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Female mate choice based upon male motor performance

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Abstract

Our goal in this essay is to review the hypothesis that females choose mates by the evaluation of male motor performance. We define motor performance as vigor, the ability to perform energetically expensive acts repeatedly, or as skill, the ability to perform difficult motor tasks well. Motor performance reflects most aspects of whole-organism performance that relate to survival, and thus should indicate, more reliably than ornaments do, individual male genetic quality and/or developmental history. Male sexual displays in many animal taxa contain elements of vigor and/or skill, and accumulating evidence suggests that females choose mates in nature based upon their evaluations of male motor performance. We note that male ornaments in many species are accompanied by conspicuous motor display, and we propose that ornaments often arise secondarily as a way to enhance the apparent skill or vigor of male motor performance. More and better methods to measure male vigor and skill are needed, as well as additional studies on the abilities of females to make discriminations of this type.

Keywords: female mate choice, male display, motor performance, skill, vigor

Charles Darwin (1859) proposed that many male sexual traits (ornaments and displays) evolve due to sexual selection by female mate choice. In spite of initial resistance to Darwin's proposal, and a subsequent century of limited attention on the topic (reviewed by Cronin 1991), the study of sexual selection currently stands front and centre within the field of animal behavior. Empirical and theoretical work on sexual selection has traditionally focused on male ornaments, most famously the peacock's (*Pavo cristatus*) tail. Sir Ronald Fisher (1930) developed a verbal model of an evolutionary process by which ornaments could evolve to become exaggerated, in spite of the expectation that such traits reduce the bearer's survival ability. Subsequently, Lande (1981) and Kirkpatrick (1982) developed mathematical models of the Fisher idea, and a vigorous debate in the literature followed on the question of whether ornaments evolve via the Fisher runaway mechanism, which requires a genetic correlation between the magnitude of the male ornament and the magnitude of the female preference, or alternatively whether ornaments evolve as indicators of male breeding value for offspring quality. Critics of the indicator hypothesis noted that the association between male ornament size and male breeding value would tend to decay, but supporters replied that the decay could be avoided if male ornaments were condition dependent (Borgia, 1979; Taylor and Williams, 1981; Pomiankowski and Møller, 1995; Rowe and Houle, 1996; Houle and Kondrashov, 2002). Kotiaho &

Puurtinen (2007) provide a more complete review of the history of these ideas.

Nevertheless, there now seems to be widespread acceptance that male ornaments are reliable indicators of male breeding value for offspring quality, and that the primary question about female mate choice concerns the origins and maintenance of preferences that result in the evolution of exaggerated male ornaments. For example, in a terms-definition box in a recent issue of *Trends in Ecology and Evolution*, Tomkins et al. (2004, page 323) defined good genes as "models of sexual selection that assume that extreme ornaments indicate the genetic quality of the bearer, defined as breeding value for fitness." Or, consider Kirkpatrick's (1987, page 45) widely cited formulation: "Sexual selection by female choice involves two characters, a male secondary sexual *trait* and a female mating *preference*." Data supporting this model, however, are incomplete. Many researchers have indeed shown that females often prefer males with exaggerated ornaments (Andersson, 1989; Hill, 1990; Møller, 1991), and some studies have reported data on sire effects (i.e. showing that males with more elaborate ornaments sire offspring with superior health, survival or developmental profiles; Petrie 1994). But, despite keen interest on the topic for more than a quarter century, no published study has put these two lines of evidence together for a single species, to show that the free choices of females in nature create stabilizing or directional selection for high values of male ornament expression, and to show simultaneously that offspring quality is associated with

the selected values of sire ornament expression.

