competitive interactions predicts the quality of mates females obtain, then this competition may be the target of sexual selection as well as natural selection for increased fecundity.

Access to defended space (i.e., territories) is one of the primary direct benefits females may obtain from their mates because territories provide many potential fitness benefits (Orians 1969; Jones 1981; Andersson 1994). The question of whether females compete for access to territories can be difficult to answer empirically because females often acquire a mate at the same time as a territory. The primary difference between these 2 scenarios is whether the female directly assesses

territory quality or mate quality. For convenience, I will instead consider evidence for this particular direct benefit in the context of mating resources over which females compete (Prediction 4), with full understanding that competition for high-quality territories may well represent competition for male direct benefits as well.

Competition for male parental care
Parental care is among the best studied direct benefit that a female might obtain from her mate, and it thus provides an excellent case study with which to examine possible female–female competition for this aspect of mate quality. In polygynous and monogamous species in which males provide parental care, females may compete over a monogamous pair-bond, using overt aggressive behaviors to ward off additional females, thus ensuring exclusive social access to a particular male (reviewed in Wittenberger and Tilson 1980; Slagsvold and Lifjeld 1994). If secondary females receive less paternal care than primary or monogamously mated females (Breiehagen and Slagsvold 1988; Kokita and Nakazono 2001) and this reduction in care leads to decreased nesting success (Clutton-Brock 1991; Kokita and Nakazono 2001, but see Dunn and Hannon 1991), selection should act on females to repel rival females that may diminish the direct benefits received from males.

Several lines of evidence support the prediction that females compete over access to male parental care (i.e., female–female competition for one aspect of mate quality). Because females that are more aggressive are more likely to be monogamously mated (Sandell 1998) and primary females are often more aggressive than secondary females (Yasukawa and Searcy 1982; Hobson and Sealy 1989; Williams 2004, but see Breiehagen and Slagsvold 1988), chasing, fighting, and other forms of aggression may deter secondary females from settling (see also Ratti et al. 1994; Kilpimaa et al. 1995). Likewise, the experimental addition of a nearby nest-box for a secondary female increases the prevalence of female–female aggression in the facultatively polygynous starling (*Sturnus vulgaris*) (Sandell and Smith 1997). If females compete for high-quality males that provide parental care, female–female aggression should also be more intense when vying for a male whose phenotype suggests that he will be a high-quality male that will provide more care than other males. In the sharknose goby (*Elacatinus evelynae*), more aggressive females are more likely to mate with a larger male, and larger males typically provide more parental care (Whiteman and Cote 2003). Thus, females do appear to compete for exclusive access to a high-quality male that will provide direct benefits.

A natural continuation of this logic, of course, is that in the absence of paternal care, female competition should be rare or should occur for different reasons (e.g., food or indirect benefits). Indeed, temporal patterns of female aggression in birds and fish (i.e., species in which males often provide care) differ markedly from mammals (i.e., species with little to no male care). In nearly, all species of birds studied to date, female aggression peaks prior to egg laying but decreases during offspring rearing (Gowaty 1981; Breiehagen and Slagsvold 1988; Slagsvold 1993; Cristol and Johnsen 1994; Sandell and Smith 1997; Elekonich 2000; Garcia and Arroyo 2002; Gill et al. 2007, but see Brunton et al. 2008). In most mammal species, females are most aggressive during the offspring-rearing period (Boness et al. 1982; Derix et al. 1993; McDonough 1994; Kapusta and Marchlewska-Koj 1998; Wolff and Peterson 1998; Rodel et al. 2008, but see Derix et al. 1993). These interspecific temporal patterns of female competition suggest that sexual selection via female competition for mate quality may be more common in species with male direct benefits (i.e., in biparental birds and fish) than in species where males do not care for offspring. Determining the generality of this suggestion will

ultimately require phylogenetically controlled tests within taxa that vary in the extent of male care. In one such comparison of burying beetles, females of the biparental species *Nicrophorus quadripunctatus* frequently compete for access to carcasses on which they rear their young, whereas female–female competition is nearly nonexistent in *Ptomascopus morio*, a species without parental care (Suzuki et al. 2005).

