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A performance based approach to distinguish indices from handicaps in sexual selection studies

B. VANHOOYDONCK,*† R. VAN DAMME,* A. HERREL* and
D. J. IRSCHICK‡

*Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium, ‡Department of Biology, University of Massachusetts, Amherst, MA, USA

Summary

1. Central to theories of the evolution of conspicuous secondary sexual traits is that sexual traits honestly reflect at least one aspect of an individual's quality. In general, the reliability of sexual traits can be explained in two ways. Either sexual traits are reliable indicators of individual quality because they are costly and the costs in terms of survival are higher for an individual of low quality as compared to an individual of high quality (i.e. handicap principle) or sexual traits are reliable because of physical constraints and thus cost-free (reliability by design).

2. The distinction between indices and handicaps thus centres on whether the sexual signal under consideration entails costs in terms of survival for its bearer. Although measuring survival directly is still the most accurate way to determine whether this is indeed the case, it is often practically impossible. We propose to introduce performance measurements because one may detect potential costs at the whole-organismal level by quantifying performance traits relevant in terms of survival and reproductive success.

3. We present some examples of sexual signals that can be classified as indices or handicaps by using our performance-based approach. We also discuss some well-cited examples which could fit the model of a handicap and propose that measurements of performance could be a feasible test of this idea.

Key-words: evolution, secondary sexual traits, handicap principle, performance

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The existence of elaborate secondary sexual traits has attracted the attention of biologists as early as the 19th century (Darwin 1871) and well before (review in Bajema 1984). Despite this long standing interest, the mechanisms by which secondary sexual traits evolve and are maintained are still debated. The honesty of sexual signals is a central feature of most theories concerning the evolution of conspicuous secondary sexual traits. Various genetic and game-theoretic models have been proposed to explain the evolution of reliable sexual signals (review in Maynard-Smith & Harper 2003). Most of these models are, at least partly, based on Zahavi's handicap principle (Zahavi 1975; Amotz Zahavi & Avishag Zahavi 1997). The handicap principle posits that sexual signals are reliable indicators of individual quality because they are costly, and because the costs in terms of survivorship are higher for an individual of low quality compared to an individual of high quality. Conspicuous traits may be energetically costly to produce and/or maintain, or they may result

in an increased risk of predation, retaliation or parasitism (Zahavi 1975; Zahavi & Zahavi 1997; Zuk & Kolluru 1998; Maynard-Smith & Harper 2003). Individuals of low quality will be deterred from investing in a sexual signal because the costs, that is, higher mortality, are not balanced by the benefits, that is, increased reproductive success. As evidenced by a large body of theoretical models, the handicap principle has proven to be extremely useful.

However, costs are not a prerequisite for reliable signalling (Hasson 1997; Maynard-Smith & Harper 2003). For example, sexual signals may represent reliable indicators of individual quality because of physical constraints (i.e. reliability by design; Hasson 1997; Taylor, Hasson & Clark 2000). The reliability of this kind of signals, called indices, rests on a direct and incorruptable link with the quality of interest (Hasson 1997; Taylor *et al.* 2000; Maynard-Smith & Harper 2003). In addition, indices differ from handicaps in that they cannot be faked whereas, at least theoretically, handicaps could be (Maynard-Smith & Harper 2003). Also, handicaps are predicted to correlate positively to some components of fitness (i.e. reproductive success),

†Author to whom correspondence should be addressed.
E-mail: bieke.vanhooydonck@ua.ac.be

but negatively influence others (i.e. survival; Maynard-Smith & Harper 2003). Indices, on the contrary, will also correlate positively with some trait that contributes to fitness in contexts other than mating (i.e. survival; Maynard-Smith & Harper 2003). The distinction between indices and handicaps is therefore based on whether survival and reproductive success exhibit a trade-off. We realize the distinction between indices and handicaps, and its usefulness, as proposed by Maynard-Smith & Harper (2003) is controversial among behavioural and evolutionary ecologists (see Searcy & Nowicki 2005). In this paper, we follow Maynard-Smith & Harper's point of view (2003) to lay out our performance approach to the study of sexual signals. However, we do not aim at solving, or taking sides in, the debate. Instead we believe that our performance approach can still be useful to elucidate, explain and understand potential (whole-organismal) costs associated with bearing conspicuous sexual traits in general.

