

A functional approach to sexual selection

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Summary

1. Sexual selection theory is a robust and dynamic field within evolutionary biology, yet despite decades of research, remarkably little is known of the mechanistic bases of mate choice and male competition.
2. Because many aspects of sexual selection involve dynamic movements, and are physically challenging, the limits of sexual selection may be defined by key functional and physiological variables (i.e. the 'functional approach').
3. We advocate the functional approach for providing mechanistic resolution on the adaptive basis of sexual structures and signals, the nature of mate choice and how males compete, among other issues.
4. An overview of recent work, highlighted in this special issue, shows that many features of sexual selection, including the outcome of male fights, the morphology and design of sexual signals, and the nature of mate choice, all appear to be dictated in large part by functional and physiological parameters.
5. We argue that the functional approach provides a potent tool for resolving several unresolved issues in sexual selection theory, particularly the nature of male quality, the handicap and indicator models of sexual selection, and the basis of mate choice.

Key-words: Sexual selection, performance, signalling, fitness, condition

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Introduction

Sexual selection theory played a key role in the Neo-Darwinian synthesis, and continues to fuel many of the most controversial topics in evolutionary biology (Andersson 1994; Johnstone 1995; Maynard-Smith & Harper 2003; Lailvaux & Irschick 2006). Indeed, much of the remarkable morphological and behavioural diversity in the animal kingdom has arisen via sexual selection. Two key processes within the broader realm of sexual selection theory are male competition and female choice. Male competition refers to antagonistic rivalries among males for access to key limiting resources, such as territories, food or females. Female choice refers to the process by which females actively choose males, presumably based on qualities that might benefit females, either directly or indirectly. Most often, these two processes have been studied from an ethological and/or life-history perspective. Life-history studies are historically rooted in discerning how organisms make decisions regarding

allocation of reproductive effort to maximise individual fitness (Stearns 1992). In the context of sexual selection, life-history approaches have focused on relationships among reproductive allocation and either mate choice (i.e. do females change their reproductive output as a function of male quality?) or male competition. Ethological perspectives have proven valuable in elucidating the behavioural bases of mate choice and male competition, and have tended to address issues such as whether females prefer particularly colourful males or whether males that are favoured by females tend to father more offspring, among other examples (Thompson, Bateson & Klopfer 1989).

These approaches (particularly life-history perspectives) tend to focus on the end product of sexual selection and less on the mechanism, and accordingly, despite tremendous progress (reviewed in Andersson 1994; Maynard-Smith & Harper 2003), certain concepts remain poorly understood, such as why some males win fights (and hence achieve greater reproductive success) than others. Other missing links remain, but a recurring theme is the lack of mechanistic detail concerning the male competition and female choice processes, or in other words,

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much of sexual selection remains a 'black box'. For example, although some researchers have shown that males with enlarged sexually dimorphic structures (e.g. antlers) sometimes enjoy greater fighting success (and sometimes greater reproductive success) compared to males with smaller dimorphic structures, we understand remarkably little about why this correlation exists. Although such simple correlations are useful, we suggest that correlations in the absence of mechanism constitute a significant limiting factor for our understanding of the broader theory of sexual selection.

In this editorial and special issue, we highlight an emerging perspective that tackles this outstanding mechanistic gap in sexual selection theory by incorporating studies of functional morphology and evolutionary physiology. We believe the subdisciplines of functional morphology and evolutionary physiology can contribute significantly to sexual selection theory because they examine how animals achieve dynamic movements (functional morphology) or sustain themselves metabolically and energetically (evolutionary physiology). Because numerous aspects of how male animals compete, and how females choose males, interface with these two arenas, they naturally form a union with sexual selection. We term the integration of functional morphology, evolutionary physiology and sexual selection as the 'functional approach' (Lailvaux & Irschick 2006).

We promote several goals in this editorial and special issue; one goal is a more standardised set of definitions that encompass the functional approach to sexual selection. We feel that this standardisation is important for researchers without a strong background in functional morphology and physiology because imprecise terms can be a significant source of confusion, particularly in collaborations with researchers from different backgrounds. We focused on this goal of standardisation both because of apparent disagreements in the literature, and from discussions with colleagues in which we found that the same term (e.g. 'performance') meant different things to different people. A second goal was to synthesise key findings, outlined below, that have emerged from recent applications of the functional approach to sexual selection.

