A functional perspective on sexual selection: insights and future prospects

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A large number of sexual selection studies have focused on examining the morphological and behavioural factors involved in male combat and female choice, such as whether large males achieve higher reproductive success compared with smaller males. However, until recently, the mechanistic reasons why such cues are linked to male dominance or female choice have been elusive. An emerging body of work shows that physiological and whole-organism performance capacities are important in individual reproductive success. Males with high performance or other physiological capacities (e.g. endurance, biting) often enjoy an advantage over males with poorer performance capacities during male–male contests. In contrast, few studies have examined links between performance and female choice. Here, we highlight recent key literature integrating sexual selection, performance and physiology. We also point to areas where a more rigorous investigation of underlying physiological processes may yield insights into sexual selection. In particular, we note that current progress in several important areas may be hampered by an inadequate physiological understanding of condition. We suggest a conceptual approach that may shed light on the physiological factors underlying condition, and we point out several other potentially important avenues for future research.

Sexual selection theory lies at the heart of evolutionary biology and has been the subject of intense debates since Darwin (1871). Indeed, recent syntheses have stressed that sexual selection is not only important for understanding the often-striking differences between males and females, but may also be a major diversifying factor in adaptive radiations (Schluter 2000; Coyne & Orr 2004). The broad field of sexual selection encompasses several different concepts, but two processes are believed to be especially important: male–male competition and female choice. In turn, these processes are thought to be a driving force in the evolution of conspicuous sexual features (e.g. horns, bright colours) often considered to be hallmarks of sexual selection. Secondary sexual characters may act as armaments for resolving male conflicts, as ornaments in a female choice context, or both (Berglund et al. 1996).

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Although the relative importance of these two processes is not well understood, both probably play a significant role within many animal populations (Andersson 1994).

To date, most studies of sexual selection have focused either on documenting the presence or intensity of male–male competition and female choice within animal populations, or relating the evolution of reproductive strategies to these phenomena. In contrast, an emerging body of work has examined sexual selection from a functional perspective, largely because many aspects of sexual selection theory are rooted in functional concepts. For example, male fighting ability is likely to be affected by an individual's physiological state and/or performance capacities. Furthermore, the 'good genes' model of sexual selection, or 'viability indicator hypothesis' (Andersson 1994), assumes a link between genetic quality and viability, frequently measured as survival (Møller & Alatalo 1999). Given the assumed general relationship between, for example, locomotor performance and survival (Jayne & Bennett 1990; Watkins 1996; O'Steen et al. 2002; Miles 2004), one might predict that males expressing good genes would also be good performers (Maynard Smith & Harper 2003). However, owing to life-history trade-offs, individuals who invest heavily in mate acquisition may

do so at the expense of functional or physiological capacities associated with survival (see Kokko 2001; Badyaev & Qvarnström 2002; Kokko et al. 2003). Thus, the study of sexual selection from a physiological perspective raises some intriguing questions: are males of high 'quality' (i.e. males showing high breeding values for total fitness; Hunt et al. 2004a) with relatively large sexual structures also males of good physiological or phenotypic quality, and are these males good fighters? Do females choose mates based on a male's intrinsic physiological state and/or functional capacities?

Although previous authors have considered these issues on specific study systems, there has been no attempt to synthesize the many disparate studies that have examined sexual selection from a functional perspective. We think that this synthesis is needed because although evolutionary biology and sexual selection have traditionally been isolated from comparative physiology and functional morphology at a conceptual level, researchers have increasingly applied methods used in functional morphology and comparative physiology to understand sexual selection. Here, we examine sexual selection in the context of two aspects borrowed from the larger fields of functional morphology and comparative physiology, namely whole-organism performance capacity and an organism's physiological state (e.g. metabolic rates, glucose levels, fat stores, etc.). Our goal is not to provide a comprehensive review, but rather to highlight key literature bearing on this topic. We do not consider studies dealing with endocrine physiology, because of the enormous literature and large amount of attention paid to hormonal effects on reproductive behaviours and because of the existence of several recent reviews on this subject (e.g. Rhens & Crews 2002). We also do not review the large literature on sensory physiology, although we note that sensory systems are of central importance to ideas of preexisting biases in female choice such as sensory exploitation or sensory trap hypotheses (Jennions & Brooks 2001).