As opposed to the extensive theoretical literature on the importance of the handicap principle to explain the evolution of conspicuous secondary sexual traits, surprisingly little empirical evidence exists on the costs of bearing the sexual trait in terms of survivorship in natural populations. Most studies revert to energetic costs or immunocompetence hypotheses. For instance, comb size in red jungle fowl is regarded a handicap. Females preferentially mate with large-combed males. However, comb size is positively correlated with testosterone levels, which in turn are negatively correlated to the number of circulating lymphocytes. Large combs may thus represent a handicap as the immune system of male jungle fowl with large combs is compromised by the effects of testosterone (Zuk, Johnsen & Maclarty 1995). However, it remains untested to which degree male red jungle fowl survival is actually affected by a decrease in immune function. Analogous reasoning may be applied to the following example of an index. The ventral surface of the abdomen of male jumping spiders (*Plexippus paykulli*) is presented to potential males or rivals. On the ventral surface, the spider's abdomen has a dark central patch surrounded by pale margins. Those margins are larger in well-fed males than in starved males. The patterning of the abdomen in jumping spiders therefore represents a reliable, unfakeable signal of a male's condition as it may indicate heritable foraging ability or health to a female (Taylor *et al.* 2000; Maynard-Smith & Harper 2003). However, it is not clear from the study whether having a fat abdomen entails costs in terms of survivorship. For instance, fat males may be slower and thus worse at escaping predators than slim males. If so, having a fat abdomen would actually be a handicap.

In general, it often remains unclear whether bearing the sexual signal entails costs in terms of survivorship. This is at least partly due to the difficulties of identifying and quantifying these 'true' costs in natural populations. The most accurate way to quantify survival

related costs is to measure survival directly, but this is usually impossible from a practical perspective. By quantifying performance traits relevant in different ecological contexts, however, one may still detect potential 'costs' at the whole-organismal level.

Performance in the strict sense is defined as the ability of an organism to execute ecologically relevant tasks (Huey & Stevenson 1979). Integrating measurements of performance has proven to be crucial to our understanding of trait evolution: only if the variation in trait design translates into variation in performance, which in turn should translate into variation in fitness, can a trait be considered to be adaptive (Arnold 1983). In the past this scheme has readily been applied to studies of natural selection in which performance variation has been linked to variation in survival (Jayne & Bennett 1990; LeGalliard, Clobert & Ferrière 2004; Miles 2004; Husak 2006). More recently, researchers have successfully applied the paradigm to studies of sexual selection whereby the variation in performance has been linked to both the variation in signal design (e.g. Huyghe *et al.* 2005; Lailvaux *et al.* 2005; Vanhooydonck *et al.* 2005a,b; Lappin *et al.* 2006; Meyers *et al.* 2006), and the variation in components of reproductive success, such as attractiveness to females or fighting ability (e.g. Perry *et al.* 2004; Huyghe *et al.* 2005; Husak *et al.* 2006a,b; Lailvaux & Irschick 2006). By introducing performance as an extra link between signal design and fighting ability and/or female preference, these authors have aimed at elucidating the mechanistic basis of this relationship. In addition, inferences between signal design and performance (cf. Vanhooydonck *et al.* 2005a) are an excellent complement to typical male–male combat or female choice studies.

In this paper, we implement Arnold's adaptive scheme (Arnold 1983) and introduce performance tests to be able to distinguish indices from handicaps. For a signal to be defined as a sexual signal, the variation in signal design must be positively correlated to the variation in reproductive success. Therefore, a trade-off between survival and reproductive success can only arise if the sexual signal has a negative effect, directly or indirectly, on survival (Fig. 1). Different pathways leading from sexual signal design to the different fitness components are possible. First, the sexual signal itself or one of its physiological/morphological determinants may have a negative effect on performance traits relevant in terms of survivorship. This in turn will result in a negative relationship between performance traits relevant in different contexts (i.e. survival vs. reproductive success), and thus in a trade-off between survival and reproductive success (Fig. 1). Here, sexual signal design can refer to any structural (e.g. crests, wings, tails) or dynamic (e.g. displays, song, calls) sexual trait. In general, we expect that if the sexual signal is a structure, the effect on performance will be direct (see Fig. 1; full line). On the other hand, if the sexual signal is dynamic, the effect on performance will be typically

