

Sexual selection on locomotor performance

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ABSTRACT

Questions: Does sexual selection operate on locomotor performance? Which taxa are likely to have locomotor performance influenced by sexual selection?

Methods: We reviewed recent literature.

Conclusions: Theory and empirical evidence support the hypothesis that sexual selection operates on locomotor performance, but tests of alternative hypotheses are rare. We provide a general framework for developing testable hypotheses. Many animal taxa show potential for sexual selection as a strong force acting on locomotor performance. These include species with male aerial display or territory defence, such as numerous bird species, gliding lizards, and flying insects, but also terrestrial ones, among which lizards have been studied the most. Locomotor performance may be an important component of female choice via its direct or indirect benefits to females.

Keywords: endurance, locomotion, performance, sexual selection, sprint speed.

INTRODUCTION

Casual observation suggests that many animals use fast speeds while undertaking a variety of important tasks during their daily lives, such as escaping predators, capturing prey items, and interacting with conspecifics. Although there are many other activities that involve locomotion, these three categories are presumed to be most relevant to fitness. The intuitive importance of traits such as locomotion to fitness has led physiologists, evolutionary biologists, and ecologists to focus research efforts on ‘whole-organism performance’ traits as potential targets of selection (Bartholomew, 1958; Bock and von Wahlert, 1965; Huey and Stevenson, 1979; Arnold, 1983; Bennett and Huey, 1990). A seminal paper by Arnold (1983) provided a methodological and statistical framework with which to study the adaptiveness of morphological and physiological traits by studying selection on performance (i.e. the morphology–performance–fitness paradigm). ‘Whole-organism performance’ is typically defined as the laboratory-measured maximal ability of an animal to perform an ecologically relevant task (reviewed in Irschick and Garland, 2001; Lailvaux and Irschick, 2006a). ‘Ecological performance’ is a measure

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of the ability of an animal to perform an ecologically relevant task in nature (Irschick, 2003; Husak, 2006a). Both of these can be distinguished from the more inclusive term ‘behaviour’. ‘Behaviour’ describes what an animal does, but not necessarily *how well* it does it (for examples, see Garland and Losos, 1994; Husak, 2006a). Studies designed to examine selection on phenotypic traits should consider these distinctions and which of the three may be the target(s) of selection. In our discussion of sexual selection on locomotion we include traits that represent a quantitative measure of a means by which individuals move through their environment. Examples include, but are not limited to, sprint speed, swimming speed, flying speed, endurance capacity (‘stamina’), agility, and manoeuvrability.

In recent years, several studies have attempted to link superior maximal locomotor performance with heightened survival (e.g. Jayne and Bennett, 1990; Miles *et al.*, 2001; Le Galliard *et al.*, 2004; Miles, 2004; Husak, 2006a, 2006b; Irschick *et al.*, 2008), but far fewer studies have attempted to directly link high performance with increased mating success. Sexual selection has been proposed to be important to the evolution of maximal aerobic capacity and locomotor endurance via territory defence and courtship behaviour (e.g. Bennett and Ruben, 1979; Bennett, 1991; Garland, 1993; Chappell *et al.*, 1997; Hammond *et al.*, 2000; Robson and Miles, 2000; Sinervo *et al.*, 2000; Miles *et al.*, 2001; López and Martin 2002; Brandt, 2003). Similar arguments could apply to other locomotor performance traits for species that utilize locomotor performance as part of a display repertoire or in territory acquisition and/or maintenance.

Since Arnold’s (1983) paper, research linking performance to some aspect of fitness has resulted in several reviews, each discussing a different component of the morphology–performance–fitness paradigm. Few, however, explicitly provide an outline for testing adaptive hypotheses concerning sexual selection on locomotor performance (Lailvaux and Irschick, 2006a; Irschick *et al.*, 2007; Miles *et al.*, 2007). Our objectives in this review are to (1) highlight studies that have attempted to link locomotor performance with mating success, (2) provide a framework for future tests of the hypothesis that sexual selection operates directly on locomotor performance, and (3) make recommendations for future research. We have not reviewed every relevant paper, and we have likely overlooked some important ones. Our goal was to provide a synthetic look at the hypothesis that sexual selection can operate directly on locomotor performance. We selectively reviewed the literature to provide useful examples for our points, trying to be as taxonomically diverse as possible.