A key element of this review is establishing a more rigorous definition for whole-organism performance than has been used in the sexual selection literature. Broadly defined, whole-organism performance capacity is any quantitative measure of how well an organism (as opposed to a cell, an enzyme, etc.) performs an ecologically relevant task (Irschick & Garland 2001). Examples include how fast a lizard can run, how hard a dog can bite, and how long a frog can croak. However, based on this simple definition, other kinds of performance can be defined, such as how quickly an animal digests food, how many offspring a female mammal can produce in a year, and so forth. We adopt a more focused definition of animal performance that has been the core of conceptually related studies over the past 25 years (Arnold 1983; Bennett & Huey 1990; Irschick & Garland 2001). Our view of animal performance is defined by dynamic movements, such as vocalization, locomotion and feeding, among others. The utility of this definition can be understood by considering human Olympics that measure performance at various tasks, including sprinting, weight-lifting and rowing, but do not measure other measures of performance, such as how many books a person can write in a year, or how much money a person can earn in a year. More importantly, a dynamical, whole-organism view of performance is most likely to be relevant for sexual selection. This is because performance represents the output from a more complex functional system, and both natural and sexual selection are expected to operate on performance first, and secondarily on other aspects (e.g. morphology).

By physiological state, we mean any quantitative measure of the internal state of an animal, such as measures of fat stores, metabolic rates, blood glucose levels, and so forth. We distinguish physiology from morphology in that the latter largely describes the various shapes assumed by animals (e.g. limb dimensions, sizes of various bones), whereas physiology provides a measure of underlying metabolic processes, digestion or muscle function, and generally has some energetic basis. As well as being influenced by factors such as nutrition, an individual's physiological state is also related to, and potentially influenced by, overall body condition. Although condition is an important concept in behavioural ecology, it is seldom rigorously defined, and hence, is the subject of some confusion, particularly with regard to how it should be measured (see Jakob et al. 1996; Kotiaho 1999; Green 2000 for discussion of the assumptions underlying calculations of condition indexes). Here, we include condition under the umbrella term of physiological state, but we also ask whether common measures of condition relate directly to measures of whole-organism performance and to other measures of physiological state.

MALE COMPETITION

Previous authors have recognized the importance of physiological state, whole-organism performance and energetics to the resolution of aggressive male–male interactions. For example, such functional concepts are implicit in Parker's (1974) notion of resource holding potential (RHP) as a determinant of victory in male contests. More recent game theory models (e.g. the sequential assessment game: Enquist & Leimar 1983; the energetic war of attrition: Mesterton-Gibbons et al. 1996; Payne & Pagel 1996; the cumulative assessment model: Payne 1998) are constructed within an explicit framework of energy costs and physical endurance capacities that affect the duration, intensity and outcomes of male contests. In addition, behavioural studies frequently refer to individual 'fighting ability' (Maynard Smith & Harper 2003 and references therein), a variable synonymous with RHP, but relatively few studies have investigated the physiological bases that might make a particular male a better fighter than another.

Game theory attempts to explain the emergence and persistence of behavioural strategies based on the costs and benefits of individual behaviour (reviewed in Dugatkin & Reeve 1998). Whereas early game theoretical models focused on symmetrical 'games' in which individuals were identical apart from their behavioural strategies, more ecologically relevant are 'asymmetrical' games in which

opponents differ in some aspect that may affect contest outcomes. The various models can be distinguished from each other by details such as signalling rate or structure; however, the important point for the purposes of this review is that decision rules in fights can be based on either (or both) of the combatants' internal states (Sneddon et al. 1998), as well as on the potential costs to a combatant, such as injuries, of persevering in an escalated fight (Earley et al. 2002).

