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13

Mate Choice and Intrasexual Reproductive Competition: Contributions to Reproduction That Go Beyond Acquiring More Mates

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How do mate choice and reproductive competition contribute to the greater success of some individuals relative to others in producing surviving young or fertilized gametes? Within evolutionary biology, the answer to this question has traditionally been sought in the salutary effects of mate choice and reproductive competition on an individual's fecundity through its ability to obtain more mates. Consequently, these traits have been closely associated in evolutionary biology with the process that Darwin (1871) termed "sexual selection." As a corollary, they have received little evaluation with respect to other potential selective advantages, as through natural selection. But why consider only more mates? Why not better quality mates? And what aspects of quality differences might competition and choice be based on? Only quality with respect to fertility, or might quality with respect to promoting offspring survival also be a basis for mate choice? Questioning traditional closure as premature, this chapter first examines the origins of the narrowed focus and then presents bases for taking a more holistic approach to the evolutionary processes associated with mate choice and reproductive competition. I use the language appropriate to sexually reproducing animals, but many of the issues apply as well to plants (see e.g., Queller, 1994; Snow, 1994; Willson and Burley, 1983).

How Did a Narrow Focus on Acquisition of Many Mates Arise?

First consider three historical origins or obstacles to a full understanding of the evolution of intersexual choice and intrasexual reproductive competition. Some traits confer an advantage with respect to natural selection, specifically to viability selection; the bearers of these traits, the individuals of higher quality, are more successful because they live longer. The traits that confer higher viability

on their bearers are those that, in general, provide advantages in dealing with the external environment, such as locating and extracting food, avoiding predation and parasites, and surviving extremes of temperature or humidity. However, for an immature animal such as a fetus, infant, larva, or embryo, enhanced survivorship is often achieved not just by its own traits to which each parent made a genetic contribution. An embryo or infant may have high viability partially as a result of some trait of its parent(s), such as large body size or high-quality parental care, even if the offspring does not itself posses that trait. This path of natural selection, parental selection, has only recently received formal treatment in genetic models (Kirkpatrick and Lande, 1989, and sequelae). Thus, we can envision two paths of selection leading to longevity, one of viability selection and the other parental selection (unfortunately termed "maternal selection" by Kirkpatrick and Lande). Traits of a parent that affect its offspring's survival contribute simultaneously to the parent's number of *surviving* offspring and to the viability (longevity) component of the offspring's fitness, a considerable complication for genetically based evolutionary models. The problem has, as a consequence, been largely ignored in the evolutionary literature. Rather, it has usually been avoided by assuming no separate parental effects (see, e.g., discussion in Arnold, 1994a). Of course, if parental effects are assumed not to occur, these effects will not then appear as potential bases for mate choice or competition.

Differences among individuals may also arise as a result of differences in traits affecting fecundity, the number of fertilized gametes that are produced in any fixed time period. Such advantage might be achieved by simply producing more gametes. However, higher gamete production alone does not lead to greater zygote production if gametes of the other sex are in limited supply. In that case, one individual's ability to produce fertilized gametes may be limited less by its own gamete production than by another member of the same sex achieving fertilizations (i.e., if one individual fertilizes gametes from a member of the opposite sex, functionally fewer gametes are available for others to fertilize). The evolutionary path or selective process by which traits evolve that are advantageous in such mating competition, was termed by Darwin "sexual selection." Darwin envisioned that a trait might evolve by sexual selection through either or both of two mechanisms, one intersexual and the other intrasexual—mate choice (or, to generalize, gamete selection) in the first instance (e.g., Gowaty 1994, Eberhard and Cordero 1995) and competition for mates (or, to generalize again, gamete competition) between members of the same sex in the second (for a recent review see Andersson, 1994, Chap. 1).

Thus, from the beginning, sexual selection and the two mechanisms that would produce it (mate choice and competition for mates) became intimately associated, despite no necessary one-to-one relationship between selection and its mechanisms. In other words, the fact that sexual selection always entails either mate choice or intrasexual competition has often mistakenly led people to act as if the converse is true, that these mechanisms are of evolutionary importance

only to the extent that they are related to sexual selection. An unfortunate consequence of this false linkage is that evolutionary conclusions regarding sexual selection have been taken as applying of necessity to mate choice and intrasexual reproductive competition in general. Choice and competition focused on quantity not quality of mates. Mate quality, if considered, was assessed by number of gametes.