Key definitions

Of foremost importance are cogent definitions of physiology and functional morphology. We define physiology as 'a branch of biology that deals with the functions and activities of life or of living matter (as organs, tissues or cells) and of the physical and chemical phenomena involved' (Merriam-Webster Dictionary 1994). 'Physiology' and 'functional morphology' are often used interchangeably, and discerning the boundaries between these fields is challenging. In the context of sexual selection, physiological studies necessarily focus on the energetic and metabolic functions of organisms, whereas functional morphological studies focus on the interaction among structure and function, including measurements of whole-organism performance, muscle anatomy and function,

and animal movement. Whole-organism performance studies have played a key role in several of the sexual selection studies outlined in this special issue, and we adopt Huey & Stevenson's (1979) definition that performance capacity is 'the ability of an organism to execute an ecologically relevant task'. Note that this definition emphasises performance output emerging from the whole organism, and excludes sub-organismal performance, such as how well an enzyme catalyses reactions. 'Function' is often confused with 'performance', but performance defines how well an organism conducts a task, whereas function describes the manner in which a structure is used. Amundson & Lauder (1994) define function as 'The use, action, or mechanical role of phenotypic features'. In the context of this special issue, two other important key definitions are 'physiological cost' and 'agonistic behaviour'. The first concept is important in understanding potential physiological costs to organisms during sexual selection interactions (e.g. female choice, male competition), which we define as 'a decrement to the organism in units of metabolic or energetic expenditure that negatively impacts fitness'. Note that the downstream effects on fitness in this case are crucial; in short, physiological decrements mean little in an evolutionary sense if they do not ultimately affect fitness. Much of this special issue is devoted to understanding the functional/physiological consequences of aggression in sexual selection context, referred to as agonistic behaviour. More specifically, agonistic behaviour refers to the complex of aggression, appeasement and avoidance behaviour that occurs between members of the same species (McFarland 1982).

Key findings

The idea of costs and trade-offs is central to sexual selection, and the functional approach provides a testable framework by quantifying physiological and performance costs and trade-offs arising from sexual displays, sexual structures and male–male (or male–female) agonistic encounters (Johnstone 1995; Berglund, Bisazza & Pilastro 1996). One theme emerging from this special issue is that male competition, either indirect (e.g. lekking, vocalisation) or direct (e.g. fighting) often comes at a high physiological cost. This idea of 'costs' associated with fighting or displaying is important because prior syntheses have stressed that the morphology and use of sexual structures is costly, and thus may be difficult (though not impossible) for a lower-quality male to mimic, such as in the 'handicap' model (Zahavi 1975; Leal 1999; Backwell *et al.* 2000; Maynard-Smith & Harper 2003). Sullivan and Kwiatkowski review a large body of literature in frogs and lizards showing that vocalisations, which are a key indicator of male reproductive success, are also energetically expensive, ensuring that few males will be capable of high-intensity and long-duration calls. In the context of agonistic male interactions, Briffa and Sneddon review how male fights in various animal species may be dictated not so

much by physical prowess *per se*, but rather the ability to either minimise or withstand the costs of fighting, such as high lactic acid build up in hermit crabs. In other words, the view that aggressive male encounters are dictated purely by size, strength and quickness may be incomplete without considering more subtle aspects of physiological state.

Functional morphological and physiological studies can also be useful for resolving older ideas about mate choice in different animal species. Kotiaho and colleagues present a careful analysis of the evolution of studies of mate choice, and point towards functional/physiological studies as being central in resolving debates regarding indirect or direct benefits to females. As shown in earlier papers, the drumming displays of spiders (Kotiaho *et al.* 1998) presents a compelling example of a signal that is both physically challenging (and hence subject to selection on functional/physiological parameters), and plays a key role in both male competition and female choice. However, as pointed out by Vanhooydonck *et al.* not all sexual signals incur a cost to the individual, such as in the case of incorruptible 'indices' of male quality. Interestingly, one of the primary advantages of the functional approach is the ability to distinguish between such indices and 'handicaps', which have rarely been rigorously addressed. Overall, these above findings may be symptomatic of a larger phenomenon; the strong functional basis of how males fight, and what they fight with, generally imply that the evolution of male sexual traits and physiology are tightly linked (Wilczynska, Rand & Ryan 2001). Interestingly, both the distributions of performance traits and male reproductive success tend to be highly skewed with relatively few very top quality individuals, and many average or poor individuals (Bennett & Huey 1990; Le Galliard, Clobert & Ferriere 2004), suggesting that physiological traits may be a primary target of sexual selection.