Energetics and Physiological State

Despite the large body of theory addressing the energetic costs of fighting in animals, few studies have directly measured metabolism and/or energetics during male combat. Direct measures of metabolic rates during fights may be difficult to obtain for some taxa, but researchers have gleaned information on energetic costs of male combat indirectly, by measuring metabolic by-products or by use of doubly-labelled water. For example, metabolic rate increased significantly as fights escalated through the three successive phases of combat in the dome spider, *Neriene litigiosa* (deCarvalho et al. 2004). Thus, aggressive behaviour is organized into phases of increasingly energetically costly behaviours that are likely to provide males with increasingly accurate information about their rival's metabolic status, as predicted by the sequential assessment game (Earley et al. 2002).

Although high metabolic rates have generally been assumed to be a cost of dominance (Røskaft et al. 1986; Hogstad 1987; Bryant & Newton 1994; Reinertson & Hogstad 1994; Whiting et al. 2003; but see Metcalfe et al. 1995), recent studies on animal signalling have reported conflicting results for resting metabolic rates. For example, negative as well as positive correlations can exist between metabolic rates and badges of dominance, even after controlling for activity levels and body mass (e.g. Senar et al. 2000). Indeed, there is no a priori reason to assume that males with high metabolic rates should be dominant over males with lower metabolic rates (Senar et al. 2000). Some evidence suggests that the opposite may be true: subordinate males may show higher metabolic rates than dominants because subordinates are likely to be involved in more challenges from other males (e.g. Sloman et al 2000). The pattern of male badges of status acting as indicators of resting metabolic rates might therefore not be general.

Investigations of the metabolic costs of fighting have also yielded less than clear-cut findings. Anaerobic respiration has been found to impose only limited costs during fights in male velvet swimming crabs, *Necora puber* (L.) (Smith & Taylor 1993; Thorpe et al. 1995), but fatigue from anaerobic activity is a limiting factor in aggressive claw waving in male fiddler crabs, *Uca lactea* (Matsumasa & Murai 2005). Elevated levels of lactate and other metabolic end products in contest losers (relative to winners) after prolonged fights have also been reported in several other taxa (cichlid fish: Neat et al. 1998; copperhead snakes, *Agkistrodon contortix*: Schuett & Grober 2000; see Table 1).

Several studies have also investigated the effects of prior nutritional state and condition on fight outcomes. For example, males with good energetic reserves are more likely to win aggressive encounters in several animal taxa, particularly flying insects (Table 1). In addition to larger fat reserves, other physiological variables, such as immunocompetence, have been found to differ between winners and losers in male damselflies (Koskimäki et al. 2004), suggesting that both fighting ability and immune function are based on physiological state (see also Rantala & Kortet 2004). However, cases also exist where fat reserves are less important than body size for winning contests (e.g. Kemp & Alcock 2003). Thus, although potentially widespread, energetic availability may not be a universal component of resource holding potential in flying insects.

Whole-organism Performance

The interaction between male combat and whole-organism performance capacities has been moderately well studied in lizards. The males of many lizard species will fight intensely for access to territories, which are often critical for acquiring matings, and potentially for acquiring food (Stamps & Krishnan 1997, 1998). At first glance, several different aspects of performance appear important for such fights, including endurance and sprint speed. Studies using several lizard species reveal that both of these aspects of locomotor performance are important for resolving disputes, and high-performance males are more likely to win in dyadic male–male contests than are low-performance males (Table 1; but see John-Alder et al. 1996; Miles et al. 2001; López & Martín 2002). To date, however, no studies have shown directly how these high locomotor performance capacities lead to victory in territorial disputes.