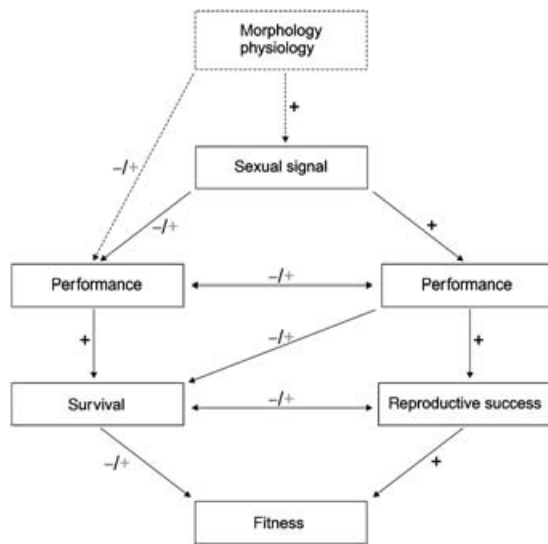


Fig. 1. Schematic representation of how performance measurements may be used to distinguish indices from handicaps. Whether a sexual signal is classified as an index or a handicap depends on whether a trade-off exists between survival and reproductive success. The variation in sexual signal design is per definition positively correlated to the variation in reproductive success, and its performance correlates (represented by the black + signs). Hence a trade-off between reproductive success and survival will arise if the variation in sexual signal itself (full line) or its morphological/physiological determinants (dotted line) negatively influence the variation in performance traits relevant in terms of survivorship. This in turn will result in a negative correlation between performance traits relevant in different contexts, and thus in a trade-off between survival and reproductive success (represented by the red – signs). If the variation in sexual signal or its morphological or physiological determinants are positively correlated to the variation in survival related performance traits, the sexual signal is an index (represented by the green + signs). Also, the same performance trait may simultaneously influence both survival and reproductive success.

via a common underlying morphological/physiological design characteristic (see Fig. 1; dotted line). For instance, in passerine birds manoeuvrability and flight endurance are important components of song flight. Both manoeuvrability and flight endurance are positively correlated to wing area, among other morphological traits (Hedenström & Møller 1992). Migrant passerines, however, benefit from having narrow wings since wing area is negatively correlated with long distance, soaring flight (Hedenström 1993; Mönkkönen 1995). Song flight in migrant passerines may thus be considered a handicap. As is evident from the example, essential to elucidating the trade-off between survival and reproductive success is our understanding of the (bio)mechanical basis of the sexual signal and of the different performance traits under consideration.

Second, at least theoretically, a trade-off between survival and reproductive success may also arise, if the variation in a reproductive success related performance trait negatively influences the variation in survival

directly (Fig. 1). We will not consider this possibility further though since we do not know of any empirical data to support this idea. The opposite, that is, the same performance trait correlates positively with both reproductive success and survival, seems more likely (Fig. 1). In that case, the sexual signal can be considered an index. Moreover, its evolution will be enhanced since both sexual and natural selection act in the same direction.

Also, performance measures offer the possibility of testing whether traits previously classified as handicaps are correctly classified. We note several well-cited examples which could fit the model of a handicap. We propose that tests of performance could be a feasible test of this idea, and may well refute it. For instance, the stripes of zebras or white patches on the rumps of waterbucks are typically viewed as a handicap (Zahavi & Zahavi 1997). On healthy animals, the white rump looks round from behind, whereas it has the shape of a pointed ellipse in thin individuals because of the atrophied hind limb muscles. According to Zahavi & Zahavi (1997) the shape of the rump may be an important signal used in predator–prey encounters, but also in male–male combat and female choice. However, since the hind limb muscles could be expected to be an important determinant of running performance and may thus be causally related to escape ability, the white rump in waterbucks may be an index (Taylor *et al.* 2000; Maynard-Smith & Harper 2003). Following an analogous reasoning, stotting in gazelles is an index and not a handicap (see Maynard-Smith & Harper 2003). Similarly, male baboon calls are assumed to honestly reflect male quality as some evidence suggests that calling is energetically expensive. If calling is indeed expensive, it could be regarded a handicap (Fischer *et al.* 2004). Alternatively, calling may not be energetically costly (Horn, Leonard & Weary 1995; Dearborn, Anders & Williams 2005), and may be reliable because it is an index of performance as the acoustic features of loud calls correlate to stamina in male baboons (Fischer *et al.* 2004). Therefore, calling may be an index of physical condition that cannot be faked. Similarly, female gobies prefer males that can display in fast water currents (Takahashi & Kohda 2004). Again, the authors claim the courtship behaviour is an honest signal because it is energetically costly (i.e. handicap hypothesis). Alternatively, display behaviour may be reliable because only males in good physical condition are able to swim in fast currents and swimming ability cannot be faked as it is functionally and causally related to morphological and physiological characteristics (review in Domenici 2003). In all these cases, measurements of locomotor performance, and the morphological and physiological determinants thereof, might prove very useful in distinguishing indices from handicaps.