A second obstacle to a full understanding of the evolution of mate choice and intrasexual competition is also an outgrowth of the history of sexual selection—this is the diversity of uses of the term "sexual selection" by various authors or subdisciplines (e.g., evolutionary genetics vs. behavioral ecology). The narrowest definitions restrict use only to differences in number of mates (based surprisingly heavily on the limited data in Bateman, 1948; see, e.g., Hrdy, 1986), or to matings, or to mates that bear one's young (see Wade and Arnold, 1980 and sequelae). More broad definitions include differences in fecundity that arise both from number of mates and from the fecundity of those mates, or even differences that also include offspring survival (e.g., discussion in Bertin and Stephenson, 1983). However, the bulk of the literature, particularly that involving evolutionary, usually genetically based, mathematical models, adheres to one or another of the most narrow definitions (see discussion in Arnold, 1994b). As a result,not only have mate choice and intrasexual reproductive competition been too narrowly linked with sexual selection, but they also have been linked in the theoretical evolutionary literature with the most narrow of definitions of sexual selection, those pertaining only to acquisition of a large number of mates. The consequence of this pair of conceptual restrictions, first to sexual selection and then to sexual selection as only relating to number of mates, is that whole areas of investigation regarding reproductive competition and choice have been relatively ignored. Moreover, the narrowing of focus is not gender neutral—to the contrary, it is quite gender biased, particularly for species with extensive and unequal parental care.

Third, sexual selection was originally defined and has been studied primarily in situations in which it is seen to operate in opposition to other forms of selection; that is, focus has been on the traits that originally led Darwin to propose sexual selection, those traits such as a peacock's tail that provide advantage in gaining mates but that place a male at a disadvantage with respect to other fitness components of viability (Andersson, 1994). This mutually exclusive categorization excludes or devalues traits that confer advantage with respect to several forms of selection. Although the advantage of such traits may be small with respect to any single form of selection, the combined effects of the several forms of selection may be greater than is the case for a trait that confers advantage only, for example, to sexual selection.

For at least three major reasons, then, intrasexual reproductive competition and mate choice inappropriately became topics linked tightly to selection on traits that are advantageous only in obtaining more mates, or in obtaining more

mates that bear one's young. As a consequence, for example, female choice has been considered relatively unimportant from an evolutionary standpoint based on evaluations of its potential impact, *vis-à-vis* male–male competition, in sexual selection (e.g., Arnold and Duvall, 1994). For the same reason, male mate choice as well as female–female competition remain virtually unstudied except in "role-reversed" species. The relative importance in sexual selection of male–male competition, female–female competition, mate choice by males, and mate choice by females has no necessary relationship to the relative importance of each of these with respect to viability, fecundity, or parental selection and, therefore, to the relative importance of each with respect to all forms of selection in total. The tendency in evolutionary biology to evaluate the importance of choice and competition based solely on sexual selection narrowly defined results in exclusion of a rich potential field of inquiry and leads to biased, potentially erroneous conclusions about the relative importance of mate choice in different social systems or on the relative importance for the two sexes. The advantages of mate choice, for example, may often be in enabling an individual to have mates of higher fertility or mates whose young are more likely to survive, and as a result, traits such as good parental care may both increase the number of surviving offspring that the caring parent leaves and gain that parent more or better mates, because members of the other sex choose mates on the basis of parental care.

A reading of the literature reveals, nonetheless, that the field is somewhat schizophrenic on the topic of mate choice and reproductive competition, especially where theory and data meet, as can be seen in the literature brought together in major topical volumes such as Bateson's (1983) on mate choice and Andersson's (1994) on sexual selection. Thus, for example, even in major reviews of mate choice in which initial note is made that choice might be based on parental care or mate fecundity, focus quickly narrows, and both evolutionary models and inferences about the importance of mate choice or intrasexual competition for males versus females are subsequently based solely on sexual selection narrowly defined (see, e.g., Halliday, 1983). Although attention rapidly focuses within the traditionally defined limits, the initial note of choice based on parental care and mate fecundity hints at a logic and a potential empirical basis that calls into question validity of the historical narrow focus and warrants exploration.

Is a Narrow Focus Justified?

