

PERSPECTIVE:

INDIRECT MATE CHOICE, COMPETITION FOR MATES, AND COEVOLUTION OF THE SEXES

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Abstract.—When Darwin first proposed the possibility of sexual selection, he identified two mechanisms, male competition for mates and female choice of mates. Extending this classification, we distinguish two forms of mate choice, direct and indirect. This distinction clarifies the relationship between Darwin's two mechanisms and, furthermore, indicates that the potential scope for sexual selection is much wider than thus far realized. Direct mate choice, the focus of most research on sexual selection in recent decades, requires discrimination between attributes of individuals of the opposite sex. Indirect mate choice includes all other behavior or morphology that restricts an individual's set of potential mates. Possibilities for indirect mate choice include advertisement of fertility or copulation, evasive behavior, aggregation or synchronization with other individuals of the same sex, and preferences for mating in particular locations. In each of these cases, indirect mate choice sets the conditions for competition among individuals of the opposite sex and increases the chances of mating with a successful competitor. Like direct mate choice, indirect mate choice produces assortative mating. As a consequence, the genetic correlation between alleles affecting indirect choice and those affecting success in competition for mates can produce self-accelerating evolution of these complementary features of the sexes. The broad possibilities for indirect mate choice indicate that sexual selection has more pervasive influences on the coevolution of male and female characteristics than previously realized.

Key words.—Darwin, male-male competition, mate choice, mating systems, sexual selection.

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Research has largely confirmed Darwin's (1859, 1871) speculations about the influence of sexual selection on evolution. Although it required more than a century to settle many of the theoretical and empirical issues, most of the scope for sexual selection as described by Darwin is now widely accepted. Here we take the argument a step farther. By using recent clarifications of sexual selection and by introducing a new distinction, we show that sexual selection has ramifications for the evolution of sexual organisms that extend considerably beyond those originally imagined by Darwin and currently recognized.

When introducing his theory of sexual selection, Darwin (1859) envisaged two distinct mechanisms. Sexual selection, he wrote, "depends . . . on a struggle between the males for the possession of the females." As an alternative mechanism of sexual selection, he suggested that "female birds, by se-

lecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect" on male features (Darwin 1859, p. 88).

The proposal that two distinct mechanisms can produce sexual selection pervaded the extended presentation in Darwin (1871). Nevertheless, perhaps the only passage in which he clearly distinguished these mechanisms was in his summary: "The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive, whereas in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners" (Darwin 1871, p. 916). For Darwin, the two mechanisms of sexual selection were associated with passive and selective females, respectively.

These two mechanisms by which individuals differ in their access to mates have become standard components of dis-

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cussions of sexual selection under the terms male-male competition and female choice, or intrasexual and intersexual selection. Nevertheless, the relationships of these two mechanisms have remained an open question (Bradbury and Davies 1987; Harvey and Bradbury 1991; Kirkpatrick and Ryan 1991; Andersson 1994; Møller 1994).

The revival of interest in sexual selection in recent decades followed two theoretical advances. First, mathematical analysis confirmed Fisher's (1930) intuitive argument that disadvantageous male traits can evolve, provided the disadvantages for survival are balanced by advantages in mating as a result of female preferences. Second, these analyses identified a less intuitive but more fundamental property of sexual selection, one that sets it apart from other examples of evolutionary trade-offs: a genetic correlation between traits of the two sexes (Lande 1981; Kirkpatrick 1982; Pomiankowski 1988). If heritable traits of one sex, often called preferences, result in proportionately greater chances of mating with those individuals of the other sex that possess complementary heritable traits, often called ornaments, then the progeny of these matings tend to inherit genes for both traits. The genetic correlation that results from this form of assortative mating can produce self-accelerating (runaway) evolution of the traits expressed in each sex, both preferences and ornaments.

Recognition of this characteristic feature has led to an operational definition of sexual selection, something that Darwin never attempted. Sexual selection is best defined as a difference in fecundity as a result of heritable differences in access to mates (Arnold and Wade 1984; Arnold 1994). Male traits and female preferences subject to sexual selection are often simultaneously subject to other forms of selection. For instance, differences in survival of males with and without ornaments (male costs), differences in survival or reproduction of females with and without preferences (female costs or benefits), or differences in survival or reproduction of offspring as a result of the genetic quality of females' mates (good genes), all can influence the spread of male ornaments and female preferences (reviewed by Pomiankowski 1988; Andersson 1994). Furthermore, female preferences might result from sensory adaptations in contexts other than mate choice (Ryan 1990, 1993). Yet in all cases, a genetic correlation between male traits and female preferences results inevitably from assortative mating. The genetic correlation provides a necessary (although insufficient) condition for self-accelerating evolution of male traits and female preferences (Lande 1981; Kirkpatrick 1982; Pomiankowski 1988).