Prediction 3: females should compete for males that will provide indirect (genetic) benefits. Independent of female–female competition for access to males or the direct benefits they provide, females may also compete over another aspect of mate quality: indirect (genetic) benefits, such as genes that confer a viability advantage to offspring ("good genes" or "compatible genes") or genes linked with female preferences ("sexy sons") (Fisher 1930; Weatherhead and Robertson 1979; Pomiankowski et al. 1991; Mays and Hill 2004). If sperm is limited (Dewsbury 1982; Wedell et al. 2002) and males attempt to conserve their sperm for new or preferred females (e.g., Pizzari et al. 2003) and if females receive some indirect genetic benefit from mating with the best male (Kirkpatrick and Ryan 1991), then females with a competitive edge could potentially benefit by acquiring more sperm from that male. Evidence suggests that preferred males are more likely to be sperm limited (Jones 2001), especially later in the mating season (Preston et al. 2001). Therefore, a female that is more adept at monopolizing preferred males may maximize the probability of fertilization by the best male if she can mate with him earlier than other females.

If females compete for genes from the best males, we should expect female–female competition on leks, where genes are essentially the only contribution from the male (e.g., Papadopoulos et al. 2009). In fact, several examples from lekking species indicate that female aggressive encounters are more intense or frequent when vying for the best male on the lek (Petrie et al. 1992; Karvonen et al. 2000; Saether et al. 2001; Bro-Jørgensen 2002). For example, female–female fights among topi antelope (*Damaliscus lunatus*) are more common at the center of the lek, where the most preferred male is located. These interactions may have very real consequences for mating success because females disrupt other females during copulation, with subordinates being disrupted more often than dominant females (Bro-Jørgensen 2002). Females in non-lekking species may also compete for access to good genes (e.g., Hasselquist et al. 1996), although it can be difficult to test this prediction empirically in systems where male direct benefits abound. A recent study on the White's skink (*Egernia whitii*) suggests one of the few examples of female–female competition for indirect benefits in a nonlekking system: More aggressive females have more extra-pair young in their litter (While et al. 2009). Although not yet tested directly, these results support the prediction that more aggressive females are better able to access the high-quality males that are most desirable for extrapair matings.

Competition over mating opportunities
Much as females may compete for access to mates themselves when mates are limited (Prediction 1), females may also compete for mating opportunities or mating resources (i.e., resources that qualify a female as a mate). As detailed above, these competitive interactions lie at the heart of one current debate regarding the scope of sexual selection in females. It is therefore especially important to identify the component of fitness affected by female–female competition for mating opportunities or mating resources. The fact that competition occurs between females in relation to reproduction is not sufficient to demonstrate competition for mates (i.e., sexual selection).

Prediction 4: female–female competition should increase when mating opportunities or resources are limited. Nesting sites can be a limiting resource for females of many species, independent

of the OSR. However, it can be difficult to determine whether females compete for access to a mate or to a critical mating resource (e.g., territory or nesting site), since the 2 often coincide temporally. In spite of this difficulty, several studies suggest that female aggression provides a competitive advantage when breeding or mating opportunities are rare. For example, in the common goby (*Po. microps*), female–female aggression was common only at sites with a shortage of nests (Borg et al. 2002), suggesting that intrasexual female competition may help secure access to a nest site and its associated male. Similarly, females are known compete with one another in close proximity to oviposition or nesting sites. In the parasitoid *Pachycrepoideus vindemmiae*, winners of aggressive interactions have at least temporarily exclusive access to an oviposition site, with losers being evicted (Goubault et al. 2007). If more aggressive females are more proficient at delaying or preventing superparasitism (i.e., multiple females ovipositing in the same host fruit), they may even improve larval growth or survival (Shelly 1999). Females burying beetles compete for access to a vertebrate carcass on which they rear their larvae. In *N. vespilloides*, when multiple females share a carcass, reproductive skew can be high: Dominant females maintain nearly exclusive access to the food supply, and they ultimately produce more eggs than the subordinate females (Eggert et al. 2008). Looking closer at the components of fitness in these last 2 examples, competitive interactions appear to directly influence food availability for offspring without affecting any component of competition for mates. Accordingly, some aspects of female–female competition for breeding resources do not fall within the purview of sexual selection via competition for mates.

If sexual selection is to shape female–female competition over mating opportunities, one key question is whether particular females are able to competitively exclude others from mating altogether, as is often the case in males (Brown 1969). Direct experimental support for this prediction comes from work on tree swallows (*Tachycineta bicolor*), a secondary cavity–nesting bird with limited nesting sites (Holroyd 1975). Female aggressiveness predicts the likelihood of obtaining a nesting cavity after an experimental reduction in cavity availability (Rosvall 2008). In this species, females that do not obtain a nesting cavity do not have alternative routes to mating or reproductive success because intraspecific brood parasitism is virtually nonexistent (Robertson et al. 1992; Whittingham and Dunn 2001). Thus, the outcome of female–female competition predicts mating success and significant reproductive skew among females (i.e., zero vs. some mates), much like sexual selection via male–male competition for territories allows certain males to be qualified as mates.