Although the theoretical literature remains focused narrowly, several threads demonstrate increasing diversity and breadth of explorations into intrasexual reproductive competition and intersexual choice outside narrowly defined sexual selection. The first is growing attention to postmating competition and choice, sperm competition (e.g., Birkhead & Møller 1992, Smith 1984) and cryptic fe-

male choice on seminal products (e.g., Eberhard and Cordero 1995). Moreover, the possibility that members of one sex compete among each other or choose mates based on mate fecundity is recognized in some models of selection, particularly for monogamous species, and the selective force in this case is termed "mate fecundity selection" (e.g., Arnold 1994b). Even these additions, however, still leave evolutionary models that consider reproductive competition only as it relates to forms of selection up to the point of conception, of zygote formation.

Might not choice and competition also arise over traits that are subject to parental selection (Kirkpatrick and Lande, 1989), those for which individual differences exist and affect not production of zygotes but survival of offspring (e.g., traits such as parental care, foraging ability, perhaps even intelligence)? No logical or biological reason has been advanced to suggest otherwise. Moreover, the limitation of restricting focus on reproductive competition to preconception events is increasingly apparent in the literature. For example, some plant population biologists have rejected sexual selection as a useful concept. The rejection is sometimes based on the difficulty of separating pre- and postzygotic selection, other times on the difficulty of distinguishing between intra- and intersexual mechanisms (e.g., Snow, 1994; Willson, 1994) Alternatively, in recognition of the importance of postzygotic activities, particularly parental care, some behavioral ecologists have argued for more inclusive definitions of sexual selection (Bertin and Stephenson, 1983). Although some authors just proceed empirically to include traits other than those relevant to number of mates, traits such as fecundity and parental care, this is done without consideration of the implications for relating their work to formal sexual selection theory (see discussion in Arnold, 1994b). Thus, some authors have rejected sexual selection for its narrowness, others have broadened the definition but thereby left it without an anchor in the formal evolutionary genetic models. Nonetheless, these efforts could each provide a beginning for some new directions if behavioral ecologists, plant population biologists, and theoretical evolutionary geneticists integrate their efforts rather than go separate ways.

Application to a Mammalian System

While studying vertebrates, particularly nonhuman primates, in which parental care is extensive and a broad range of reproductive competition seems potentially very important (Hrdy 1977, Smuts 1985, Wasser 1983), I was puzzled as to why so little of that competition was recognized or captured by evolutionary models of selection, and I alternately ignored sexual selection or tried to convince colleagues who model sexual selection to broaden their definitions of sexual selection. Neither proved to be a very satisfactory or productive approach. I therefore started trying to explore and locate primate reproductive competition more broadly within studies of selection and, as a corollary to that

effort, to respond to the challenge posed by colleague's surprise at the suggestion that primate males should choose their mates on the basis of certain traits—echoing a common view in evolutionary biology, my colleague asked why one could possibly think that males would have to choose mates; surely a male with priority of access can have all mates at little or no cost, unless the mating systems are monogamous or polyandrous, situations that are quite rare in mammals (but see, for example, Dewsbury [1982] for a review of sperm limitation in mammals).

When would mate choice be advantageous? To the extent that individuals of one sex, say females, differ in quality, those individuals of the other sex, males in this case, that exercised mate choice would be at an advantage unless those potential choosers could have all the mates at less cost than would be required for choosiness. Likewise, unless individuals of either sex have unlimited (uncostly) reproduction, intrasexual competition should be expected for mates of high quality, in addition to or instead of competition for a greater number of mates. Only if we demonstrate, in any particular system or in general, (1) that the requisite variability in mate quality is absent, (2) that reproduction is unlimited for the potential choosing sex, or (3) that the costs of choice are too great, is it reasonable to assume that choice is unlikely or can be ignored as a potential selective mechanism. In the analysis below, focus is on the presence of conditions that would lead to male mate choice, because this is one of the most ignored of the four "cells" of intrasexual competition and intersexual choice, and because it is the one that contrasts most with the approach that focuses on "male competition is all." Nonetheless, the evidence and conclusions point directly to the potential for female–female competition as well (e.g., Hrdy, 1977; Hrdy and Williams, 1983).