Our first objective here is to show that a distinction between two forms of mate choice, direct and indirect, clarifies the relationship between Darwin's two mechanisms of sexual selection. A review shows that male competition for mates inevitably depends on conditions set by females and, consequently, that male competition for mates is inseparable from what we shall call indirect female choice. Like direct mate choice, this indirect mate choice produces assortative mating and consequently the genetic correlation that characterizes all sexual selection. Our second objective is to indicate the expanded scope for sexual selection suggested by this perspective. The possibilities for indirect mate choice reveal that the evolution of male and female characteristics in sexual organisms is much more extensively intertwined

than currently recognized. To establish these points, we begin with some basic features of the mechanisms of sexual selection.

MECHANISMS OF SEXUAL SELECTION

A principle we shall follow in our terminology is a distinction between proximate (behavioral or physiological) and ultimate (evolutionary) mechanisms. To mark this distinction, we shall use the term "selection" only for evolutionary mechanisms. The common term "intrasexual selection" confuses these mechanisms and has had various meanings in the past. Huxley (1938a, p. 431) suggested this term for any "competition between individuals of one sex in the struggle for reproduction," a usage even broader than the current definition of sexual selection in general. Current discussion of intersexual and intrasexual selection tends to focus on proximate mechanisms that can produce sexual selection.

Instead of intersexual selection, a more accurate term is competition for mates. An analogy with ecological competition (Park 1962; Andersson 1994) suggests two forms of competition for mates. On the one hand, interference competition for mates includes all behavioral interactions between individuals of one sex, including assessment, threat, fighting, and deception, that affect their access to mates. Like its ecological analog, it requires direct behavioral interaction between individuals. On the other hand, exploitation competition for mates includes any behavior that increases access to mates, except direct interactions with other individuals of the same sex. Examples include sequestering of mates, persistence in advertising for mates, or efficiency in locating mates (Ghiselin 1974; Wells 1977; Alcock 1980). For instance, in a study of thirteen-lined ground squirrels *Spermophilus tridecemlineatus*, mating success of males correlated primarily with efficiency in locating estrus females and not with the outcomes of interactions between males (Schwagmeyer and Wootner 1986).

The analogy with the forms of ecological competition clarifies the importance of limitations on reproductive success. Only when the availability of mates limits reproduction can competition for mates occur. This limitation, which often applies to males, requires that any male mating with a female reduces the expected reproduction of all other males. When some other factor limits reproduction, such as the availability of nutrients or sites for eggs, situations that often apply to females, then careful choice of mates evolves rather than competition. This sexual difference in limiting factors for reproduction leads to the evolution of competitive males and choosy females and, by extension, to complex sexual differences in mating behavior and parental care. Many authors have framed this conclusion in somewhat different terms (Trivers 1972; Emlen and Oring 1977; Trivers 1985; Clutton-Brock and Parker 1992). Exceptions to the pattern of male competition and female choice, among both vertebrates and invertebrates, tend to prove the rule that factors limiting reproduction determine the evolution of choice or competition for mates (Gwynne and Simmons 1990; Gwynne 1991; Vincent et al. 1994).

Instead of intersexual selection, a more accurate term is mate choice. Mate choice includes all behavior by an indi-

vidual that restricts membership in its set of potential mates (those individuals of the opposite sex likely to mate with it). "Restrict" is the key term in defining mate choice, although it is not emphasized in previous definitions (Halliday 1983). In contrast, competition for mates consists of behavior, sometimes even coercion, that tends to expand an individual's set of potential mates. Mate choice is distinguished by a decrease, rather than an increase, in the set of potential mates.

In ordinary language, "choice" has broad connotations of consciousness and deliberation. Darwin (1871, pp. 467–468) explicitly encouraged thinking in these terms. He repeatedly referred to females' "taste" and "sense of beauty." He attributed some of this taste to universal preferences for regularity and symmetry but recognized that the sense of beauty might also be "capricious," an idea akin to our current concept of arbitrary preferences. Female taste suggested too much complex cognition by nonhuman animals for some of Darwin's contemporaries and followers (Wallace 1889). Debate about mate choice continued until Fisher (1930) and Huxley (1938a,b) argued persuasively that mate choice only requires some neural mechanism, peripheral or central, that allows individuals to discriminate between features of potential mates. This capability has received extensive experimental investigation (reviewed by Kirkpatrick and Ryan 1991; Andersson 1994; Møller 1994), and heritable preferences are components of all current mathematical models of sexual selection (reviewed by Pomiankowski 1988). This focus on preferences, however, has obscured the full range of proximate mechanisms that influence mate choice.

Preferences represent what we propose to call direct mate choice, in which differences in responses to possible mates affect an individual's chances of mating with them. Thus, direct mate choice requires discrimination, as the term is commonly used in behavioral studies, among the features of possible mates. Any behavioral or morphological features could serve for such a discrimination, for example the lengths of tails, the concentrations of pheromones, the fundamental frequencies of calls, or the rates of display.