Recent work also shows strong linkages between the overall size and/or colour of enlarged male sexual structures and whole-organism performance capacities that play a key role in the sexual selection process. Studies of whole-organism performance capacities (e.g. sprint speed, endurance and biting) have played an instrumental role in the growth of functional morphology and evolutionary ecology (e.g. Huey & Stevenson 1979; Arnold 1983; Bennett & Huey 1990; Irschick & Garland 2001), and now are rapidly making forays into the arena of sexual selection, particularly for understanding the role of sexually dimorphic structures. Extravagantly sized and coloured male sexual structures represent some of the most mysterious and least understood hallmarks of the sexual selection process. Work with *Anolis* lizards shows that lizards with enlarged throat fans (dewlaps) tend also to exhibit high bite forces, a crucial trait for polygynous lizards that often bite one another during male encounters (Vanhooydonck *et al.* 2005a, 2005b). Interestingly, Vanhooydonck *et al.* provide additional data showing that possession of a large dewlap, at least in smaller males, does not result in trade-offs with other

performance variables, such as clinging and sprinting, supporting the idea that the dewlap is a reliable 'index' of male quality. Some research also indicates a dominance and reproductive advantage for male lizards that can bite particularly hard (Lailvaux *et al.* 2004; Huyghe *et al.* 2005; Lappin & Husak 2005; Husak *et al.* 2006a, 2006b). More generally, this work demonstrates the usefulness of using whole-organism performance capacities as a metric for testing theories in sexual selection. In this context, providing a quantitative metric of male quality that can be compared among individuals within species, as well as among divergent species is crucial. Because of their long use in physiological and functional studies, performance measures present well-understood links to variation in morphological structures on the one hand, and aspects of ecology and life-history on the other hand.

The functional approach also shows great promise for elucidating the mechanisms that lead to alternative male mating strategies. Miles *et al.* show how analyses of hormones, immunocompetence and whole-organism performance capacity (e.g. sprint speed, endurance) provide new insights into the evolution of male morphs, exemplified by the classic rock-paper-scissors game for the lizard *Uta stansburiana* (Sinervo *et al.* 2000). Although researchers know a great deal about the social behaviour, and reproductive consequences of different kinds of male morphs in various taxa (e.g. fish, insects), far less is understood about why some morphs are able to dominate others during direct encounters among males. The functional approach provides a testable framework for examining whether such social differences are also manifested in structural, functional and physiological differences that may be the primary predictors of dominance in social situations.

One of the primary advantages of the functional approach is the ability to attack sexual selection from an evolutionary perspective. Phylogenetic methods have revolutionised many aspects of biology, including sexual selection, but generally have not been applied to the functional approach to sexual selection outlined here. Pioneering studies showcased the utility of incorporating phylogenetic perspectives for studies of physiology (e.g. Huey & Bennett 1987), but researchers have been slow to take the next step by incorporating sexually selected traits. However, Oufiero and Garland show how a phylogenetic approach is useful for understanding the evolution of sexual traits, such as the elongated tail fins of many fish species. This example is particularly instructive because it demonstrates the dual nature of many sexual traits, in this case mate attraction and swimming, and how an evolutionary approach can dissect their relative roles to a greater extent than within-species studies.

The approach that Oufiero and Garland describe can be expanded to many other kinds of sexual signals. For example, one could examine a clade of species that vary in several parameters, including the size of male sexual structures, performance and physiological state. One approach would be to determine whether, as the relative size of sexual signals decreases or enlarges, the

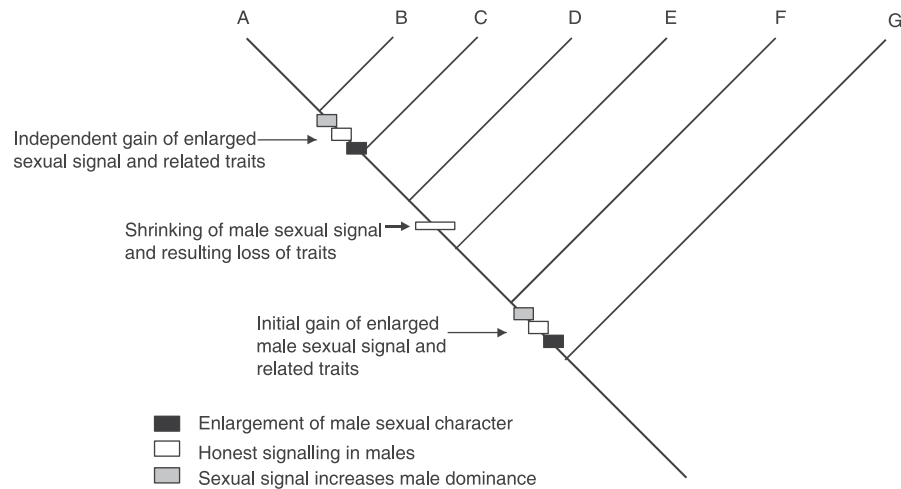


Fig. 1. A hypothetical example of the phylogenetic distribution of male sexual structures (i.e. enlargement or diminishment), the distribution of honest signalling, and the distribution of male dominance (as related to sexual structure size).

relationship between the size of the signal and performance also changes (i.e. honest signalling). In other words, does the evolutionary ‘shrinking’ and ‘expanding’ of sexual structures (or enhancement or diminishment of colour) relate to the use of the structures as honest signals within species? One could also determine whether the morphological state of sexual structures correlates with female choice or male dominance within some species, and not others, and hence, test which ecological factors might be the underlying causal factors (Fig. 1).