Stepping back, the foundation for a broader view of sexual selection by female choice was put forward 9 years before the Lande paper, by Robert Trivers, who wrote: "As in other aspects of sexual selection, the degree of male investment in the offspring is important and should affect the criteria of female choice. Where the male invests little or nothing beyond his sex cells, the female has only to decide which male offers the ideal genetic material for her offspring..." (Trivers 1972, page 167). This view looks beyond ornaments per se; it predicts that sexual selection by female choice should occur wherever there is asymmetry in parental investment, and that females should evolve the ability to discriminate among potential mates, using whatever information is available. Consider the situation in mammals, where asymmetry in parental investment is extreme. With few exceptions (e.g. Bradbury 1977), male mammals do not possess sexual ornaments analogous to the elongated tail feathers or brightly colored plumage of birds. In the few mammalian species in which males have some conspicuous coloration (Fernandez & Morris 2007), it is doubtful that the coloration constitutes a character that is opposed by natural selection. Many male mammals do possess characters that are associated with intrasexual selection, such as weapons (Emlen 2008), large body sizes and pugnacious dispositions, but they do not possess nonutilitarian ornaments that serve female choice.

The virtual absence of male ornaments in mammals forces one of two conclusions: either sexual selection by female choice does not occur in mammals, or alternatively, it does occur, but the criteria by which females evaluate males involve something other than ornaments. In this article, we review the evidence that, across a wide range of taxa, females evaluate males largely based on male motor performance, especially within mating displays. This hypothesis has numerous precedents (e.g. Ryan and Keddy-Hector, 1992; Rowe and Houle, 1996; Irschick et al., 2007) but remains largely unappreciated in the broader literature on sexual selection. We also examine the idea that motor performance provides particularly reliable information about male genetic quality, condition and developmental history, superior to information that could be derived from ornaments alone.

Motor Performance as Vigor

Motor performance as we define it includes two somewhat overlapping aspects of behavior. The first is vigor, a term used by Darwin (1859, 1871). Vigor is an individual's ability to perform energetically expensive motor acts repeatedly. Consider the pronghorn, *Antilocapra americana*. Within this species, the mate-sampling strategy of females forces males into many energetically demanding acts of harem defense (Byers et al. 1994), and the males that sire the greatest number of offspring are typically those that are able to defend a harem for many successive days during rut (Byers 1997). Moreover, this female mate sampling is costly to females (Byers et al., 2005, 2006), and nearly all females each year converge in their choices, without copying, on a small subset of males in the population. The males in this subset, all having demonstrated vigor by their ability to defend a harem over many days, provide superior breeding value for offspring survival (Byers & Waits 2006). Other examples of traits indicative of vigor that females might use to evaluate males include the leaping and the climbing and diving displays of snipe, genus *Capella* (Sutton 1981), the diving and shuttle displays of several species of hummingbirds (Stiles 1982), the leaping displays of blue-black grassquits, *Volatinia jacarina* (Costa and Macedo, 2005; Aguilar et al., 2008), wing-clapping displays of flappet larks, *Mirafra rufocinnamomea* (Norberg 1991), the chasing behavior of house flies

Fannia canicularis (Land & Collett 1974), the leg-waving displays of many wolf spiders (Hebets & Uetz 1999) and the energetically expensive waving of the enlarged cheliped in fiddler crabs, genus *Uca* (Salmon et al., 1978; Matsumasa and Murai, 2005). Additional examples include the lengthy bouts of flying in some male bird displays (Mather & Robertson 1992), the sustained, energetically expensive vocalizations of many anuran amphibians (Prestwich, 1994; Welch et al., 1998) and of some ungulates (Wyman et al. 2008), sustained stridulation in some orthoptera (Hedrick, 1986; Prestwich, 1994; Prestwich and O'Sullivan, 2005), sustained flashing displays of fireflies (Lewis & Cratsley 2008) and persistence on leks by displaying males (Leuthold, 1966; Vehrencamp et al., 1989; Deutsch, 1994; Isvaran and Jhala, 2000). Indeed, one of the most striking aspects of many male mating displays is their repetitive nature. Certainly, the vigorous repetition of a display can serve other functions, such as repelling rivals, or simply increasing the likelihood of attracting a female, but to the extent that repetition is energetically costly, or to the extent that repetition exposes the signaler to danger or risk of retaliation, it becomes a way in which the quality of males can be compared. In addition, females may be able to assess vigor by observing male fighting and similar forms of competition, by indirectly detecting the outcome of male-male competition, or by inciting male competition and selecting the winner (Cox and LeBoeuf, 1977; Byers et al., 1994; Bro-Jorgensen, 2002). In many lek-breeding species, females prefer to mate with males that occupy territories at the spatial centre of the lek (Hoglund and Lundberg, 1987; Apollonio et al., 1992; Kokko et al., 1999; Isvaran and Jhala, 2000; Bro-Jorgensen and Durant, 2003). Here, to the extent that males compete for central locations, the female preference is for vigor.