Discrimination among possible mates is, however, not necessary for mate choice. Any other behavior that restricts the chances of mating with particular individuals we propose to call indirect mate choice. This form of mate choice is indirect because individuals never respond differently to the behavioral or morphological features of possible mates. In some cases, they might not even perceive them. Nevertheless, their behavior makes it less likely that they will mate with certain individuals of the opposite sex than with others. Their set of potential mates has decreased.

VARIETIES OF INDIRECT MATE CHOICE

Prominent possibilities for indirect mate choice include (1) advertisement of copulation or fertility, (2) evasive behavior when approached by the opposite sex, (3) aggregation with other individuals prepared to mate, (4) synchronization with other individuals prepared to mate, and (5) mating at predetermined locations. Copying of other individuals could augment the effects of any of these forms of indirect mate choice. In each case, the behavior (or morphology) of one sex establishes conditions under which individuals of the

opposite sex compete for access to mates. By setting the conditions for competition, an individual indirectly chooses a mating partner.

Advertisement of Copulation or Fertility.—As an example of indirect mate choice, consider the loud calls of female elephant seals *Mirounga angustirostris* during copulation (Cox and LeBoeuf 1977). When a subordinate male attempts copulation, these calls alert any nearby dominant male, who often supplants the subordinate. Note that females need not discriminate subordinate and dominant males. Instead, by calling whenever any male attempts copulation, they initiate a chain of events that increases their chances of successful copulation with dominants. Their choice of mates is thus an indirect consequence of their behavior.

This example, one of the first detailed reports of female behavior that incites competition between males, serves to illustrate an important point about direct and indirect mate choice. A correlation between mating success and features of individual males, such as size, dominance, or display, is not sufficient evidence for direct choice of these features by females. Instead, experiments or controlled observations must demonstrate that females in fact respond differently to males differing in these features. Indirect choice can produce the same correlation of mating success with male traits without any discriminating responsiveness by females.

The behavior of female elephant seals also includes an element of direct choice, as they are more likely to call in response to advances of subordinate males than to those of dominant males (Cox and LeBoeuf 1977). Nevertheless, it is clear that loud calls announcing attempted copulations serve to provoke interference competition between nearby males and thus produce indirect consequences for mating. Conspicuous vocalizations by females occur during copulation in a variety of birds (Montgomerie and Thornhill 1989) and mammals, including primates (Hamilton and Arrowood 1978; Hauser 1990; O'Connell and Cowlshaw 1994), and often seem to incite competition between males.

Advertising copulation is a special case of advertising fertility. Females of many species produce signals alerting males that they are now or will soon be fertile. Distinctive signals by fertile females, including visual (sexual swellings of some primates, swollen bellies of gravid fish), acoustic (infrasonic calls of elephants, calls of some birds), and olfactory (pheromones of moths and mammals), attract and thus stimulate interference competition among males (Clutton-Brock and Harvey 1976; Hrdy and Whitten 1986; Payne et al. 1986; Montgomerie and Thornhill 1989; Poole 1989; Pagel 1994). In some frogs, simple splashing by gravid females might suffice to incite competition between nearby males (Kluge 1981).

Particularly striking are insects in which females mate immediately after or just before eclosion from pupae (Crankshaw and Matthews 1981; Schöne and Tengö 1981; Thornhill and Alcock 1983, table 7.5). These females often have no direct contact with males before copulation. It is difficult to imagine how they could exercise direct mate choice. Yet signals indicating their imminent fertility can provoke interference competition between males and create selection for exaggerated traits. For instance, heliconine butterflies have evolved characteristically long wings. A male's long wings

serve to prevent other males from landing on an occupied female pupa (Deinert et al. 1994).

Advertising fertility often takes the form of signals that attract potential mates. Such attractants, like the sex pheromones of female moths, can evolve in conjunction with almost incredibly sensitive (but possibly otherwise disadvantageous) receptors in the opposite sex. Although such signals serve to attract mates, they can also serve to restrict the signaler's set of potential mates in two ways. First, by provoking exploitation competition among males, an attractant restricts a female's mates to those able to detect and locate the source quickly. In addition, by inciting interference competition among the males attracted, a female increases her chances of mating with those successful in dominating rivals. If she produced no attractant, or one not as detectable, she would mate more nearly at random. As a consequence, like other forms of advertising fertility, attractants can result in indirect mate choice.

Evasion.—Evasive behavior by receptive females can also serve as indirect mate choice. Prolonged chases are a feature of courtship in a number of birds and mammals. Barn swallows *Hirundo rustica* are a clear example (Møller 1994). These chases have at least two possible indirect influences of mate choice. First, only males in sufficiently good condition can catch evasive females; second, such chases tend to attract other males and thus stimulate competition between males, either interference or exploitation, depending on whether males fight or simply race to reach the female first.