If whole-organism performance abilities are important components of fighting ability, then game theory predicts that male signals or armaments should be indicators of performance capacity. For instance, Guderley & Couture (2005) demonstrated a link between muscle condition and likelihood of victory in fights between male sticklebacks, and suggested that males are able to assess the physiological status of opponents prior to combat. Several studies using lizards have shown an interaction between display behaviour and locomotor capacity. For example, headbobbing or pushup displays, which are considered critical for lizard male–male contests (Jenssen et al. 2000), may be constrained by endurance ability (Brandt 2003). Thus, threat posturing may act as a handicap restricting the endurance ability of displaying males. Male armament size and performance have also been linked to male–male interactions in invertebrates. Victory in fights between male horned dung beetles, *Euoniticellus intermedius*, is determined by size-adjusted horn size (Pomfret & Knell 2006), which is also correlated with two types of performance abilities used by males during fights (Lailvaux et al. 2005). Given the opportunities for assessment of horn size during fights in this species (R. Knell, unpublished data) males probably acquire information on a rival's performance abilities from the size of his horn.

Table 1. Summary of studies showing a link between male combat (MCO) or female choice (FCH) and functional traits

Species	Selective context	Male functional trait	Effect on interaction outcomes	Reference
Insects				
Odonata				
Calopteryx maculata	MCO	Energetic reserves	Positive	Marden & Waage 1990; Marden & Rollins 1994; Plaistow & Siva-Jothy 1996
Calopteryx virgo	MCO	Immunocompetence	Positive	Koskimäki et al. 2004
Orthoptera				
Gryllus bimaculatus	MCO	Immunocompetence	Positive	Rantala & Kortet 2004
Coleoptera				
Euoniticellus intermedius	MCO	Locomotor endurance; pull-resisting force	Positive	Lailvaux et al. 2005; Pomfret & Knell 2006
Hymenoptera				
Hemipepsis ustulata	MCO	Energetic reserves	None	Kemp & Alcock 2003
Lepidoptera				
Hypolimnus bolina	MCO	Energetic reserves	None	Kemp 2002
Pararge aegeria	MCO	Flight performance	None	Kemp et al. 2006
Diptera				
Cuterebra austeni	MCO	Energetic reserves	Positive	Kemp & Alcock 2003
Scathophaga stercoraria	MCO	Energetic reserves	Positive	Blanckenhorn et al. 2003
Crustaceans				
Uca lactea	MCO	Anaerobic endurance	Positive	Matsumasa & Murai 2005
Necora puber	MCO	Metabolic rate; endurance	None	Smith & Taylor 1993; Thorpe et al. 1995
Spiders				
Neriene litigosa	MCO	Metabolic rate	Positive	deCarvalho et al. 2004
Hygrolycosa rubrofasciata	FCH	Metabolic rate	Positive	Kotiaho et al. 1996; Kotiaho et al. 1998; Mappes et al. 1996; Kotiaho 2000; Rivero et al. 2000
Fish				
Gasterosteus aculeatus	MCO	Energetic reserves; muscle condition	Positive	Chellappa & Huntingford 1989; Guderley & Couture 2005
Tilapia zillii	MCO	Energetic reserves; anaerobic respiration	Positive	Neat et al. 1998
Poecilia reticulata	FCH	Locomotor endurance	Positive	Nicoletto 1991, 1993; Kodric-Brown & Nicoletto 2005
Rhinogobius brunneus	FCH	Condition; swimming performance	Positive	Takahashi & Kohda 2004
Lizards				
Anolis carolinensis	MCO	Bite force; jumping ability	Positive	Lailvaux et al. 2004
	FCH	Bite force; jumping ability	None	Lailvaux & Irschick 2006
Anolis cristatellus	MCO	Locomotor endurance	Positive	Perry et al. 2004
Sceloporus occidentalis	MCO	Sprint speed	Positive	Garland et al. 1990b
Urosaurus ornatus	MCO	Sprint speed; locomotor endurance	Positive	Robson & Miles 2000
Gallotia galloti	MCO	Bite force	Positive	Huyghe et al. 2005
Snakes				
Agkistrodon contortix	MCO	Anaerobic endurance	Positive	Schuett & Grober 2000
Birds				
Gallinula chloropus	FCH	Energetic reserves	Positive	Petrie 1983
Mammals				
Clethrionomys glareolus	CO	Aerobic capacity; metabolic scope	None	Radwan et al. 2004