Like birds, mammals are vertebrates that are characterized by high levels of parental care. Unlike birds, however, mammals have intense amounts and extensive periods of postzygotic parental care that are tied particularly to physiological and morphological characteristics of females—gestation and lactation—and most mammals have female-biased adult sex ratios, polygynous social systems, relatively great body-size sexual dimorphism. These are all traits that evolutionary biologists, particularly students of sexual selection, associate with reproductive competition predominantly through male–male competition, perhaps complemented by female mate choice (usually assumed to be congruent in outcome with male–male competition). Males are assumed to have high variance in reproductive potential; females are assumed to have little or no variance (i.e., males but not females vary in quality, males but not females are considered to be mate-number-limited in reproductive success, and males are assumed to be effectively unlimited in the number of females by which they could produce young). Much of the evolution of mating systems and parental care, characterized by philandering, indiscriminant males and nurturing, sexually cautious females, is taken as a natural and inevitable part of this package, shaped particularly by sexual selection narrowly construed.

A very different picture emerges when, without restricting attention to the number of mates acquired, one takes a close look at actual male and female life histories. One can do so illustratively using baboons, a "type-specimen" of the classical evolutionary scenario, a highly dimorphic and polygamous species in an order, primates, that has some of the most extensive maternal care. We particularly focus on the questions "Can a male have it all?" and "Are all females the same quality?".

Most monkeys and apes are to varying degrees polygamous and sexually dimorphic in body size (e.g., Smuts, Cheney, Seyfarth, Wrangham, and Struhsaker, 1987). The females of most species produce only a single young at a time and do so at infrequent intervals. Baboons are among the largest of the monkeys, adult males are approximately double the body mass of females, and adult females outnumber adult males. The savannah species that are widespread throughout Africa live in multimale, multifemale groups, as do most cercopithecine primates. As with other mammals, gestation and lactation bias care to the female parent. Monkeys and apes have very dilute milk, which leads to a need for frequent suckling throughout the day, and, in most cases, mothers also provide transport for the young, which develop very slowly by mammalian standards (see, e.g., discussion in Altmann and Alberts, 1987 and references therein). These patterns of life-history and parental care provide a classical sexual selection scenario in which males are thought only to fight among themselves for reproductive priority of access.

Is this the whole story? Can males have it all? Do females vary in quality? Data for over two decades of longitudinal studies on the population of baboons in Amboseli, Kenya, suggest otherwise for this system.

Most primates are highly seasonal in reproduction like the vast majority of mammals. A result of this seasonality is that, with rare exceptions (e.g., Pereira, 1991), if any females are in estrus and fertile, multiple females will be, even in relatively small groups of females. Primate groups that contain more than five females often contain more than one adult male, and those that contain at least ten females almost always have several adult males. Even a male with priority of access to estrous females can maintain exclusive access only by mate guarding, and he can guard only a single female at a time.

A few primate species, including gorillas, chimpanzees, humans, and baboons, are relatively aseasonal and breed throughout the year, a situation that will reduce the incidence of overlapping fertile periods in females that cycle at random with each other and might, thereby, increase the need for mate-guarding.

The relatively aseasonal species should fit classical sexual selection models even better than other primates. Nonetheless, even for these species, a simple binomial model of independent cycles, applied to a group of only a dozen females, yields the finding that about 40% of the time that any female is within the five most fertile days of her cycle, at least one other female will be as well (i.e., estrus periods often overlap even in the absence of synchrony). If the group is larger, or

if the females exhibit any degree of cycle synchrony, this frequency of overlapping cycles will be even greater. Examination of our data for three groups of baboons ranging in total size from 25 to 75 and including 10 to 20 females over a ten-year period, revealed that the proportion of overlapping fertile periods ranged from 40–80% (unpublished). In summary, then, we can answer the question of whether primate males in multimale groups can "have it all" or whether they might have to choose among females that are simultaneously in estrus—males often will be faced with more than one female in estrus, and, because other males will, in general, go to a female who is not being monopolized in a consortship, even males, say, of high dominance status will be faced with a choice, a choice that means compromising complete paternity assurance with one female in order to have some access to another.

We note at this point, but will not explore in detail herein, that if two females are simultaneously in estrus, they will not, in general, both be able to have complete paternity assurance with the same male in a multimale group, and if males base subsequent care of offspring on their degree of paternity assurance, a female's access to only a single male during her time of conception might affect her ability to garner paternal care from him later (but see alternatives motivated primarily by considerations of female tactics against the threat of infanticide by nonfathers; e.g., Hrdy, 1979). Therefore, the same scenario that sets the stage for male choice might also lead to female–female competition if males vary in quality and the females favor the same male. Alternatively, this scenario might lead to behavior by females, such as staying close together, that would more readily permit a single male to monopolize two females.