THE ADVANTAGE OF BETTER LOCOMOTION

The potential advantages of being a better locomotor performer can fall into two categories that have historically been used to distinguish mechanisms of sexual selection: intra-sexual selection (male competition) and inter-sexual selection (female choice). We treat each of these in turn below. The exact nature of the mating advantage is likely to be taxon-specific, but this is implicit in the nature of the morphology–performance–fitness paradigm. There is no ‘ideal performance trait’ that will be relevant to the fitness of individuals in all species. Thus, choosing appropriate and relevant performance traits is critical and requires knowledge of the natural history of the study species (Garland and Losos, 1994; Irschick and Garland, 2001; Irschick, 2003). We first develop a framework for testing sexual selection hypotheses, and then review our work using this framework. We then give examples of other taxa in which sexual selection may operate on locomotor performance.

TESTING HYPOTHESES

Often sexual selection operates in opposition to natural selection (Andersson, 1994), frequently making it easier to develop mutually exclusive predictions about the phenotypic effects of natural versus sexual selection (e.g. Ryan *et al.*, 1982; Endler, 1983). However, both natural and sexual selection may favour better locomotor performers (Arnold, 1983; Pough, 1989; Irschick and Garland, 2001; Irschick *et al.*, 2007). Thus, it is important to simultaneously test for the effects of both to fully understand the relative strength of each and their corresponding effects on the phenotype. Our suggested framework provides ways to distinguish between the effects of natural and sexual selection on the evolution of performance.

Sexual selection may operate directly on locomotor performance in cases where the performance trait provides a direct advantage in mating success through male competition or female choice (see above; Fig. 1). Evidence for this hypothesis comes partially from the finding that variation in locomotor performance predicts significant variation in genetic reproductive success (or some suitable proxy). However, multiple alternative hypotheses could explain this relationship (Fig. 1). Thus, the mechanism by which the performance trait

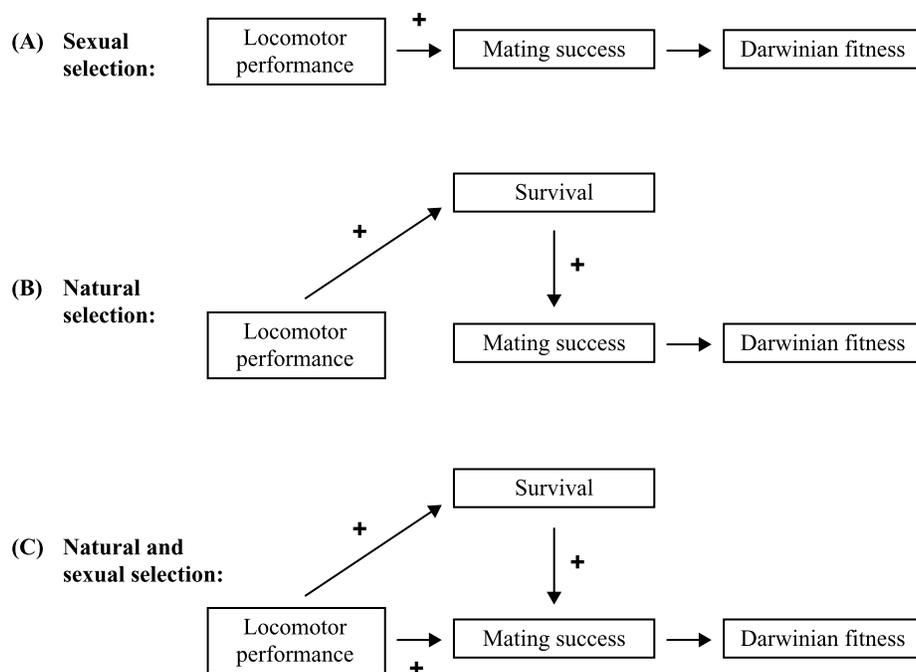


Fig. 1. Schematic representation of alternative hypotheses that might explain a positive relationship between locomotor performance and reproductive success. Panel (A) represents the situation where the locomotor performance trait directly influences mating success via male competition or female choice. Panel (B) represents the situation where better locomotor performers survive better than poor performers and, hence, have higher reproductive success. Here, locomotor performance is not involved in male competition or female choice and is thus under the influence of natural selection, not sexual selection. Panel (C) represents the situation where locomotor performance contributes to both survival and mating success directly. Here, locomotor performance is favoured by both evolutionary forces.

is used to enhance mating success and the physiological basis for variation in the performance trait must be considered before it is concluded that sexual selection operates on locomotor performance.