Forced copulations in ducks often include chases (McKinney et al. 1983). Despite the clear risks for females in some species, such chases might nevertheless stimulate both interference and exploitation competition by males for access to these females. Chases, in conjunction with long-range advertisement of estrus, are also prominent features of courtship in some tree squirrels (Koprowski 1993). In eastern gray squirrels *Sciurus carolinensis*, males attracted to a female on her single day of estrus pursue her persistently. A female always mates with the first male to relocate her after she has temporarily evaded a group of suitors.

Evasive behavior can represent a form of direct choice as well. If a female flees from any approaching male but then decides whether to accept the male based on how fast or persistently he pursues, she has exercised direct mate choice. If, as apparently in the case of the squirrels, she flees from any male and then mates with any who catch her, she has practiced indirect mate choice.

Aggregation.—Aggregation of receptive females can promote competition among males for access to mates. For example, female red deer *Cervus elaphus* aggregate during the rut more than at other times of the year (Clutton-Brock et al. 1982), and female seals and sea lions aggregate even within the restricted areas available on shore, despite risks of increased pup mortality (Bartholomew 1970; Stirling 1983). Males of these species herd females and compete among themselves for control of the resulting harems. Aggregation by females might have consequences unrelated to mating. Female red deer, for instance, appear to take advantage of optimal grazing in autumn. Nevertheless, behavior by a female that facilitates herding by males also has indirect consequences for mate choice.

Female red deer can avoid herding, and indeed they frequently change harems during the rut (Clutton-Brock et al. 1982). Individual females might differ in their level of "herdability," specified by a rate of leaving aggregations and a probability of returning when herded by a male. The herdability of females in relation to the rates of herding by individual males would determine the sizes of female aggregations, and females would tend to accumulate in aggregations with more actively herding males by a sort of kinesis. The herdability of a female would thus indirectly influence her probability of mating with males active in herding, a capability often associated with superior physical condition and success in excluding nearby competitors. This mechanism for aggregation resembles the proposal that females in lekking deer accumulate in those males' territories where they are least often chased by intruding males (Stillman et al. 1993).

Herding by males can differ markedly between closely related species. A dominant male hamadryas baboon *Papio hamadryas* accumulates a small group of females that never stray far from him without promptly eliciting threat or attack. In contrast, olive baboons *P. anubis* live in groups of mixed sex without such exclusive associations of females with particular males. A female olive baboon translocated from her own group to a group of hamadryas can learn within 1 hr, as a result of repeated attacks by a male, to stay in that male's harem (Kummer et al. 1970). This study, however, included only eight such tests, and an unspecified number resulted in escape by the female olive baboon. We also do not know whether a male hamadryas can successfully herd several female olives at once. Further experimentation in the field could clarify the behavioral mechanisms that result in aggregation of females by herding males.

Synchronization.—Competition between males for access to females depends on an interaction between the spacing and timing of females' receptivity. Synchronization of receptivity can reduce competition between males for access to mates (Emlen and Oring 1977; Knowlton 1979). This consequence of synchronization requires that access to one fertile female precludes access to another. For example, in the colonially nesting Brewer's blackbird *Euphagus cyanocephalus*, females respond contagiously to each others' precopulatory displays, behavior that could enforce monogamy on their mates (Horn 1970). In other circumstances, near synchronization in combination with aggregation of females can increase competition for mates. In sage grouse *Centrocercus urophasianus*, over 30 females can mate with a single male within 3 h in one morning (Wiley 1973). Other males are prevented from mating because the females aggregate mostly within one male's territory.

Even when females aggregate for advantages of avoiding predators or finding food, they can independently influence male competition by the location and timing of copulations. Colonial blackbirds and their relatives illustrate a diversity of male competition in species with similar nesting aggregation. Female Montezuma oropendolas *Psarocolius montezuma* and boat-tailed grackles *Quiscalus major* often copulate on or adjacent to their nests in dense colonies. As a consequence, a dominant male can effectively exclude others from copulating with the 10–30 females, at least while they are in

the colony (Post 1992; Webster 1994a; Poston 1995). Female common grackles *Q. quiscula* and Brewer's blackbirds also nest relatively synchronously in colonies of 10–30. They usually copulate only with a male that has closely accompanied them for days previously (Horn 1970; Wiley 1976). Female yellow-rumped caciques *Cacicus cela*, related tropical icterids nesting in colonies of 10–50, always copulate away from the colony (Robinson 1985, 1986a,b). Although a male can only accompany one receptive female at a time, females' fertile periods are staggered throughout a long nesting season. Consequently, a few males can monopolize most of the matings.

Despite overall similarities in the spatiotemporal dispersion of nesting females, males of these five colonial icterids have remarkably different forms of interference competition for mates. The differences in male competition result from differences in the conditions for copulation set by females. In this way, females indirectly restrict their sets of potential mates.