Do females vary in quality? Even if males are faced with a choice among females, partner selectivity would not be expected if females did not vary, or, to paraphrase a former U.S. president's evaluation of redwood trees, "If you've seen one female, you've seen them all." Only to the extent that females of larger body size or better condition have different conception probabilities or more ova are females considered variable from the perspective of sexual or fecundity selection, and from that perspective, the amount of variability among females is usually assumed to be much smaller than the potential cost of male mate choice, including any reduction in mate numbers that might be entailed by male mate choice. So one can ask, are primate females all the same, or do they vary in fertility, and do they vary in other ways that might provide an advantage to a choosy male?

At least within natural social groups, primate females do vary in fertility, not usually in potential litter size but in probability of conception, often as a function of age, dominance status, or nutritional condition (e.g., see Harcourt, 1987; Lee, 1987; Silk, 1987; also Packer, Collins, Sindimwo, and Goodall, 1995). For example, adolescent and sometimes primiparous females are less fertile than are older females in baboons, and high-ranking primate females have often been found to have higher probabilities of conception than females lower in the female dominance hierarchy. In addition, females in very good nutritional condi-

tion are more fertile than those in poorer nutritional condition when comparisons are made across groups or populations that differ in nutritional condition, and such nutritionally based fertility differences might also be important within groups as well. For wild baboons in Amboseli, for example, adolescent females take more than twice as many cycles to become pregnant as do more mature females (an average of ten cycles versus three or four). Furthermore, among mature females, those in good nutritional condition take only one or two cycles versus the three or four cycles of those under more stringent, completely wild-foraging regimens. Because females vary in conception probabilities, a male that chose at random between two females that differed in conception probabilities would, on average, have fewer mates that bore his young (the narrow definition of sexual selection) than a male that favored more fertile females. Mate choice, therefore, would, under this scenario, probably be favored by sexual selection, even in the narrow definition of sexual selection if we are considering only relatively short time frames. Considered across the full reproductive span, during which some of the same mates are encountered repeatedly, mate choice of individuals who are consistently of higher fertility would be favored by mate fecundity selection (Arnold, 1994b; attribution to one or the other classes of selection may depend on the time scale of analysis (see also Arnold & Duvall 1994).

Even if one would want to restrict explorations of potential bases for mate choice to a discussion of conception probabilities, a discussion of "mates that bear ones young" should not be based solely on female fertility. In particular, if a female does mate with more than one male (i.e., if complete mate monopolization does not occur) the question arises as to which sperm fertilize an egg. So-called "sperm competition" has become an area of increasing interest *within studies of sexual selection,* but the very name and the history of this topic itself provides an interesting example of an unbalanced, gender-biased approach. Particularly when considering species that have internal fertilization, why would one *a priori* characterize the differential fertilization success of sperm from different males as a matter of male–male competition and not one of female choice (see e.g., Eberhard and Cordero 1995, Gowaty, 1992)? Consider a fully intact, mature female with sperm within her body from a variety of donors; is it more likely that she would have mechanisms for (as well as "interest" in) choosing those sperm most advantageous to her or that the sperm and their associated products would have the field to themselves to determine the outcome? Developments on this topic during the past decade demonstrate how much richer the science when balance or biological plausibility rather than implicit human biases structure the conceptual framing as well as the empirical investigations (see Andersson, 1994; Gowaty, 1994). Moreover whether the mechanism is choice or competition, a problem arises in deciding whether differential fertilization falls under sexual selection or mate-fecundity selection in Arnold's (1994) nomenclature. The assignment depends on whether the selection results in all offspring being fathered by one male (sexual selection)

or whether the selection results in different nonzero proportions of offspring being obtained by more than one male (fecundity selection). [If litter size is one (the case for most primates and some other mammals, such as most ungulates, cetaceans, and kangaroos), then this would fall under sexual selection when only single pregnancies are concerned, perhaps fecundity selection if we considered an individual's full reproductive span.]