Relative armament size has also been linked to other types of whole-organism performance besides locomotor capacities. For example, residual bite force is positively related to the residual size of the dewlap (a male secondary sexual character displayed in several social contexts, including male—male interactions) in several species of *Anolis* lizards (Vanhooydonck et al. 2005a, b). This finding is consistent with empirical studies suggesting a role for bite force in influencing fight outcomes. Indeed, males of several species are known to bite each other directly in the latter stages of escalated conflicts (e.g. McMann 1993; Molina-Borja et al. 1998) (see also Neat et al. 1998), and lizards with strong bite forces appear better able to acquire high-quality territories (Lappin & Husak 2005). Furthermore, recent studies have shown that males with large size-adjusted bite forces win male fights in

several polygynous lizards (Lailvaux et al. 2004; Huyghe et al. 2005; S. P. Lailvaux & D. J. Irschick, unpublished data).

Performance-based tactics used for competing with rivals may also differ intraspecifically. Male colour morphs of the lizard species *Uta stansburiana* are associated with both alternative reproductive tactics and different endurance capacities (Sinervo et al. 2000). Similarly, territorial male pupfish, *Cyprinodon pecosensis*, show significantly higher swimming endurance than do nonterritorial males (Kodric-Brown & Nicoletto 1993). Use of performance-based fighting tactics can also depend on an individual's size and/or age (e.g. Hu & Morse 2004; Irschick & Lailvaux 2006). For example, sexually mature *A. carolinensis* males may rely on either bite force or jumping ability to win size-matched fights, depending on their size (Lailvaux et al. 2004; but see Jenssen et al. 2005). Thus, social and ecological context may affect the utility of different performance types in fights (see also Pasi & Carrier 2003).

Whereas the above studies reported positive relationships between armament size and performance, a handful of studies have provided evidence that armament size can impede performance ability (see also Basolo & Alcaraz 2003 for a female choice example). For example, performance decrements may be incurred by mechanical obstruction (e.g. in the dung beetle *Onthophagus taurus*, the large horns of male guarder morphs restrict movement in narrow tunnels; Moczek & Emlen 2000), or by increasing drag (e.g. the large eyestalks in male *Cyrtodiopsis whitei* flies; Swallow et al. 2000). In both cases, however, the affected performance abilities are apparently unrelated to fighting ability. Poor performance in these species can therefore be viewed as a cost of sexual selection similar to increased predation rates suffered by males with conspicuous ornamentation (Andersson 1994; Stuart-Fox et al. 2003; see also Hunt et al. 2004b).

FEMALE CHOICE

Discrimination amongst potential mates may be advantageous to females for several reasons (Andersson 1994), and mating biases or preferences are consequently shown by females of many animal species. Female choice often favours costly male ornaments that signal honest information about individual condition, although other aspects of individual 'quality' may be relevant as well. Here, we briefly review female choice from a functional perspective, and ask what insights such an approach might reveal.

Energetics and Male Ornaments

Male ornaments are generally considered energetically costly to produce (see Kotiaho 2001 for a review and cautionary note), and of these ornaments, male vocalizations are particularly expensive. For example, the metabolic rates of calling males may exceed those of resting males by factors of 100−220% in frogs and toads (Gerhardt 1994 and references therein). Prolonged breeding seasons are often associated with declines in body mass and condition, and calling rate and growth rate are negatively

correlated in at least one species of frog, *Rana virgatipes* (Given 1988). Finally, males incur a further energetic cost during the act of amplexus that may limit their opportunities for future reproductive encounters (McLister 2003).

Energetic costs of auditory signalling in a female choice context have also been reported in several invertebrate taxa. For example, abdomen drumming in male wolf spiders, *Hygrolycosa rubrofasciata*, which produce an audible sound directed at females (Kotiaho et al. 1996; Kotiaho 2000; Rivero et al. 2000; Parri et al. 2002), is costly (Kotiaho et al. 1998): males provided with more food were able to drum longer than males provided with less food (Kotiaho 2000), and males that were induced to drum more often also lost mass more rapidly. These studies provide a rare and instructive example of the interactive effects between physiology (energetic reserves) and performance, demonstrating how individuals with high levels of performance both obtain a clear benefit (access to females) and incur a physiological cost.