Mating at Predetermined Locations.—Mating at locations known in advance to members of the opposite sex can also stimulate interference competition for mates. In some cases, such locations are learned at least in part from other individuals and thus are traditional. On coral reefs in the Caribbean, female bluehead wrasse *Thalassoma bifasciatum* tend to spawn at specific locations at the down-current end of a reef. Large bright males defend these sites from other males, at least on small reefs, and spawn with visiting females. The general location of these sites has advantages, as the fertilized eggs drift away from predators on the reef. Yet the exact locations are an arbitrary result of tradition among females. Following experimental replacement of all fish on a reef, the new fish select slightly different sites for spawning (Warner 1988, 1990). When only males are removed and replaced or when a male moves his territory, females remain faithful to their preferred sites (Warner 1987). Evidently females choose sites and not individual males. The tendency of females to return to the same site and to copy the choices of other females sets the conditions for male interference competition. Some lekking birds and mammals also show evidence of traditional locations for mating (reviewed by Wiley 1991).

Mating at a predetermined location is a particularly clear example of mate choice that requires no discrimination between features of potential partners. Females do not have to respond to differences in size, brightness, or behavior of males. If any of these attributes influences the outcome of competition among males for access to preferred sites, then females that choose these sites mate with partners that tend to have these attributes. Competition between males for opportunities to mate can result in correlations between mating success and features of males, such that females tend to mate with males that have these features (Arak 1983, Andersson 1994), but it is not so well appreciated that the behavior of females determines the opportunities for males. Choice of a predetermined site by females often results indirectly in mating with males that have particular features, even when females do not or can not make discriminations among these features.

Use of predetermined mating sites need not involve previous experience. In many insects receptive females approach

prominent landmarks, with the consequence that male interference competition for mates focuses on these sites (Thornhill and Alcock 1983, table 7.4; Wickman et al. 1995). "Hill-topping" behavior by many butterflies and other insects is a prime example. Males compete for perches with advantages in intercepting females arriving to copulate (Shields 1967). Mating in sunspots has the same effect for woodland butterflies. In these cases, choice of mating sites by females evidently does not require previous experience or copying of other females (Davies 1978).

Mating locations that males can identify in advance also include habitats optimal for nesting, oviposition, or foraging. If females mate in these habitats, then they also determine the conditions for which males compete for territories. This sort of indirect mate choice might often occur in species with resource-defense polygyny. The red-winged blackbird *Agelaius phoeniceus* is perhaps the best studied case (Searcy and Yasukawa 1983, 1995). Females choose safe nesting sites, rather than individual males. Nevertheless, male red-wings whose territories contain more nesting females are often (although not always) significantly larger than those with fewer females (Searcy 1979, Yasukawa 1981). This association of males' features with mating success is an indirect consequence of female behavior. Females usually copulate near their nests. Males apparently identify the same habitats favored by females and compete to defend territories as large as possible there. During absences of a territorial male to feed, a female sometimes mates with an intruding male (Westneat 1993). Consequently, by mating near locations chosen for nesting, females indirectly choose males successful in competition for territories and able to spend as much time as possible there (for a similar situation, see Frederick 1987).

Although this form of indirect mate choice could apply to many species with resource-defense polygyny, few experiments have definitely established that females choose features of microhabitat. None excludes the possibility that females might also exercise some direct mate choice (Howard 1978; Pleszczyńska 1978; Alatalo et al. 1986).

Copying.—Copying other females could enhance the effect of any form of mate choice, including each of the forms of indirect choice. In some cases, females copy others' direct mate choices (Dugatkin 1992; Kirkpatrick and Dugatkin 1994), but in other cases females might copy others' indirect mate choices (Wiley 1991; Gibson and Höglund 1992; Pruett-Jones 1992). Aggregation, synchronization, and use of particular sites can all involve responses of females to each other. Receptive female sage grouse and fallow deer *Dama dama*, for instance, are attracted to other females (Wiley 1973; Clutton-Brock and McComb 1993). Copying might occur mostly among inexperienced females. Older females could switch to repeating their previous behavior, as demonstrated in guppies *Poecilia reticulata* (Dugatkin and Godin 1993). Studies of mating systems have in general tended to focus on male-male interactions and to ignore the possibility of female-female interactions (Ahnesjö et al. 1993), although these latter often set the conditions for male competition.

VARIETIES OF DIRECT MATE CHOICE

The distinction between indirect and direct mate choice should not be confused with other recent classifications of

mate choice. In particular, we wish to avoid confusion with active choice and passive attraction (Parker 1982, 1983; Searcy and Andersson 1986). Passive attraction, it is proposed, occurs when females mate with particular sorts of males yet appear not to reject some males in favor of others. A proposed example is choice of the first mate encountered and consequently often the loudest or most conspicuous.

The distinction between active choice and passive attraction recalls Darwin's contrast between females that remain passive and those that select. The distinction is perhaps again motivated by a sense that choice requires some minimal level of cognition. However, a distinction between active and passive females remains as problematic now as it was then. Response to the first stimulus encountered involves discrimination of signals above and below a threshold. This filtering might occur in the peripheral nervous system, in which case a stimulus evoking a response would generate some minimal excitation of particular sensory cells. The filtering might instead occur in the central nervous system, in which case a stimulus would achieve some minimal match with a cognitive criterion. In either case, a stimulus that fails to meet a criterion for response is rejected (Sullivan 1989; Wiley 1991, 1994; Forrest and Raspet 1994). Both are forms of direct mate choice based on discrimination of the attributes of males.