The first step in taking a performance-based approach to sexual selection is to determine which performance traits are important to the inter-dependent fitness components of survival and reproductive success (Irschick and Garland, 2001; Husak and Fox, 2006). Intuition based on observation and natural history data provides a good start, but quantitative data (i.e. 'ecological performance') on the importance of potential performance traits are important for testing hypotheses about the nature and strength of selection (Husak and Fox, 2006). Knowing if, when, and how much individuals in a population use a locomotor performance trait allows hypotheses to be generated *a priori* about whether natural or sexual selection operate on that trait. For example, if a species uses only 25% of its maximal sprint speed ability while escaping predators, 95% while chasing prey, and 10% while chasing male rivals, then fast speeds likely provide a survival advantage and not an advantage in mating success *per se* (see Irschick and Garland, 2001; Husak and Fox, 2006). Finite resources can then be better devoted to testing a natural selection hypothesis (i.e. a survival advantage to faster individuals), rather than a sexual selection hypothesis (i.e. an advantage in mating success to faster individuals). Alternatively, a species may use 95% of its maximal flight speed ability while chasing rivals, but only 10% and 25% for catching prey and escaping predators, respectively. Here, sexual selection may be an important force shaping flight speed and can help elucidate how fast speeds may increase mating success (Fig. 2). Or the performance trait could be endurance capacity and not speed. If endurance capacity is more important for males seeking out females (compared with males finding food or escaping predators), then sexual selection may shape that locomotor trait (Fig. 2).

Locomotor performance may relate to reproductive success simply because better performers survive better to reproduce more: the classic case of natural selection (Fig. 1). For example, Miles *et al.* (2001) proposed that natural selection, not sexual selection, favoured male Galapagos lava lizards with greater locomotor endurance because of predation risk associated with conspicuous male coloration and behaviour. Hence, investigators should determine the relative importance of locomotor performance traits to survival probability in both sexes and over ontogeny [at least in discrete age classes (Husak, 2006b)]. If survival is

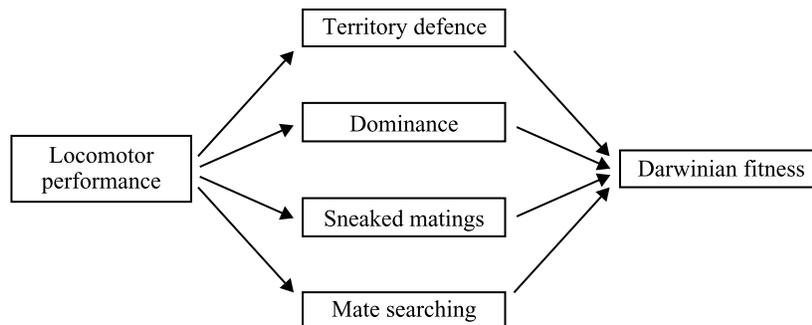


Fig. 2. Schematic representation of alternative hypotheses to explain how locomotor performance can give males an advantage in male competition for access to females. One or all of these pathways is possible. Examinations of parentage patterns in the population and individual behaviour in nature can help make mutually exclusive predictions for these hypotheses.

enhanced by better locomotor performance in breeding males, then statistical analyses (such as path analysis) should be employed that include survival as an additional link between performance and fitness, which may significantly explain variation in reproductive success (Fig. 1). ‘Ecological performance’ data will help to clarify the mechanism by which better locomotor performance provides a survival advantage. If better locomotor performers do not have enhanced survival but do have more offspring than slower individuals, then further data are needed to determine why this is so (Fig. 2).