Studies on wolf spiders provide multiple lines of support for the hypothesis that display vigor is used in mate choice. Mature male *Hygrolycosa rubrofasciata* court females by striking their abdomens against the substrate (typically dry leaves) in an action termed "drumming." Drumming increases an individual's metabolic rate 22-fold over resting metabolic rate (Kotiaho et al. 1998b), and is condition dependent (Mappes et al. 1996). Males with high drumming rates survive better in both laboratory and field conditions (Mappes et al., 1996; Kotiaho et al., 1999), and have superior mobility and the ability to evade predators (Lindström et al. 2006). Female *H. rubrofasciata* prefer the sound of drums of longer duration and males that drum more actively (Kotiaho et al., 1998a; Parri et al., 2002).

Recently, courtship intensity or vigor was shown to influence female mate choice in other wolf spider species. Nutritional enrichment enhanced courtship intensity in *Pardosa prativaga*, and nutrient-enriched males experienced higher mating success (Lomborg & Toft 2009). Similarly, *P. milvina* males in better condition court at higher rates and survive predation better than do males in poor condition (Hoeffler et al. 2008), and females prefer to mate with males performing more body shakes and leg raises (Rypstra et al. 2003). Male courtship rate in *P. milvina* is repeatable for most male-female pairings, and females that mate with males with high courtship rates tend to produce more offspring, which in turn emerge sooner and show greater probabilities of survival (Hoeffler et al. 2009). *Schizocosa* wolf spiders are well known for their elaborate courtship dances and associated ornaments (Hebets and Uetz, 2000; Stratton, 2005; Framenau and Hebets, 2007). In *S. ocreata*, multiple aspects of courtship signaling rate and duration are important in female mate choice (Delaney et al., 2007; Gibson and Uetz, 2008). In *S. uetzi*, the rate of male leg raises influences female mate choice (Shamble et al. 2009). Although *S. uetzi* males possess foreleg ornamentation that is condition dependent, female choice appears to be based on courtship rate, irrespective of foreleg ornamentation (Shamble et al. 2009).

Results from studies on *Photinus* beetles parallel those from studies of wolf spiders. In both field observations and photic play-back experiments, female *Photinus* choose males that display higher flash pulse rates and durations, which in turn might be limited by male vigor (Demary et al., 2006; Lewis and Cratsley, 2008).

Vigor should provide a highly reliable indicator of male quality, for at least two reasons. First, vigor cannot be faked, as may be possible for an ornament; vigor cannot be decoupled from overall organism performance. Second, vigor is a summed expression of a male's near-complete if not entire functional genome, and thus captures myriad aspects of organism performance, such as immune function, parasitism profile, limb proportions, locomotor efficiency, gut anatomy and digestive efficiency, motivational system and behavioral efficiency, and growth and developmental history. All of these factors listed above shape display vigor in a manner that is independent of the receiver. Display vigor may also be affected by receiver-dependent costs, such as increased probability of retribution from other males, or increased exposure to predators (Searcy & Nowicki 2005).

Motor Performance as Skill

The second aspect of male motor performance that females might use when comparing prospective mates is the skill with which an individual performs a challenging action, which could be a single motor pattern or a linked series of motor patterns. A challenging action is one that requires a degree of precision in the activation and coordination of motor units that is greater than that needed for everyday activities or that is close to the limit of production possibilities imposed by an animal's anatomy and physiology. Motor skill and performance abilities are regularly considered in the study of behaviors that are linked to survival, such as feeding or locomotion. In contrast, their impact is considered only rarely in the study of sexual selection and animal signals.