Similar costs might be expected in passerine birds, which also show elaborate auditory courtship displays. However, although field observations suggest that bird calling is energetically expensive (e.g. Thomas 2002), support for this notion from laboratory studies is equivocal. Energetic costs have been reported in some species (Eberhardt 1994), but not others (Oberweger & Goller 2001; Franz & Goller 2003; Ward et al. 2003, 2004), even though singing is typically associated with increased metabolic rates. It is often difficult to determine how expensive calling should be before it imposes a fitness cost (see Kotiaho 2001 for a general discussion of the distinction between expenditure and cost in sexual selection studies). Mechanical efficiency is a likely cause for the relative cheapness of songbird calls, but calling is also energetically cheap in some nonpasserine birds, such as roosters (Horn et al. 1995). Bird vocalizations may have an anaerobic component (Weathers et al. 1997), although this is considered unlikely (Ward et al. 2003). However, bird song may yet be costly, because singing might be affordable for a bird that is able to maintain energy balance, but expensive for a bird that is close to starvation (Ward et al. 2003). In this respect, an interaction between resource availability and energy expenditure may be important for bird song, as it is for drumming in wolf spiders (see above).

Finally, energetic expenditure can also be affected by external factors, including parasitism (Schall et al. 1982; Horak et al. 2004; Whiteman & Parker 2004). Parasite-mediated sexual selection (PMSS) posits that male ornaments advertise parasite resistance (Hamilton & Zuk 1982; Clayton 1991; Andersson 1994), and although few studies have quantified the energy costs of parasitism on male ornament expression, desert gerbils, *Gerbillus dasyurus*, infected with ectoparasites show a 16% increase in metabolic rate (Khokhlova et al. 2002). Similarly, immune activity can elevate energy expenditure (Martin et al. 2003) and affect song characteristics in some birds (Garamszegi et al. 2004). Male ornamentation is associated with immune function in several taxa (reviewed in Møller et al. 1999; see also Ahtiainen et al. 2004), but despite some intriguing hints at the links between energetics,

immunity and ornamentation (e.g. Møller et al. 1996; but see Adamo 2004), no studies to our knowledge have explored these relationships directly within a single system.

Whole-organism Performance

Links between female choice and male performance capacities have been examined in only a few studies. For example, females show a preference for male ornaments that are correlated with swimming ability in the guppy *Poecilia reticulata* (Nicoletto 1991, 1993; see also Kodric-Brown & Nicoletto 2005), even though the offspring of preferred and nonpreferred males do not differ significantly in performance ability (Nicoletto 1995; but see Evans et al. 2004). In contrast, females do not prefer high-performance males in the lizard *A. carolinensis* (Lailvaux & Irschick 2006). Thus, insufficient data exist on this topic to draw any firm conclusions. However, recent work suggests that males who invest heavily in sexual advertisement may do so at the expense of other fitness components, such as survival (Hunt et al. 2004a, b). Thus, sexual advertisement may come at the cost of important functional traits, including performance. An understanding of the patterns of resource allocation between performance and sexual advertisement is therefore essential in assessing the relationship between male performance and female preferences.

