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Review

Physiological control of elaborate male courtship: Female choice for neuromuscular systems

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ABSTRACT

Males of many animal species perform specialized courtship behaviours to gain copulations with females. Identifying physiological and anatomical specializations underlying performance of these behaviours helps clarify mechanisms through which sexual selection promotes the evolution of elaborate courtship. Our knowledge about neuromuscular specializations that support elaborate displays is limited to a few model species. In this review, we focus on the physiological control of the courtship of a tropical bird, the golden-collared manakin, which has been the focus of our research for nearly 20 years. Male manakins perform physically elaborate courtship displays that are quick, accurate and powerful. Females seem to choose males based on their motor skills suggesting that neuromuscular specializations possessed by these males are driven by female choice. Male courtship is activated by androgens and androgen receptors are expressed in qualitatively and quantitatively unconventional ways in manakin brain, spinal cord and skeletal muscles. We propose that in some species, females select males based on their neuromuscular capabilities and acquired skills and that elaborate steroid-dependent courtship displays evolve to signal these traits.

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1. Introduction

1.1. Sexual signals and exaggerated displays

Sexual selection was proposed by Charles Darwin (1859, 1871) to explain the origin of traits that seemed to contradict his theory of evolution by natural selection. Within this overarching theory, he found it difficult to explain how, for example, the large, decorative tail of a peacock could evolve when it seemed obvious that the tail had survival costs such as increasing the male's vulnerability to predation and reducing the efficiency of his flight. Typical of Darwin, he envisioned a relatively simple, but powerful solution, referred to as sexual selection. He posited that the peacock's tail would evolve if the gain in reproductive success provided by the tail outweighed its costs. Sexual selection swiftly became a popular branch of biological investigation, now attracting empirical and theoretical biologists alike. The field grew to encompass traits that served to increase reproductive success by both enhancing mate choice (by possessing ornaments) as well as by increasing success in male-male competition (possessing armaments that increase fighting success). The benefits of some traits seem relatively easy to explain, such as armaments like the antlers of deer, that are advantageous in male-male competition and that lead to increased access to females (Andersson, 1994). The origins of other traits are more difficult to comprehend, and likely reflect features that females identify for discrimination of males for purposes of mating. A particularly dramatic category of behavioural ornamentation are the *elaborate courtship displays* performed by males of many species. Despite their presence in most animal taxa, we know very little about the genomic, physiological and anatomical mechanisms underlying the evolution of elaborate courtship behaviours. Scientists have been seeking answers as to why specific phenotypes, and not others, evolve. A variety of theories have arisen that attempt to capture the great diversity of signals females might use to assess males including the handicap hypothesis (Zahavi, 1975), the parasite hypothesis (Hamilton and Zuk, 1982), Andersson's concept of honest indicator (Andersson, 1994), and the immunocompetence hypothesis (Folstad and Karter, 1992). Yet there remains the particularly challenging question as to what actually drives the evolution of specific behavioural repertoires associated with some courtship displays.

It is widely believed that *courtship behaviours carry information that females use in assessing male quality*, the basis of their choice for copulation. In some cases, male displays borrow from behaviours that are already employed in other facets of the animals life, such as the ritualized behaviours well-described by Huxley (1938) and Tinbergen (1965). In some cases, *courtship behaviours seem designed to show off the male's physical ornaments*, likely amplifying the value of these signals (Guilford and Dawkins, 1991; Rowe, 1999). Such seems to be the case for the display of the extraordinary tail of the male peacock (Petrie et al., 1991). It is important to recognize that behavioural features that are used only during periods of reproduction are by their very nature transient and likely provide information to females about the male's current physical condition. In contrast, physical ornaments that are permanent (static) or that require extensive periods of growth likely reflect the male's condition over longer spans of his life (Maynard-Smith and Harper, 2003). Elaborate courtship displays that transiently display long-held physical ornaments may serve to signal to females both the short- and long-term condition of the male (Maynard-Smith and Harper, 2003).

Birds are a taxonomic group with extraordinary variation in male mating displays (Lack, 1968). As noted by Darwin "Secondary sexual characters are more diversified and conspicuous in birds. . .The males sometimes pay their court by dancing, or by fantastic antics performed on the ground or in the air" (Darwin, 1871). Some of the most spectacular of these displays are performed by species that have promiscuous mating systems in which males provide no direct benefits to females and females must rely on courtship and ornaments to gather information on mate choice. In those species in which males gather in *leks*, the females are able to compare several males displaying simultaneously (Hoglund et al., 1995). Well studied lekking species of the temperate-zone include the male sage grouse, *Centrocercus urophasianus* (Vehrencamp et al., 1989) and the greater prairie chicken, *Tympanuchus cupido* (Nooker and Sandercock, 2008). Males of both of species gather in large groups where they perform a dance display that shows off their courtship plumage, which is accompanied by production of unusual drumming sounds produced by airflow through specialized air sacs. Other examples include the well-known birds-of-paradise, a family of tropical Australasian birds that mate promiscuously with males performing truly exceptional courtship displays. The male superb bird-of-paradise, *Lophorina superba*, has two blue iridescent shields on his breast which create astonishing contrasts when he opens his black wings in his *ballerina* dance (Frith and Frith, 1988). Male Carola's parotia bird-of-paradise, *Parotia carolae*, perform a hop and shake dance, spreading their wings into a *tutu*-like formation to enhance their iridescent colours and the wire-like feathers protruding from their heads (Scholes III and Sodhi, 2006). *Some birds enrich their courtship by the construction of specialized display arenas*. Males of many bowerbird species, such as the satin bowerbirds *Ptilonorhynchus violaceus* and the great bowerbird, *Chlamydera nuchalis*, not only perform exaggerated movements and vocalizations during their display but also build their bowers which they decorate with coloured objects that contrast with their plumage (Endler and Day, 2006; Endler et al., 2005; Patricelli et al., 2003).

Of relevance to the focus of this review, many of the courtship displays highlighted here include movements that are strikingly unique, quite dissimilar from normal body movements used in normal daily life, such as when foraging for food, when interacting in