We suggest that skill in the performance of challenging actions is probably equivalent or perhaps better than vigor as an indicator of overall organism performance. In addition to general health, skill necessarily reflects musculoskeletal, nervous and sensory system construction and function, and may thus be a particularly reliable indicator of developmental stability. Nowicki et al. (1998) hypothesized that one kind of behavioral display, birdsong, should provide a particularly reliable indicator of male quality, because the development of brain nuclei that constitutes song learning occurs when young birds are energetically and nutritionally challenged. Support for this "developmental stress" hypothesis appeared in a number of studies (reviewed by Podos et al. 2009). For example, Nowicki et al. (2002) showed that swamp sparrows, *Melospiza georgiana*, partially deprived of food during early life developed smaller brains, smaller song control brain areas and reduced song learning, as compared to control birds. In a parallel example, it is now established that human children born prematurely tend to exhibit lasting deficits in sensory-motor performance (Foreman et al. 1997).

Is it reasonable to assume that animals can perceive differences between conspecifics in the skill of their motor performances? We suggest that it is, and that animals probably have underappreciated perceptual sensitivities in this arena. Consider an example from our own experiences: almost every adult human can run a short distance, leap in a forward arc, land on one foot, and continue running. However, only a few adults, who we call dancers, can execute this motion in a way that we perceive as beautiful. Additionally, humans easily perceive performance differences between professional dancers, the actions of which must be nearly identical yet still readily distinguishable. Humans also routinely make what must be very

fine discriminations among the motor performances of musicians and athletes. Humans can even detect differences in dance quality that are correlated with the degree of fluctuating asymmetry of the dancer (Brown et al. 2005). It is improbable that humans are the only animal species with this kind of perceptual sensitivity.

Sexual selection theory predicts that females choosing mates should evolve strong discrimination abilities that allow them to discern males with the most elaborate or intricate sexual traits (Trivers 1972) and to resist the courtship efforts of males that do not quite make the grade (Holland & Rice 1998). Many studies on sexual selection have shown that females can indeed discern slight differences between exaggerated male ornamental variations. Yet we have few data that speak to this possibility for motor performance, undoubtedly because of the difficulty in quantifying both the variation in male motor displays and the variation in female responses. With regard to visual discrimination, our understanding of perceptual abilities might be guided by analogous data on predatory behavior in mammals. Numerous accounts of predators that hunt mobile prey describe a two-stage process in which the predator first rushes a group of prey and then selects a single individual to pursue (Schaller, 1972; Holekamp et al., 1997; Peterson and Cicucci, 2003). Holekamp et al. (1997, page 4) described this hunting method in spotted hyenas, *Crocuta crocuta*, as follows: "The hunting methods utilized by our study animals matched those described previously by Kruuk (1972), Mills (1990) and Cooper (1990). That is, our study animals typically first rushed a group of prey animals, stood briefly to observe the prey animals' locomotor behavior, selected one target individual, then chased that individual down over distances ranging from 75 m to 4 km." Usually, human observers are unable to detect the subtle deficit that the predators identify, and the human observers tend to describe the perceptual ability of the predators as "uncanny" (Holekamp et al. 1997). The elaborate stotting that prey such as Thomson's gazelles, *Gazella thomsoni*, perform at the beginning of a predator attack suggests that the predators are capable of detecting slight differences in the motor performance of prey (FitzGibbon & Fanshawe 1988). It is also well known that predators efficiently identify weak, injured or sick prey (Mills, 1990; Quinn and Cresswell, 2004; Martin et al., 2006; Wright et al., 2006). In summary, natural selection on predators has probably enhanced animals' ability to detect subtle differences in the motor performance of potential prey. We suggest that it is similarly likely that sexual selection has created parallel capabilities in females to detect subtle differences in the motor performance of potential mates. In the remainder of our essay we ask what aspects of performance could serve as reliable indicators of skill, reviewing relevant data in birds, mammals, and arthropods.