Condition and Condition Dependence

Condition is commonly understood to be a summary of the general health and vigour of an organism, and is narrowly defined as the acquired resources available for allocation to various fitness-enhancing traits (Rowe & Houle 1996, Hunt et al. 2004a; Tomkins et al. 2004). The allocation of resources to a particular trait denies those resources being allocated to another trait in the future; this is the basis for trade-offs between traits. Although this view of condition has proven useful in understanding the expression of organismal traits such as male ornaments (reviewed in: Andersson 1994; Cotton et al. 2004), as well as providing insight into some female mating preferences (e.g. Wagner & Hoback 1999), its relevance for both whole-organism performance and other more direct aspects of physiological state (e.g. fat levels) is unclear. For example, although only males in good physical condition are able to court females in fast water currents in some fish species (Takahashi & Kohda 2004; Kodric-Brown & Nicoletto 2005), the traditional 'black-box' approach gives us little insight into which mechanistic, physiological processes are affected by condition in these cases. Similarly, while the expression of male ornaments is often explained as being condition dependent, it is generally not known whether ornament expression compromises functional traits by limiting resource availability. Indeed, the relationship between performance and condition has, to our knowledge, never been examined experimentally.

The evolution of condition has, like the condition-dependent nature of performance, received little attention

(Tomkins et al. 2004). In red junglefowl, *Gallus gallus spadiceus*, comb size is both heritable and genetically correlated with an index of condition (Parker & Garant 2004). Thus, more than simply underlying signal expression, condition dependence may also be selected for through female choice (Bonduriansky & Rowe 2005; see also Badyaev 2004). Females might therefore select indirectly for males of good physiological 'quality', as predicted by the handicap hypothesis (Zahavi 1975). More directly, Blanckenhorn et al. (2003) showed that lipid and glucose levels (likely components of condition) are positively associated with male mating success in yellow dung flies, *Scatophaga stercoraria*, over several generations (but see Otronen 1995). This work is a rare example of a selection study examining physiological variables (Endler 1986; Kingsolver et al. 2001) and it shows that physiological traits (and, potentially, condition) can respond to selection pressures imposed by females (see also Bonduriansky & Rowe 2005).

DISCUSSION

Synthesis

Functional approaches to sexual selection have produced several noteworthy findings, particularly with respect to male combat. Although endurance rivalry has been recognized as a key component during male competition for females (Andersson 1994), performance traits other than endurance (e.g. sprint speed, bite force) also affect the outcome of male fights. Indeed, the importance of particular performance traits during male combat varies between species and taxonomic groups (see Table 1). Several studies also have demonstrated links between whole-organism performance capacities and the expression of secondary sexual male characters. In at least one case (the dung beetle *E. intermedius*), the same secondary sexual trait signals multiple kinds of performance, each of which influences the outcome of male fights (Lailvaux et al. 2005). If fighting ability indeed consists of a composite of different kinds of performance capacities, then researchers should consider measuring multiple aspects of performance capacity (in addition to male armament expression) when attempting to predict the outcome of male fights. Furthermore, the possibility exists that multiple components of fighting ability may trade off against each other. Although no trade-offs between performance traits were evident in Lailvaux et al.'s (2005) laboratory study, life-history theory predicts that such trade-offs might be expected under resource-limited conditions such as those experienced by animals in nature (Zera & Harshman 2001).

In contrast to male combat, we found little evidence directly linking female choice to male performance capacity. Furthermore, the few studies conducted on this topic were confounded by the lack of information regarding trade-offs between male performance and total fitness. For example, our own review provides evidence that 'high-performance' males are good fighters, but whereas good fighters tend to be preferred by females in some species, in

others they are not (reviewed in Wong & Candolin 2005). Females from several species may even 'eavesdrop' on fights between males, and in some cases, may associate preferentially with winners (e.g. Doutrelant & McGregor 2000; but see Ophir & Galef 2003). Thus, females may sometimes prefer males who are good fighters (and, potentially, good performers), although this phenomenon depends on the species in question (Wong & Candolin 2005). A general implication is that the evolution of sexual dimorphism in performance may be driven largely by male competition (i.e. sexual selection), as well as concomitant selection from other environmental sources (e.g. natural selection).

The energetic costs of male ornament expression are reasonably well studied, but determining the true fitness costs to ornamented males remains a significant challenge (Kotiaho 2001). In this regard, the finding that individuals with expensive ornaments or displays incur fitness costs only under limited resources (e.g. Kotiaho 2000) has some intriguing implications. For example, fitness costs of parasitism or other immune challenges could be similarly evident under ecologically realistic resource-limited conditions, particularly in species where the relations between resource acquisition, ornament expression and survival change across life-history stages. Thus, resource availability may be central to the fitness costs imposed by ornament expression.