Below we discuss some examples of conspicuous sexual traits in greater detail. More specifically we show how performance traits can be used to classify these traits as an index or as a handicap.

Indices

Horn size in male horned dung beetles (*Euoniticellus intermedius*) is a sexually selected trait. Males guard and mate with females inside tunnels dug by the latter and will fight, using their horns, with other males within the tunnels for access to females. Horn size appears to be the most important predictor of contest outcome as the male that is able to resist the greatest force prevents himself from being pushed out of the tunnel (Lailvaux *et al.* 2005; Pomfret & Knell 2006a). Moreover, horn size appears to be positively correlated to both pulling force (i.e. the force required to push a beetle out of a tunnel) and maximal exertion (Lailvaux *et al.* 2005). Also, measuring the immune response in dung beetles during maturation does not show an obvious trade-off between horn size and immunity (Pomfret & Knell 2006b). Since, no costs seem to be associated with bearing a long horn, at least with respect to the traits measured so far, horn size may in fact represent an index.

Anolis lizards are characterized by the possession of a conspicuous secondary sexual trait, called a dewlap. Dewlap extensions are an important component of anoline display behaviour in various contexts. In aggressive male–male interactions the dewlap is believed to represent a ‘threat’ or ‘challenge’ to potential intruders (Greenberg & Noble 1944; Jenssen, Orrell & Lovern 2000; Perry *et al.* 2004). Dewlap size has also been shown to be an honest indicator of at least one component of fighting ability, that is, bite strength in territorial *Anolis* lizards (Vanhooydonck *et al.* 2005a,b), although its role in resolving male conflicts in anoles remains equivocal (Tokarz, Paterson & McManh 2003). Moreover, females appear to choose males based on dewlap characteristics and appear more receptive towards males that are performing dewlap extensions (Greenberg & Noble 1944; Crews 1975). Lastly, the dewlap functions as a pursuit-deterrent signal in a predator–prey context (Leal & Rodríguez-Robles 1997a,b; Leal 1999).

Surprisingly little empirical data are available on potential evolutionary mechanisms influencing dewlap size in *Anolis* lizards. Echelle, Echelle & Fitch (1978) posited that both at the intra- and interspecific level anoline dewlap size represents an ‘optimum’ at which a compromise is reached between conflicting selective pressures. Previous studies have shown that in some organisms conspicuous sexually selected traits, such as bright colouration or acoustic displays, are costly in terms of viability (Rosenthal *et al.* 2001; Godin & McDonough 2003; Bernal, Rand & Ryan 2006; Husak *et al.* 2006c). Similarly, relatively large dewlaps might be selected against because of their increased conspicuousness towards predators. In addition, large dewlaps may hamper locomotor performance as an extended dewlap may interfere with the front limbs while moving around on or between branches. If this hypothesis is correct, dewlap size could be

regarded a handicap. However, correlating dewlap size with body size, bite and jumping performance in a population of *Anolis carolinensis* does not point in that direction (Vanhooydonck *et al.* 2005b). In this case, bite force represents a performance trait mostly relevant in a sexual context, whereas locomotor performance is expected to be of prime importance while foraging and escaping predators (see Vanhooydonck *et al.* 2005b). In addition, the role of body size is specifically considered in mediating the relationship between dewlap size and performance as body size is one of the most important factors determining fighting ability (see Maynard-Smith & Harper 2003) and female preference (see Rosenthal & Evans 1998).

In small mature males, dewlap size appears to be an indicator of body size, bite strength and jumping performance. Thus, dewlap size in male *A. carolinensis* does not seem to incur a locomotor cost, and should not be regarded a handicap, at least not with respect to the traits under consideration here. The fact that *Anolis* typically extend their dewlaps while sitting stationary (Greenberg & Noble 1944), whereas the dewlap is folded back during movements (personal observation), might explain why large dewlaps do not seem to impair locomotor performance. Whether individuals with larger dewlaps are more conspicuous to predators remains to be tested. We note, however, that there is some evidence of directional selection on dewlap size in the largest mature males (Vanhooydonck *et al.* 2005b).