Motor Skill in Bird Displays

A significant body of research has focused on the production, perception, and evolution of vocal displays in birds. Studies of sexual selection on birdsong have traditionally focused on the hypothesis that song complexity, especially repertoire size, is a primary guide for female choice. There is significant disagreement, however, about the extent to which this hypothesis is supported by available evidence, in spite of several compelling data sets correlating repertoire size and male mating success (Haselquist et al., 1996; Reid et al., 2004). A recent review by Byers & Kroodsma (2009), for instance, questions the biological validity of assays used to infer female preferences for large repertoires, and also notes that small repertoires persist in many songbird lineages, with corroborating evidence in the evolution of some clades for repertoire reductions rather than expansions. An alternative

set of characteristics to which females may attend more generally, independent of repertoire size, concerns male vocal skill, as reflected, for example, in the production of particular syllables and phrases and in the consistency with which vocal elements are repeated across renditions (Lambrechts, 1996; Gil and Gahr, 2002; Podos et al., 2009). Studies of vocal mechanics during the last 25 years have illustrated that song production by male birds is intrinsically challenging, involving the simultaneous control and coordination of breathing, syrinx modulations (the left and right sides having separate innervations) and vocal tract modulations including those of the trachea, mandible and oropharyngeal cavity (Nowicki, 1987; Podos and Nowicki, 2004; Suthers, 2004; Riede et al., 2006). Even acoustically simple songs, such as that of the northern cardinal, *Cardinalis cardinalis*, are appropriately regarded, given the complexity of their production mechanism, as an “extraordinary feat of virtuosity” (Suthers 2004). Mechanical limits on vocal production are particularly evident when birds sing high-bandwidth frequency sweeps that are packed together in rapid trills. There is a performance trade-off between these two song components (Podos, 1996, 1997): at some limit, a bird cannot sing faster trills without truncating bandwidth or cannot increase bandwidth without slowing the trill rate. Other vocal components that may reveal male vocal skill include the production of constant note frequency ratios (Christie et al. 2004), of song repertoires with high proportions of trilled songs (Schmidt et al. 2008), and of high-frequency notes with consistency (Byers 2007).

Some evidence suggests that birds can discriminate among the song components that reflect vocal skill. For example, female canaries, *Serinus canaria* (Draganoiu et al. 2002) and swamp sparrows (Ballentine et al. 2004) prefer (laboratory copulation solicitation display tests) trills that are close to mechanical performance limits; male chestnut-sided warblers, *Dendroica pensylvanica*, that sing high-frequency notes with greater consistency attract more extra-pair mates (Byers 2007); male chickadees, *Pocile atricapillus*, with the most consistent internote ratios are most dominant at feeders (Christie et al. 2004); male blue tits, *Cyanistes caeruleus*, with highly consistent intersong intervals tend to sire more offspring (Poessel et al. 2001); and territorial male nightingales, *Luscinia megarhynchos*, are repelled more effectively by playback of song bouts that include higher proportions of trilled songs (Schmidt et al. 2008). In satin bowerbirds, *Ptilonorhynchus violaceus*, male attractiveness to females is strongly correlated with the number of other species' songs that the male mimics, and with the accuracy of the mimetic copies (Coleman et al. 2007). We suggest that there are probably many other aspects of birdsong that represent “Olympian” performances, and in which relevant variation among singers is defined by how closely individuals can approach the physically maximum possible performance. Indeed, the prevalence of sensorimotor song development in birds may be a reflection of the fact that song is physically challenging to produce, and that practice is required to enable accurate model reproduction (Podos et al. 2009).

In the New World manakins (Pipridae), males of many species produce non-vocal courtship sounds by extraordinary movements of their wings (Bostwick and Prum, 2003; Bostwick and Prum, 2005). Several of these sounds are produced as birds slap the dorsal surfaces of their wings together at very high repetition rates, close to the contraction speed limits of vertebrate muscle. Males often perform these movements in the midst of horizontal or vertical leaps. It seems likely that these amazing motor performances represent the outcome of an evolutionary process in which females chose males based upon their skill in performing elaborate courtship leaps (Prum 1997). We suggest that birdsong represents a similarly derived state of advanced motor performance. However, because the motor acts

in song are of smaller amplitude and are largely contained inside the bird, their difficulty is not as readily apparent.