Finally, we have highlighted empirical studies that have begun to address the evolution of male ornament condition dependence. In a recent review, Badyaev (2004) established a useful framework for understanding the evolution of sexual ornamentation. Badyaev (2004) notes that secondary sexual traits might be expected to be highly integrated with physiological quality and that trade-offs between secondary sexual trait expression and physiological processes are likely to be important, at least at the initial evolutionary stages of ornament expression. Furthermore, selection for greater condition dependence is probably contingent on 'organism-wide costs of trait elaboration' (Badyaev 2004, page 983). One resulting prediction is that some components of sexual ornamentation may reflect specific organismal processes better than others (Badyaev 2004). We think that this conceptual approach holds promise for understanding the physiological processes underlying condition (see Tomkins et al. 2004 for a related discussion of genetic condition). In addition, studies that examine secondary sexual trait expression or components of fighting ability with physiological processes in mind may prove helpful for understanding the factors driving and constraining the processes of sexual selection.

Future Directions

We suggest several promising avenues for extending the functional approach to sexual selection synthesized here. First, we note the lack of studies using a phylogenetic approach for understanding how function influences sexual selection processes. For example, do species that differ in their degree of territoriality also differ both in performance traits related to fighting ability and in the manner in which they fight? A phylogenetic perspective might similarly reveal the relative importance of female choice and male competition for the evolution of male ornaments and linked functional capacities. Second, manipulative experimental studies would be useful for teasing apart the large number of potential correlated traits that influence male fighting success and female choice. Measures of fighting ability and ornament expression under resource-limited conditions may reveal physiological and performance costs and trade-offs that are not evident under standard laboratory regimes. We found few studies that directly linked common measures of condition to more ecologically relevant measures of performance and physiological state, and thus we lack an understanding of the physiological processes involved in resource allocation. For example, although fat reserves have been used as an index of male condition in several male dominance studies, the energetic contribution of fat reserves to the resolution of male fights is unclear; indeed, male dominance is unrelated to fat reserves in some species (Ekman & Lilliendahl 1993; Gosler 1996; Kemp & Alcock 2003).

Quantitative genetic life-history studies examining trade-offs among ornament expression and whole-organism functional traits that might reflect ornament costs (e.g. metabolic rate, energetic efficiency) represent an exciting area of future research. Such an approach poses difficulties, as genetics studies of physiological trade-offs over an individual's lifetime may be impossible for some species, and even for model systems, the nature of trade-offs among various functional traits may differ between species. However, even a general understanding of the potential costs of ornaments in terms of affected physiological processes would be invaluable. For example, trade-offs between ornament expression and muscle function could affect both male performance and behaviour, resulting in fitness costs that might not be evident under the current view of condition. Thus, a proper physiological understanding of condition may direct us towards 'hidden' costs of male ornament expression, similar to hidden performance costs of reproduction (e.g. Veasey et al. 2001). Although recent studies have examined links between performance and fitness (e.g. Miles 2004; Le Galliard et al. 2004), we are aware of no published studies that have directly examined links among sexual traits, performance and reproductive success. Strong evidence exists for genetic variation of whole-organism performance (van Berkum & Tsuji 1987; Garland et al. 1990a; Le Galliard et al. 2004), suggesting a potential role for indirect benefits in male combat as well as female choice (Moore 1990; but see Zeh 2004). Natural and sexual selection might therefore both act in the same direction (e.g. both act to increase the size of a trait), or, more interestingly, they may oppose one another, particularly if performance is subject to life-history trade-offs against other sexually selected traits. As a final line of future research, one cannot ignore the fact that many physiological and performance traits change seasonally, and thus, the relationships among sexual and functional traits, including performance and physiology, may be dynamic.

Acknowledgments

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