We also advocate microevolutionary studies that examine both the survival and the reproductive basis of sexually selected traits, and their links to functional traits. For example, one microevolutionary approach would be to conduct detailed studies of both paternities (thus quantifying reproductive success) and survival within an animal population, and then relating both parameters to the relative size, colour and shape of prominent sexual signals, as well as to functional traits that might dictate both female choice and male competition. An important new study (Husak *et al.* 2006a) shows the promise of this approach; by integrating studies of paternity (i.e. reproductive success), survival, performance and hormone levels within a marked population of Collared lizards (*Crotaphytus*), they were able to definitively provide a complete link among sexual traits (head size), performance (sprint speed and bite force), and both survival and reproductive success.

More generally, our hope is that the functional approach will enable researchers to more exactly test and define ideas of male ‘quality’, and thus making a large leap forward in testing models of male competition and female choice. The concept of male ‘quality’ has remained elusive to researchers in sexual selection, in part because this term has a strong anthropomorphic bias and can imply different things in different contexts or in different organisms. We suggest that vague notions of male quality will continue to hamper progress in the broader field of sexual selection, and that detailed and

quantifiable measures of performance capacity and physiological state represent a practical and meaningful way to examine male quality. Recent ‘good genes’ models propose that females should choose males that provide the greatest genetic benefit for their offspring (Kokko 1998; Hunt *et al.* 2004). However, this approach, although valuable, primarily identifies the genetic end product of mating, and provides little insight into the mechanism. Within this framework, we do not argue that functional traits alone dictate male competition and female choice (although we argue they often do), but rather suggest that they represent logical, practical and quantifiable measures that can be compared among individuals and species.

Finally, we believe that researchers working in the field of sexual selection rely far too much on simple measures of body condition (e.g. relative body mass, relative body fat, etc.) as convenient measures of male ‘quality’ (see Jakob, Marshall & Uetz 1996 for an insightful review). One of the most important lessons over the past 100 years of functional morphological and physiological studies is that morphology alone is often a poor predictor of organismal function (Lauder 1996; Wainwright *et al.* 2005). Ironically, behaviour is often the culprit; by dramatically altering behaviour, animals can change the relationship between morphology and performance, as any three-legged dog demonstrates. In the same manner, animals with markedly different condition indices have the potential to exhibit the same level of organismal performance for a variety of tasks. Further, one cannot assume that high levels of performance or even male dominance will translate into female preferences (Ophir & Galef 2003). As an alternative to simple measures of condition, we advocate more intensive functional and physiological measures (in combination with condition) that are more relevant, from the perspective of fitness, to the organism in question. For example, consider a theoretical example of an invertebrate (e.g. a spider) that engages in prolonged male fights, and

for which one could also assess condition via the width of the abdomen or some similar measure. Because of the close link between endurance capacity and male fighting in this group, one could measure both condition and locomotor endurance (i.e. amount of time to run around a circular track until exhaustion), and examine interactions between condition and endurance, and between both variables and male fighting success. Again, the emphasis should be on choosing functional measures that relate directly to some aspect of how males fight or how females choose. Researchers may also be surprised to learn that such additional measures are not as difficult or as time-consuming as they might imagine. Nevertheless, an obvious drawback is that greater effort will have to be invested for a given sample of animals (potentially resulting in smaller sample sizes), but we also believe that the potential explanatory power of the resulting data will be dramatically increased.

The functional approach outlined here obviously cannot serve as a panacea for all the problems that bedevil sexual selection theory. A reasonable criticism is that the functional variables discussed in this special issue may not be the true target of sexual selection, but rather could be correlated with some other, more important, metric of male quality. We tend to reject such an argument because one could make the same claim for any study in which a researcher correlates different sets of traits, or for any experimental biologist who examines the effect of a manipulated variable on some other trait. Nevertheless, researchers using the functional approach should carefully consider whether the functional variables chosen are biologically meaningful. Part of this debate revolves around whether quality is a multivariate phenomenon (see Hamilton & Sullivan 2005) or perhaps better explained by a few key variables. Resolution of this issue will be challenging, but the functional approach makes no *a priori* statement on either model, and, as with any other behavioural study, a solid understanding of the natural history of the study organism is essential. In the case of sexually selected traits, behavioural observations of organisms in the field can provide valuable insight into which parameters of male 'quality' are most likely to be direct targets of natural and sexual selection. In conclusion, we encourage researchers in the sexual selection field to seek out collaborations with functional morphologists and evolutionary physiologists to more fully implement the functional approach outlined in this special issue. Likewise, we encourage functional morphologists and evolutionary physiologists to broaden their research programs to incorporate sexually selected traits.

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