What are the potential evolutionary implications for mate choice of postzygotic events? Do differences among females affect the probability that the offspring a male conceives will survive—to birth, through infancy, to maturity? The answer is a clear "yes." First pregnancies are less likely to lead to surviving offspring in many vertebrates, including primates. Among the Amboseli baboons, for example, first conceptions have half the chance of survival through infancy as do those of higher parity (Altmann, Hausfater, and Altmann, 1988). Maternal nutritional status, dominance status, or quality of maternal care often predict offspring survival and age of offspring reproductive maturity (e.g., Altmann et al., 1988; Bulger and Hamilton 1987; Lee, 1987; Packer et al., 1995; Silk 1987; Rhine, Wasser, and Norton, 1988; Smuts and Nicolson, 1989). In their significant modeling departure, Kirkpatrick and Lande (1989) have begun an exploration of these factors in models of parental selection and parental effects.

Clearly male mate choice based on female parity, parental ability, and perhaps on female dominance status or nutritional condition very well might have arisen and be maintained through sexual and other forms of selection. Likewise, one might reasonably expect that some female traits, particularly female competitiveness and female parental care, perhaps female foraging ability and ability to respond advantageously to changing environments, have been selected, not just through forms of natural selection because of advantages in survival and in the survival and quality of offspring, but also through selection *on females* as a result of male mate choice. It does not seem far-fetched to propose that the evolution of extremely high degrees of parental care of foraging skill, for example, may owe much to intrasexual competition and intersexual mate choice.

Mate choice by males on the basis of female fertility (e.g., maturity/age) and on the basis of female traits that lead to offspring survival and fertility (e.g., dominance rank, maturity, family size, parental care) will lead in primates to a male having more zygotes per unit time and more surviving young per unit time (choice of time units important in many species). Mate choice by males may have the same consequences for the chosen females if males vary in quality and those that are able to choose are the same ones that are otherwise of higher quality. Traits that affect viability and fecundity may, therefore, also be subject to sexual selection through mate choice by affecting the probability of obtaining a mating that leads to conception, and these traits may evolve more rapidly than they would in the absence of mate choice.

When mate choice by males is considered, however the potential restriction that makes the system more like temporary monogamy is often remembered; the

first chooser just gets first choice of a mate, the next gets choice of remaining members of the opposite sex, and so on (i.e., the "sampling" may be without replacement, not with replacement). When mate choice by females is considered, however it is usually assumed (except in monogamous situations) that all females would choose the "best" male, the one that would win in intrasexual competition. Nonetheless, to the extent that several males may choose/compete for the same female, that female may have more ability to choose sperm or have higher conception probability just from the fact of multiple mates.

Finally, it is important to remember that mating is intrinsically a dyadic behavior; not only are the choices potentially contingent on prior choices in a small-sample, nonreplacement situation, but also both partners in the mating are potentially choosing simultaneously, unless one is prevented from doing so (in which case we would expect that partner to evolve choice mechanisms at a later reproductive stage if she/he can). With internal fertilization, females will in general have the potential for more control at later reproductive stages than do males.

In conclusion, the selective setting for the evolution of male mate choice is multifaceted. The selective advantages of such choice will fall within several types of selection, the relative apportioning depending both on how various evolutionary biologists label types of selection (see diverse approaches in AmNat supp, 1994; Andersson, 1994) and empirically on the species and perhaps even the population under consideration. Some investigators may consider the distinction between sexual selection, fecundity selection, viability selection, and parental selection to be artificial or too problematic (see AmNat supp 1994), and for some purposes one might not need to focus on those differences in selective forces in any case. Nonetheless, the type of selection is in some instances important for the evolutionary implications (e.g., see Kirkpatrick and Lande, 1989, regarding the time lag in response to parental selection). Focus on any one type of selection, however, will not give a full appreciation of mate choice, competition for mates, or the traits that may be the subject of mate choice. Moreover, in contrast to tradition, the parallel action of several types of selection acting in the same direction may need to be modeled and evaluated as is done when investigating selection at different levels of demographic action (individual, deme, etc.). Both theoretical and empirical studies are needed, ones that are not reductionist or prejudgmental, but rather that include all forms of selection on traits that may be subject to several forms of selection that may often act in the same direction. A richer rapprochement between behavioral ecology and more theoretical and genetic evolutionary studies will surely emerge, as well as an evolutionary biology that is truer to the complexity of the reproductive biology of the lives under study. The biases and omissions that have occurred in the study of reproductive competition are in many ways male biased. Their redress, however, will lead to a more full understanding of the evolution of both male and female behavior.

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