Although dewlap size in *A. carolinensis* fits the performance-based description of an index (sensu Maynard-Smith & Harper 2003), it does not meet the ‘reliability by design’ criterion as it is not physically, functionally or mechanistically constrained in a strict sense (sensu Hasson 1997). Examples exist, however, in which the relationship between sexual trait design and performance is a functional one. For instance, adult male collared lizards (*Crotaphytus collaris*) perform gaping displays during agonistic encounters with rivals. During these displays the jaw adductor muscle complex, which is an important determinant of bite force, is clearly visible (Lappin *et al.* 2006). As has been documented in other lizard species (Gvozdik & Van Damme 2003; Lailvaux *et al.* 2004; Perry *et al.* 2004; Huyghe *et al.* 2005), bite strength in *Crotaphytus* lizards predicts the outcome in staged contests and reproductive success (Lappin & Husak 2005; Husak *et al.* 2006a,b). Thus, mouth-gaping in collared lizards may serve as an index. Similarly, in veiled chameleons (*Chamaeleo calypttratus*) preliminary data on crest height, a sexually selected trait, and bite force in six individuals, show the two variables are positively correlated ($r = 0.97$; $P = 0.002$). Since the jaw muscles responsible for generating bite force attach along the entire crest (Rieppel 1981; Rieppel & Crumley 1997), a higher crest will lead to a greater bite force, thus suggesting that crest height in *C. calypttratus* represents an index. However, both for the collared lizard as the

chameleon example, we need data on other performance traits, such as locomotor tasks, to rigorously test whether the sexual traits under consideration influence these traits, and ultimately survival, in one way or the other and complies with the performance-based description of an index (*sensu* Maynard-Smith & Harper 2003).

Handicaps

Darwin's finches, and songbirds in general, make use of acoustic signals in contexts of male–male competition and female choice. Sound production depends on the configuration of the vocal tract, which consists of the trachea, larynx and beak. Vocal performance capacity, or the ability to produce rapid, broad-band trills, seems an important criterion for female songbirds in mate selection, probably because vocal performance is an indicator of male quality as it may be related to physical condition or developmental history (Nowicki, Peters & Podos 1998; Buchanan 2000; Draganoiu, Nagle & Kreutzer 2002; Ballentine, Nowicki & Hyman 2004; Ballentine 2006). Among individuals, vocal performance varies as a function of vocal tract morphology, and particularly bill morphology (Podos 1997, 2001; Ballentine 2006).

In addition, the bill in most birds shows important morphological adaptations to feeding ecology (Ballentine 2006). Extensive research on the Darwin's finches of the Galápagos islands has shown that feeding ecology is the primary selective force that has resulted in the remarkable morphological diversification of songbirds (Schluter, Price & Grant 1985; Grant 1999; P.R. Grant & B.R. Grant 2002). By quantifying seed hardness and bill morphology in the medium ground finch (*Geospiza fortis*), researchers found that individuals with deeper bills ate harder seeds and were better able to survive severe droughts as during these extremely dry periods hard seeds are the only food items available to ground finches (Bowman 1961; Abbott, Abbott & Grant 1977; Boag & Grant 1981; Grant 1981; Price 1987). Bill depth therefore appears to be under strong natural selection (Price *et al.* 1984; Grant & Grant 1995).

Recent studies in which vocal performance and its morphological correlates were quantified in a population of *G. fortis* showed that vocal deviation, a composite performance measure of the temporal and frequency structure of song, is positively correlated to beak depth (Podos 2001; Huber & Podos 2006). Since a high vocal deviation is indicative of poor vocal performance, birds with tall beaks appear to be poor singers. In the same population, however, beak depth is positively correlated to bite strength (Herrel *et al.* 2005). Thus, individuals with deeper beaks can bite harder and will therefore be able to crack harder seeds. Since the relationship between beak depth and vocal performance is opposite to the one between beak depth and bite force, vocal performance and bite force

should trade-off in *G. fortis*. Song in the medium ground finch can therefore be regarded a handicap, as being a better vocal performer comes at the cost of being worse at cracking hard seeds. In this case, the trade-off between a performance trait presumed to be relevant in terms of survivorship (i.e. bite force) and vocal performance, a function relevant in terms of reproductive success results from a conflicting underlying morphological requirement (i.e. tall vs. shallow beak). We note, however, that on rare occasions, having small beaks may be advantageous in a feeding context as well. Recently, Grant & Grant (2006) showed that when *G. fortis* competes intensely over seeds with the large ground finch (*G. magnirostris*), the smaller-beaked *G. fortis* individuals are at a survival advantage.