Males of many bird species court females, as do wing-sonating manakins, using whole-body acrobatics. Display flights are especially common. In his review of the display flights of snipe, Sutton (1981, page 474) wrote: “All but one of the 13 currently recognized species of the scolopacid genus *Capella* display in the air during courtship, though aerial display is not restricted to the breeding season. Display flights are accompanied by hooting, bleating, neighing, or whinnying sounds that are widely believed to be non-vocal and that almost certainly are produced by vibration of some or all of the tail feathers.” Such non-vocal sounds are produced repeatedly as individuals make long series of climbs and dives. During dives, sound amplitude increases with dive speed, reaching a sudden crescendo as the bird pulls out of the dive to climb. Even more spectacular U-shaped dive displays occur in some hummingbird species (Johnsgard 1997). Of Allen's hummingbird, *Selasphorus sasin*, and Anna's hummingbird, *Calypte anna*, Larimer & Dudley (1995, page 1064) wrote: “... the display usually begins with a long steep dive initiated 20–35 m above a conspecific bird. When the diving bird is about 1 m of the display target and moving probably at maximal velocity, an abrupt pullout ensues during which radial accelerations must be substantial.” Larimer & Dudley (1995) calculated that the birds dive at a velocity of 17 m/s, and make U-turns of radius 3–4 m at the bottom of the dive, resulting in radial accelerations of 70–100 m/s², with forces on the wings that are up to 10 times body mass. Recently, Clark (2009) showed that the courtship dive of Anna's hummingbirds has a peak average velocity of 27.3 m/s, the highest known length-specific velocity of any vertebrate. During the pull up from the dive, males experience centripetal accelerations nine times that of gravitational acceleration; taken together, these values suggest that male courtship dives reveal the physical performance limits of individual males (Clark 2009). These birds also capitalize on the high forces at maximum dive velocity to produce high-pitched tones by vibrations of their tail feathers (Clark & Feo 2008). Acrobatic flight displays occur in many of the shorebirds, gulls and alcids (Charadrii); in this suborder, the presence of acrobatic displays is associated with evolutionary reduction in male size, presumably because lower mass permits greater performance in difficult flight maneuvers (Székely et al. 2000).

Like some manakins, hummingbirds and snipe, male flappet larks produce non-vocal sounds during flight displays (Norberg 1991). Displaying males produce these sounds by slapping the ventral surfaces of the wings together while accelerating upward in flight at a steep angle. Without changing the amplitude of wing beats, displaying males increase wing beat frequency from 11/s to 24/s, which requires a doubling of power consumption compared to normal flight. Slow-motion analysis of the displays of blue-black grassquits reveals that the “jumps” of males are actually short, almost vertical flights, in which, in some birds, the male's wings meet dorsally to produce short clicks analogous to those produced by manakins (J. Podos & R. H. Macedo, unpublished data).

In addition to acrobatic aerial displays, modified walking or hopping, sometimes combined with short flights, occurs in the display actions of many birds. These actions often look unnatural because of the extremely rapid motions that they entail. For example, red-capped manakin, *Pipra mentalis*, male courtship involves backward “slides” along a branch by tiny, imperceptibly fast movements of the male's feet (Prum 1990). Other manakin males incorporate very rapid short flights and acrobatic hops in their displays to females, often occurring in synchrony with sonation (Prum and Johnson, 1987; Thery, 1990; Bostwick and Prum, 2003). High-speed hops, pivots and glides and other unusual movements occur in the

courtship displays of males in many species of the birds of paradise (Aves: Paradisaeidae). For example, Scholes (2008, page 498) wrote that courtship movements of males in the genus *Parotia* include "(1) horizontal perch pivot; (2) sidle/head tilting; (3) hop/charge; (4) stand/hops and shake; (5) the various ballerina dance phases; and (6) dance/bounce. There are four distinct ballerina dance phases..." In addition to highly acrobatic and rapid movements in courtship displays, males in the manakins and in the birds of paradise often have brightly colored, highly modified plumage that certainly falls into the class of characters that are commonly called ornaments. We suggest that modified plumage in the dancing manakins and birds of paradise, and probably in many other ornamented species, has arisen as a secondary adaptation to enhance the visual stimulus value, or the apparent quality of motor performance, of male display.