A clearer classification of forms of direct mate choice might distinguish three levels of match between a female's criterion for a response and the attributes of individual males. A cognitive match would involve central neural filtering, such as, presumably, a preference for a visual or acoustic pattern. A sensory match would involve peripheral neural filtering, such as responses to particular colors or frequencies of sound. A morphological match between the female and a potential mate would require no neural processing at all. Morphology of females that allows only males with matching morphology to mate represents structural, rather than behavioral, discrimination among males (Eberhard 1985, 1990).

All three forms of criteria for direct mate choice can result in sexual selection for exaggerated traits in the opposite sex. A sensory threshold for females' responses creates selection for more intense or conspicuous signals by males, just as an appropriate cognitive criterion in females would favor more exaggerated ornaments in males. Furthermore, the evolution of all three forms of criteria for direct mate choice face the same trade-off between benefits and costs. A stricter criterion (higher threshold) entails both any increased benefits of a more narrowly specified choice and also any increased costs of a longer search. As a result, there is an optimal threshold (or strictness of criterion) for any response (Wiley 1994).

Another frequent distinction in discussions of mate choice contrasts absolute and relative choice, often called sequential and best-of-N choice (Janetos 1980; Real 1990). The latter requires either simultaneous or repeated exposure to different potential mates and a choice based on comparison among them. The criterion for response is thus relative rather than absolute. The important point in the present context is that all of these forms of mate choice require discrimination of males' attributes and thus represent forms of direct mate choice.

COMPLEXITIES IN MATE CHOICE

Patterns of mating success among males probably often result from combined influences of direct and indirect mate choice by females. The natterjack toad *Bufo calamita* provides a case in point (Arak 1983, 1988). A proposed example of passive attraction, this species actually illustrates a combination of simple forms of direct and indirect mate choice. In the field, mated males average significantly larger than unmated. As in other toads, the dominant frequency of males' calls correlates strongly with body size. Yet, in experiments with tape-recorded calls in the field, females do not discriminate between males' calls differing in dominant frequency, not even between calls at the high and low extremes of the population. These results rule out cognitive forms of direct mate choice.

Nearly half of all females enter the breeding pond near the densest aggregation of calling males and then mate with the first male they encounter. Larger males call more frequently and produce more intense calls. Thus, even if females approach the first male with a call exceeding some threshold of intensity, this behavior represents simple direct choice of louder and thus larger males. This direct choice is reinforced by indirect choice. Larger males displace nearby smaller males. Thus, by entering the pond near an aggregation of calling males and then choosing the first male encountered, females indirectly choose those males most successful in defending large areas in aggregations of males and thus most successful in competition with other males.

Notice that relatively nonspecific forms of direct mate choice, such as a preference for loud males, can lead indirectly to much more specific mating. In boat-tailed grackles, males as well as females produce loud, distinctive vocalizations preceding and during copulation (Poston 1995). By copulating only with a loud male, a female assures that her mate can compete successfully with other males. In this case, a relatively nonspecific preference for males that make themselves conspicuous preceding copulation can lead to mating with the most dominant male in the area. This case of simple direct mate choice resembles many cases of indirect mate choice in that relatively nonspecific responses by females can lead to highly specific mating associations.

EVOLUTION OF INDIRECT MATE CHOICE

Our review of possibilities for indirect mate choice reveals that much female behavior not normally considered a part of mate choice nevertheless restricts a female's set of potential mates. In all cases, these indirect forms of mate choice by one sex serve to set conditions for competition for mates by the other sex. Conversely, competition for mates inevitably depends on conditions set by some form of indirect mate choice.

These possibilities take on additional significance when we consider that indirect mate choice evolves in the same way as direct mate choice. The mathematical models of sexual selection developed in the last two decades specify the mechanisms of choice only in general terms. They assume a function that determines the mating association between females with a preference and males with a trait or ornament (Lande 1981; Kirkpatrick 1982). Polygenic models can ac-

commodate any of several psychological functions that specify the expression of the preference. Allelic models assume that females with an allele for preference mate only or disproportionately with males with an allele for the trait.

In all cases, the proximate mechanisms that result in these mating associations between females with heritable preferences and males with heritable ornaments are not specified. Instead of preferences and ornaments, we can substitute, respectively, any of the mechanisms of indirect mate choice and the corresponding traits contributing to success in competition for mates. In either case, male success in mating could conceivably increase as a linear or a nonlinear function of a male trait (relative preferences) or could vary around optimal values for a trait (absolute preferences).