A more extreme version of competitive exclusion is the physiological or behavioral suppression of subordinate females in group living or communally breeding animals (Wasser and Barash 1983; Reeve and Sherman 1991; Solomon and French 1997; Clutton-Brock et al. 2006; Fitzpatrick et al. 2008; Saltzman et al. 2009). In communal breeders in particular, skew among females is typically higher than skew among males, with one dominant female breeding and several subordinates assisting in parental care. Overt aggression among females is thought to play a role in reproductive suppression by preventing ovulation or increasing stress in subordinates (McLeod et al. 1996; Saltzman et al. 1997; Young et al. 2006, but see Sapolsky 2005). Even without complete reproductive suppression, this active competition may successfully delay reproduction in rivals by interrupting mating, delaying ovulation, or increasing stress (Wasser and Starling 1988; Hohmann and Fruth 2003). While these examples of intense female–female competition clearly predict important reproductive variance, females do not apparently compete for mates in any direct way. Competitive interactions that establish dominance

(and thus, the likelihood of mating at all) may be a form of indirect mate competition, by which more aggressive females are allowed to mate. However, similar to female–female competition for territories, this example may be difficult to parse into natural and sexual selection, with 2 mechanisms targeting the same outcome.

CONCLUSION

Female–female competitive interactions lead to a number of possible fitness benefits for the winning female, suggesting that traits conferring a competitive edge among females are unlikely to exist merely as nonadaptive by-products of selection on males. Furthermore, patterns of overt aggression among females map onto the availability of resources and mates, and the direct or indirect benefits provided by those mates. These patterns reveal specific currencies of differential mating success and the evolutionary mechanisms shaping competitive interactions among females. At one end of the spectrum of relative parental investment, with extensive female-only care, sexual selection appears to play a lesser role, with fecundity and mortality selection shaping female competition to protect offspring or acquire the food necessary for prolonged maternal care. In the absence of male direct benefits, females appear to compete for access to genetic benefits from high-quality males. When males provide parental care, females also may compete for exclusive social access to those high-quality males. In either case, if all females cannot mate with the best male and if males vary in the direct or indirect benefits they provide, then sexual selection should favor females who are more adept at gaining access to these high-quality mates. In short, both natural and sexual selection favor female–female competition in a number of contexts. Whether the selective advantage of overt aggression outweighs potential costs is an empirical question for future research, one that is a key step in addressing whether the overall selection differential for female–female competition is positive.

Aspects of female–female competition appear very similar to their male counterparts, with some notable differences. The availability of mates influences female–female competitive interactions in species with standard and reversed sex roles (Darwin 1871; Trivers 1972; Eens and Pinxten 2000). When males are limited, the frequency and intensity of female–female competitive interactions increases (Prediction 1). In addition to this competition over access to mates, there are additional ways in which female competition affects mating success without influencing the number of mates, per se. Overt aggressive behaviors also increase when females compete for high-quality mates that provide either direct benefits (Prediction 2) or indirect benefits (Prediction 3). While the number of males may not be limiting to females outside of role-reversed species, the number of high-quality mates may be limiting (Petrie 1983; Altmann 1997), and competition for these males constitutes a form of mating competition. Accordingly, sexual selection may favor females that outcompete other females for male parental care, indirect genetic benefits, and nesting sites held by preferred males.

As a consequence, it is clear that if we restrict sexual selection to competition for the quantity of mates without including competition for high-quality mates, we ignore a potentially important component of mating success, particularly in females. If mating success is strictly limited to mate number, then 2 individuals with one mate each have equal mating success. If, however, one of these mates is high quality and the other low quality, should we not also consider the former individual to have higher mating success than the latter? And, if competitive interactions between these 2 individuals determined this outcome, should we not also consider this process part of sexual selection? The answer to these questions essentially boils down

to differences in the quality and quantity of mates. In light of empirical evidence that mate quality impacts fitness in many systems (Andersson 1994), it may be overly simplistic to ignore mate quality in measuring mating success and sexual selection.

The gray area of sexual selection centers around female–female competition for territories or other mating resources that qualify an individual as a mate (Prediction 4) because many of these examples affect female survival and fecundity as well as mating success. Competition among females for nesting sites required for both mating and reproduction, for example, provides a nearly identical parallel to sexual selection via male–male competition for females and territories, although some instead consider this process social selection in both sexes (West-Eberhard 1983). Females that are more aggressive may obtain access to resources that allow them to mate (or mate more, or mate with better mates), thus couching this process in the overarching theme of sexual selection (i.e., competition over mates). Females also may compete over resources that directly affect fertility, fecundity, or offspring survival without affecting competition for mate quantity or quality, and thus, this sort of intrasexual competition does not fit within sexual selection.