Motor Skill in Mammal Displays

There is growing evidence that mammals are able to detect subtle differences in the motor performances of conspecifics. Pelletier et al. (2004) found that bighorn rams, *Ovis canadensis*, that were chemically immobilized by researchers for radio-collaring suffered almost immediate rank challenges upon returning to the ram group, even though the researchers could detect no movement deficits. Pelletier et al. (page 1165) concluded that "Subordinate rams appeared to detect some subtle 'vulnerabilities' in captured rams just after the release..." It seems likely that such perceptual capabilities are enhanced by selection for distinguishing among potential mates or rivals. Stereotyped acrobatic displays by males have been described infrequently for mammals, but it is unclear whether this is because such displays in mammals are uncommon, or because descriptions of what female mammals do in nature when they choose mates are so rare. In the pronghorn rut, males sometimes perform an act, called a circle chase (Byers 1997), that appears to be a display of speed and agility. In a circle chase, a male rushes at a single female in his harem. The female runs away but not in a clear attempt to escape. She runs in tight loops of about 50–70 m radius, close to the harem, frequently changing direction in fast dodging turns, with the male following closely (usually within 1–2 m) behind, matching every direction change. The chased female does not run at top speed, and the male does not attempt to close the gap. Other females in the harem commonly watch the circle chase. The chase ends after about 30–60 s, and the female rejoins the harem. It is not clear whether the male initiates the circle chase or whether he responds to a subtle movement of a female in his harem. The circle chase clearly has the potential to act as a male display of running ability and agility.

In other mammals, the actions of females at the moment of copulation seem to act as tests of male agility. Bison, *Bison bison*, females commonly run from the tending bull at the moment that he achieves intromission, and males often maintain intromission until ejaculation by running behind the female on their hindlegs for up to 100 m (Lott 2002). Even more spectacular running copulations occur in bighorn sheep (Hogg & Forbes 1997). Coursing rams (Hogg 1984) rush a tending ram and the ewe that he is guarding. If the ewe runs, the coursing rams pursue, leap onto the ewe's back and copulate with her while she runs. This male tactic is unusually successful (Hogg & Forbes 1997) and clearly favors the success of males that demonstrate extreme agility. Male sac-winged bats, *Saccopteryx bilineata*, attract and defend harems of females with conspicuous and energetically expensive hovering display flights (Voigt et al. 2001). Males are smaller than females in this species, and may be so partly because natural selection on small size favors improved flight maneuverability (Voigt et al. 2005). This interpretation must be viewed with caution, how-

ever, because males are smaller than females in a majority of bat species that feature multiple mating systems; further information on the relative contributions of multiple selective pressures on sexual size dimorphism in bats awaits a comparative study, analogous to that which has been conducted on shorebirds (Székely et al. 2000).

In many mammals, intrasexual competition among males is pronounced, resulting in substantial sexual dimorphism in body size and weapons. This has led some to conclude that intrasexual competition in male mammals precludes the opportunity for sexual selection by female choice (Clutton-Brock & McAuliffe 2009). However, to the extent that the outcome of competition among male mammals is governed by vigor or skill, female mammals can select for motor performance by preferring and choosing the winners of male–male competition. In pronghorn (Byers et al., 1994; Byers, 1997), females at estrus sometimes incite fights between males. The inciting female appears to watch these fights closely and then immediately mates with the winner. In some mammals that breed on leks, males compete to occupy spatially central territories; females can choose males that have won this competition simply by exerting a preference to mate on central territories.

In many mammals and other taxa, it may be difficult or impossible in practice to disentangle the effects of male–male competition and female choice for male motor performance as determinants of male mating success. However, we suggest that more successful discriminations than one might expect will be brought to light with further descriptions of the sampling behavior of individual females in nature before and at sexual receptivity. A general weakness of sexual selection work to date, especially in mammals, is that there are few studies on the unrestrained behavior of individual females in nature as they sample and choose mates.