Direct mate choice produces assortative mating between females with preferences and males with corresponding ornaments. In an analogous way, indirect mate choice, in which female behavior or morphology sets conditions for interference competition between males, produces assortative mating between females with one set of traits and males with a complementary set of traits. As a consequence of assortative mating, progeny carry alleles for both sets of traits. This genetic correlation, whether produced by direct or by indirect mate choice, can generate self-accelerating (runaway) evolution of these traits. All conclusions about the coevolution of males and females in models of sexual selection apply to indirect as well as to direct mate choice.

The evolution of preferences also depends on their consequences for fecundity and survival of females and their offspring (Heisler 1984, 1985; Kirkpatrick 1985; Andersson 1986; Pomiankowski 1987; reviewed by Pomiankowski 1988). When a preference has direct costs for females and no influence on heritable viability of offspring, the only evolutionary equilibrium under most conditions is extinction of the preference. In this case, self-accelerating evolution of male and female traits does not occur. However, if direct costs for females are offset by sufficiently increased viability of offspring, then preferences can evolve to fixation in a self-accelerating process (Pomiankowski 1988). In addition, these mathematical analyses of sexual selection leave open the possibility that costly preferences might evolve when direct costs are frequency dependent (such as search costs) or when the genetic correlation of preferences and traits is sufficiently strong. The important point here is that all of these conclusions apply equally to direct and to indirect mate choice.

INDIRECT MATE CHOICE AND EXAGGERATED MORPHOLOGY OF FEMALES

Following Darwin and Fisher, we expect sexual selection to produce exaggerated traits in males, at least in the usual case of competitive males and choosy females. The mathematical models of sexual selection make it clear, however, that exaggeration should occur both in male traits and female preferences. In the case of direct mate choice, the obvious consequence is exaggerated, even bizarre, male morphology. In this case, the exaggeration of female preferences has no obvious structural manifestation and requires an experiment to appreciate. In the case of indirect mate choice, in contrast,

an exaggeration of the mechanisms of female choice by sexual selection might produce bizarre morphology in females.

Consider, for example, the elaborate perineal swellings (called sexual swellings) that advertise fertility in some primates. Pagel (1994) recently emphasized that these swellings seem to exceed the minimum necessary for communication of a female's imminent fertility. He suggested that sexual selection could produce these exaggerated signals as a result of competition, not between males, but between females for access to males. Sexual swellings would thus represent a female equivalent of the plumes of male birds. Competition between females should occur, however, only when access to males limits reproduction. This situation seems unlikely for females in multimale primate troops, the social structure associated with exaggerated sexual swellings (Clutton-Brock and Harvey 1976).

An alternative suggestion is that sexual swellings incite competition between males (Clutton-Brock and Harvey 1976). They would thus be a form of indirect mate choice. If attraction of competitive mates or promotion of promiscuous matings resulted in higher viability of offspring, sexual swellings could have net benefits, despite some direct costs for females. Runaway evolution might then lead to exaggerated morphology for advertising fertility as an extreme mechanism of indirect mate choice.

This example makes it clear that explanations for the evolution of sex-specific female morphology depend critically on the nature of limitations on female reproductive success. Only when access to mates limits reproductive success of females should females evolve mechanisms of intrasexual competition for mates. Otherwise, sex-specific female structures might instead evolve as exaggerated mechanisms of indirect mate choice.

INDIRECT MATE CHOICE AND ASSESSMENT OF MATES

Indirect mate choice also fits models of assessment of mates (Andersson 1986; Grafen 1990a,b; Iwasa et al. 1991; Price et al. 1993). These models assume that females benefit by mating with males in better physiological condition. Females, however, cannot directly judge a male's condition but only the level at which he expresses some signal. Expression of the signal affects both a male's mating success and, in conjunction with his physiological condition, his survival. There is a unique equilibrium for these conditions: females prefer the highest level of a costly signal (one for which the level of expression is inversely related to a male's survival) and males express the signal as an increasing function of condition. In other words, females prefer honest, costly signals, and males produce such signals.

Although the terminology of these models suggests direct female choice, indirect choice serves just as well. The conclusions only require that female behavior results in a tendency to mate with males producing costly signals. If a form of indirect female choice sets conditions such that male competition depends on costly traits, then this indirect choice would evolve.

In some situations, indirect mate choice might permit more reliable assessment of mates than would direct mate choice. Errors by females in discriminating signals do not change

the equilibrium in the preceding models of mate choice, but they do reduce the expected advantage to females because they less often choose optimal mates. As a consequence, if there is any advantage to choosing a mate in the best condition, females should favor the most reliable indicators of male condition (Andersson 1982, 1986; Grafen 1990b). By an extension of this argument, females might evolve mechanisms of indirect mate choice, instead of direct preferences for signals, whenever indirect mate choice can identify males in peak condition more reliably than can direct mate choice.