Selection should favor competition among females if variance in female competitive ability maps onto even slight variance in any component of fitness, whether sexually or naturally selected. For females, variance in mating success may be less dependent on mate number than on mate quality, which in turn may affect quality or even lifetime quantity of offspring. While quality is a more subtle measure of mating success than quantity, the critical condition for selection to favor female–female competition is a positive selection differential, even if the magnitude of the payoff in females is smaller than in males. It would be a mistake to confuse this potentially smaller fitness payoff of intrasexual competition in females with a lack of sexual selection in females.

PRIORITIES FOR FUTURE RESEARCH

Behavioral ecologists should continue to address the many questions about the nature of intrasexual competition in females and its role in the framework of sexual selection. Based on the above discussion, I suggest 4 specific avenues for research:

1. Do females compete for breeding resources and mate quality more so than males? A central tenet of mating systems and sexual selection theory is that the sexes differ fundamentally in their route to reproductive success, with male reproductive skew based on competition for mates, and female reproductive skew based on access to resources that affect fecundity (Bateman 1948; Trivers 1972; Wade and Shuster 2005). With growing interest in sexual selection in females and the entities over which females compete, and fewer biases against the study of sexual selection in females (Berglund et al. 1993; Gowaty 1997), we may finally be poised to rigorously test these sex differences. These tests must include large-scale empirical studies of whether females compete more for resources than do males (Clutton-Brock 2010; Roughgarden and Akçay 2010). They also must extend the predictions laid out here to include other ways in which both sexes might compete for high-quality mates or mating resources, looking at competitive interactions that are more subtle than overt aggression (e.g., rituals, signaling, etc.). As was common with the burst of research on sexual selection in males beginning about 30 years ago, comparative studies are needed to explore patterns of female–female competition while controlling for differences in mating system, parental investment, and phylogenetics.

2. How easily can both sexes compete? In the last decade or so, both theoretical and empirical works have explored conditions under which mutual mate choice is likely (Bergstrom and Real 2000; Kokko and Johnstone 2002; Kraaijeveld et al. 2007; Clutton-Brock 2009), with less focus on the conditions under which mutual mating competition occurs. In future work on sexual selection, it will be essential to identify the extent of simultaneous intrasexual competition in both sexes as well as the spatiotemporal dynamism of competition in one sex versus the other.

3. Do the same rules govern male and female contests? Because males and females may compete over different entities and receive different benefits from winning a competitive interaction, they may be expected to follow different rules of engagement as well. Consistent with this view, resource-holding power (e.g., age, size, or territory tenure) does not always predict the outcome of female–female interactions (Koivula et al. 1993; Dale and Slagsvold 1995; Draud et al. 2004; Stuart-Smith et al. 2007), as it often does in males (Parker 1974). Instead, resource value (e.g., territory quality) may be more important in predicting the victor (Shelly 1999; Kokita 2002; Draud et al. 2004). Along similar lines, the dear enemy hypothesis predicts a more aggressive response to strangers than neighbors and has been largely supported in males (Temeles 1994). In female New Zealand bellbirds (*Anthornis melanura*), however, the opposite appears to be true, perhaps because of sex differences in the relative threat posed by neighbors versus strangers (Brunton et al. 2008). In humans as well, there is some indication that male–male competition and female–female competition follow different rules, with the former being characterized by overt violence and aggression and the latter by more subtle expressions of aggression, such as gossiping and ostracizing (Campbell 1999; Geary 2002). Although it is premature to draw any definitive conclusions, these studies leave open the possibility that sex differences in intrasexual competition extend beyond the function of aggression and into the nature of contest rules.

4. How does mate quality affect theoretical models of sexual selection? With mating success typically focused on the number of mates, measures of mate quality are generally not incorporated into quantitative genetic models of sexual selection (Wade and Arnold 1980; Kokko et al. 2006; Klug et al. 2010, but see Johnstone et al. 1996; Jones and Ratterman 2009). Although there are difficulties with assigning quality to fitness measures (Moore et al. 1997; Wolf and Wade 2001), if female–female competition for mates targets quality more so than quantity, it will be important for future models to explore how this difference in the nature of intrasexual competition affects the strength of selection (Gowaty 1997).

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