Motor Skill in Arthropods

Courtship displays in dipteran flies often involve swarming dances, complex aerial pursuits and/or elaborate displays on the ground (Downes 1969). Long-legged flies in the family Dolichopodidae show courtship displays that involve many complex flight maneuvers (Land and Collett, 1974; Land, 1993; Zimmer et al., 2003). Lunau (1992) suggested that the physiological constitution (speed or agility) of the males may be indicated through these dynamic courtship movements. In the copepod *Temora longicornis*, females cruise through the water leaving a chemical trail that is detectable by males for up to 10 s. Upon encountering a trail, males follow and attempt to catch the female (Doall et al., 1998; Weissburg et al., 1998). In this scenario, it seems likely that directional selection for male skill, supported by superior sensory and locomotor systems, would be favored by sexual selection.

Fiddler crabs provide a rare instance in which male display characteristics and female choice have been studied predominantly in the field under natural conditions. Males in the genus *Uca* produce species-specific visual and acoustical displays that involve body lifts, leg extensions, and movements of both major and minor chela (Salmon et al. 1978). In *Uca perplexa*, video analyses revealed that subtle differences in male movements influence female choice. Males that were visited by females in the field completed the downward component of the chela wave more rapidly than their neighbors, and the interval between the end of one wave and the start of the next was shorter (Backwell et al. 1998). A subsequent study found similar results: the waves of males that were visited by females were distinct from those that females passed by (Murai & Backwell 2006). These studies suggest that females are not only capable of detecting subtle differences in male courtship skill, but that they base their reproductive decisions upon such subtleties.

Predictions

Courtship displays that involve strenuous and/or skilled motor acts are common in animals. We predict that significant variation exists among males in the deployment of these displays, with respect to vigor or skill, or both. We also predict that aspects of display performance will correlate with aspects of male quality (e.g. current condition, developmental history, immune function, breeding value for offspring performance), or with direct contributions that males make to the female. Furthermore, as the intended receivers of most courtship displays, we expect that females are capable of discerning slight differences in male display performance and, most importantly, we predict that female mate choice decisions are based upon these subtle differences in the performance of male courtship displays.

In species where motor performance is crucial for survival, we predict that male displays will reflect these motor challenges, not only in overall display complexity, but also in their specific display components. For example, we expect broad patterns of display complexity to correlate with natural history, such as is seen in spiders where the most elaborate courtship displays are found in taxa that are also active hunters (i.e. jumping spiders, lynx spiders, wolf spiders), while those adopting sit-and-wait strategies tend to have less complex courtship displays (Foelix 1996). We also expect that specific courtship elements will often mimic movements essential to an individual's motor repertoire; for example, flying animals that rely on speed and agility for either prey capture or predator evasion will incorporate flight speed and maneuverability into their courtship displays as a reflection of their motor performance. Finally, for taxa in which motor performances are produced in tandem with the presentation of ornaments, we predict that motor performances will be found to have evolved first, and that the subsequent elaboration of ornaments may have served to enhance the visual appearance of display performances. Testing many of these predictions will require detailed analyses of display structure, and such detailed analysis is becoming more and more feasible with the development of new technologies. Phylogenetic comparative analysis will also aid in the reconstruction of pathways of ornament and display evolution.

Summary

We suggest that sexual selection by female choice for male motor performance is more common than currently appreciated. Motor performance refers to vigor and/or skill. Vigor and skill are closely linked to whole-organism performance, and thus should be especially useful indicators of individual genetic load (Rowe and Houle, 1996; Whitlock and Agrawal, 2009), individual developmental history, and current health and condition. These are testable hypotheses. Vigor and skill are certainly more difficult to document and measure than are ornaments, but modern technology (e.g. high-speed videography, acoustic analyses, telemetered EMG) can help overcome this limitation. It seems likely that females are selected to be able to perceive slight differences in motor performance of conspecific males, although the degree of perceptual sensitivity is at this point unknown. We also predict that in many species, the ornaments that troubled Darwin and that many researchers now believe to be the target of sexual selection by female choice will be found to have evolved as secondary enhancers of male motor display.

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