As is the case with indices, handicaps will be most easily discerned when the sexual signal, or one of its morphological or physiological determinants (*cfr.* the beak in Darwin's finches), is functionally and causally related to a component of fitness. For instance, quantification of bite force and locomotor performance in male *Gallotia galloti* lizards suggests that head size is a handicap. Head size in these lizards is an important determinant of fighting ability (Molina-Borja, Padron-Fumero & Alfonso-Martin 1998) as male *G. galloti* with large heads bite harder and win more fights in staged encounters (Huyghe *et al.* 2005). However, head size has a negative effect on locomotor performance (i.e. endurance and acceleration capacity; data taken from Huyghe *et al.* 2005). Although no empirical data exist on whether a decrement in locomotor performance actually translates into higher mortality in *G. galloti*, locomotor performance has been shown to be relevant when feeding and/or escaping predators in other lizard species (Irschick & Losos 1998, 1999; LeGalliard *et al.* 2004; Miles 2004; Husak 2006). Therefore, large-headed males bite harder and are dominant over small-headed males but they suffer from diminished locomotor skills that may impair their ability to effectively escape predators. Preliminary data on a limbless burrowing skink, *Acontias perzevali*, reveal a similar pattern: whereas head size, a sexually selected trait, correlates positively to bite force, it has a negative effect on burrowing speed (unpublished data). In an analogous fashion, one of the classic examples of the handicap principle, that is, the tail of swallows, can be explained. In male barn swallows the extremely elongated tail streamers appear to be costly in terms of foraging efficiency and flight performance (review in Møller 1994; Møller *et al.* 1998; but see Norberg 1994; Hedenström 1995). Consequently, tail elongation has been shown to negatively influence male viability (Møller 1991; Møller & de Lope 1994; Saino, Bolzern & Møller 1997).

Limitations

In this study, we posit that a performance based approach can be used to distinguish indices from

handicaps. We do recognize, however, that our approach has some drawbacks. Whereas a trade-off among various performance traits relevant in different ecological contexts supports the notion of a handicap, finding a positive or no correlation among different performance traits does not necessarily prove the sexual signal under consideration is indeed an index. In the latter case, the potential negative influence of some unexamined function on survival and reproductive success and its potential negative relationship with the sexual trait remains untested. For instance, traditional performance measures, such as bite force or locomotor performance may correlate positively with the sexual signal, whereas the relationship with other physiologically based traits such as immune functions or hormone concentrations may not (e.g. Zuk *et al.* 1995; Skarstein & Folstad 1996; Møller *et al.* 2000; Ahtiainen *et al.* 2005; Kristiansen *et al.* 2006). Since in most cases it is impossible to study all these traits in concert, handicaps may go unnoticed. Only if immune functions and/or hormone concentration are also directly linked to the above mentioned 'traditional' performance measures, their effect will become evident using our approach. For instance, in some lizard species higher testosterone concentrations are correlated to increased locomotor performance (John-Alder *et al.* 1996; Klukowski, Jenkinson & Nelson 1998; Sinervo *et al.* 2000). However, a negative or no relationship between hormone levels and performance has also been found (Meylan & Clobert 2004; Husak *et al.* 2006a). Similarly, in birds, song performance may or may not correlate to circulating hormone levels and parasite load (Garamszegi 2005). It is clear that an integrative approach in which morphological, physiological, performance and sexual traits are studied in concert will be essential to our understanding of the evolution of conspicuous sexual traits (cfr. Husak *et al.* 2006a).

Also, as mentioned above, our performance approach will be most useful when the sexual signal, or one of its morphological or physiological determinants, is functionally and causally related to a component of fitness. We realize our approach will be limited to a purely correlational analysis in studies of the evolution of so-called badges of status, such as bright colouration (review in Whiting, Nagy & Bateman 2003). In addition, for our performance approach to the indices–handicaps distinction to work, it is necessary to have *a-priori* knowledge on which performance traits are in fact ecologically relevant for the organisms under study. For instance, we need to know which performance traits are relevant in different ecological contexts and how they relate to survival and reproductive success. Moreover, these relationships may well differ among species and study systems. Yet, we believe that performance measurements may allow one to detect potential costs at the whole-organismal level by specifically quantifying those performance traits relevant in terms of survival and reproductive success.

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