Indirect choice could have advantages over direct choice when it sets conditions for prolonged interference competition by the other sex. For instance, mating at particular sites or in aggregations of receptive females often favors males that have established dominance over many rivals for prolonged periods. Boat-tailed grackles demonstrate this possibility clearly, as successful dominant males have survived in competition with rivals for years (Post 1992; Poston 1995). In lekking species, males interact with each other for weeks before females arrive for mating (Wiley 1991), and males' relationships can develop over years (McDonald 1989a,b). In many species in which males defend groups of females from rivals, males' relationships are determined over years. In many territorial species as well, males' interactions establish territorial locations and boundaries over weeks or years.

Indirect mate choice could have further advantages when females have limited time to compare potential mates (Wiley 1991, 1994). When the sexes associate only for mating, as in many lekking species, or choose mates and territories quickly after arrival on breeding grounds or after maturity, as in territorial birds and many insects, females have little opportunity for direct comparison of potential mates. With such constraints on the time available for choice, indirect mate choice could often provide a more reliable behavioral mechanism for choosing a mate than would direct choice.

The term "indirect" mate choice should not suggest less specificity than direct mate choice. As noted above, relatively nonspecific behavior in indirect mate choice can result in much more specific mating associations. On the other hand, direct mate choice can involve considerable uncertainty. The specificity of females' direct choice for morphological or behavioral features of males is in fact often low. An objective for the future is a comparison of errors in different forms of mate choice.

Indirect mate choice might also incur fewer costs. Costs of searching are the principal constraint on the evolution of direct choice of mates (Pomiankowski 1988; Real 1990). These costs include an array of possibilities, such as lost time and energy, exposure to predators, possibility of forced copulation with undesired males, and lost opportunities as a result of not finding a mate as good as a prospect already passed by. Many of these costs of mate choice might be less for indirect rather than direct choice. Investigations of the possible advantages and disadvantages of mate choice have thus far not considered indirect mate choice.

ADAPTATIONS FOR MATE CHOICE IN RELATION TO ECOLOGICAL ADAPTATIONS

For two decades, explanations for the evolution of mating systems have operated on two premises: the spatiotemporal

distribution of females is determined by ecological considerations (trophic relationships of feeding and avoiding predation); the distribution of males is then determined by the distribution of females (Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Bradbury et al. 1986). Recognition that female aggregation and synchronization can result in indirect mate choice broadens the perspective on the evolution of female distribution.

In particular, the evolution of female spatiotemporal distribution depends both on ecological consequences and on consequences of indirect mate choice. Indirect mate choice raises the possibility of self-accelerating sexual selection of arbitrary female aggregation or synchronization. It also might affect a female's immediate reproductive success or the genetic quality of her progeny. These advantages of indirect mate choice could balance ecological disadvantages.

It is conceivable, for instance, that aggregation of nesting female birds could evolve because of its advantages in indirect mate choice, despite some disadvantage (or no advantage) from exposure to predators or distance to food. There seems to be no ecological advantage of aggregation for nesting female boat-tailed grackles (Post 1994) and some disadvantages for female oropendolas (Webster 1994b). Instead, as described above, copulation within colonies is the females' principal mechanism of indirect mate choice.

Female behavior presumably evolves to minimize any conflicts between ecological advantages and advantages of indirect mate choice. The exact expression of indirect choice could minimize these conflicts. Further understanding of these possibilities, however, will require more attention to the possibility that the spatiotemporal distribution of females is influenced by adaptations for indirect mate choice as well as by ecological adaptations.

Because indirect mate choice includes any behavior that restricts membership in an individual's set of potential mates, other than direct discrimination of their attributes, it could include many kinds of behavior with no immediately apparent connection with mating. Our listing of possibilities is not likely to be exhaustive. In particular, additional possibilities might well occur in the complex social systems of primates, including humans. An individual's set of potential mates is surely influenced by subtle alterations in behavior or morphology. The multiplicity of behavioral mechanisms that might result in indirect mate choice suggests a sweeping recommendation: no study of mate choice should exclude, without explicit investigation, any behavior preceding mating, even long before mating. Sexual selection no doubt has more pervasive influences on the evolution of both sexes than currently realized.

CONCLUSION

This expanded perspective on sexual selection developed from a classification of behavioral mechanisms of mate choice. By emphasizing a distinction between direct and indirect mate choice, we reached two conclusions. First, Darwin's two mechanisms of sexual selection, mate choice and competition for mates, are inseparable. It seems likely that competition for mates by one sex always depends on conditions set by indirect mate choice by the other sex. Even

when male-male competition takes exaggerated forms, females are not "passive," as Darwin originally suggested. Instead, indirect mate choice by females sets conditions for male competition. Studies of sexual selection and mating systems thus far have largely overlooked this aspect of mate choice.

Second, indirect mate choice evolves in the same way as direct choice. In special cases, indirect mate choice might lead to runaway evolution of both male and female traits, just as direct mate choice might. Furthermore, in situations in which females have limited opportunities to interact with males before mating, indirect mate choice might allow more reliable and less costly identification of competitive mates than would direct choice. Future research on sexual selection and mating systems should strive to redress the imbalance in our attention to direct and indirect forms of mate choice.

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