Selection on traits that are physiologically or genetically linked to locomotor performance may obfuscate results from sexual selection studies (see Oufiero and Garland, 2007). For example, the effects of testosterone on vertebrate male morphology, behaviour, and signal production are well documented (reviewed in Husak *et al.*, 2007; Miles *et al.*, 2007), and many of those secondary sexual characteristics may be subjected to sexual selection. As a hypothetical example, bite-force capacity – an important determinant of dominance in lizards (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006b) – may be signalled to rivals by display behaviour, both of which may be mediated by testosterone concentrations (see Husak *et al.*, 2007; Vanhooydonck *et al.*, 2007) (Fig. 3). If locomotor performance is also mediated by testosterone concentrations, then a correlation between locomotor ability and mating success may be erroneously interpreted as evidence for sexual selection operating on locomotion (Fig. 3). Thus, in this hypothetical example the direct targets of sexual selection are bite-force performance and display behaviour, not locomotor performance. The broad phenotypic effects of testosterone make this a very possible scenario of which investigators should be mindful when designing studies in vertebrate taxa. The general effects of hormones on locomotor performance are not consistent across vertebrate taxa (reviewed in Miles *et al.*, 2007), suggesting that hormone mediation of performance traits may be evolutionarily labile (see Hau, 2007). It is also possible that hormones influence multiple performance traits, including locomotor performance traits, such that a suite of interrelated traits increases mating success. In this case, path models and tests for correlational selection (Sinervo and Calsbeek, 2003) should be used to determine the relative contribution of each to fitness. Again, understanding how performance traits are used in nature will shed light on the relevance of those traits to fitness and whether they are simply the product of correlational selection.

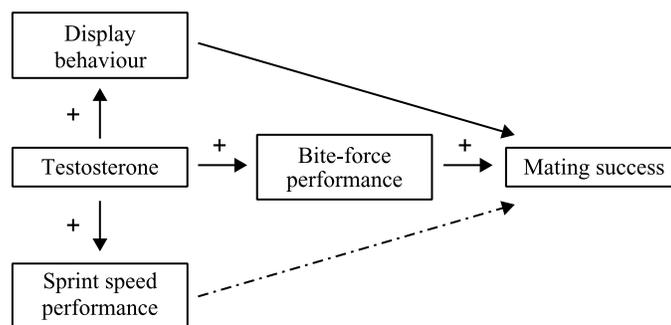


Fig. 3. Schematic representation of how a spurious correlation (indicated by the dashed line) can be revealed between locomotor performance and mating success. Here, sprint speed is correlated with testosterone concentrations, the latter of which also mediates display behaviour and bite-force performance, which are the actual targets of sexual selection.

Because there can be complex interactions among traits due to pleiotropic effects (e.g. the testosterone example above) or correlational selection on suites of traits (Jang and Greenfield, 1998; Blows *et al.*, 2003; Sinervo and Calsbeek, 2003; Brooks *et al.*, 2005), studies that seek to determine which phenotypic traits influence fitness should take a multivariate approach, testing for non-linear selection (see also Irschick *et al.*, 2008) and correlational selection. These issues have recently been reviewed elsewhere (Blows and Brooks, 2003; Blows *et al.*, 2003), but we feel that they will contribute substantially to our understanding of how sexual selection might operate on locomotor performance (e.g. Sinervo and Calsbeek, 2003), especially where trade-offs exist among sexually selected traits and/or there are alternative adaptive peaks in the fitness landscape. On the flip side, the phenotypic effects on other traits that result from sexual selection on locomotion (due to pleiotropic effects or trade-offs) should also be considered in future investigations using multivariate methods (Phillips and Arnold, 1989).

To summarize, we believe that future research should address the following questions to determine whether sexual selection acts directly on locomotor performance: (1) What locomotor traits are used during male competition or in female choice? (2) Are the locomotor traits used in those contexts used at a near-maximal level? (3) Are those traits used in any other context, such as predator escape or prey capture? (4) Do those traits predict survival? (5) Do those traits predict mating success? (6) Are the locomotor performance traits correlated physiologically or genetically to another trait that may be under sexual selection? (7) What are the relative impacts of natural selection, relevant locomotor performance traits, and correlated traits on reproductive success? (8) Is selection linear or non-linear, and is there correlational selection on other traits?

As an example of our approach, we review our work on collared lizards (*Crotaphytus collaris*). We investigated the role of sexual selection on the evolution of maximal sprint speed capacity. Adult male collared lizards, but not females or younger males, use more than 90% on average of their maximal sprint speed capacities when responding to unfamiliar males in their territories (Husak and Fox, 2006). Faster territorial males have larger territories and overlap more females (Peterson and Husak, 2006), resulting in the siring of more offspring by faster males (Husak *et al.*, 2006a). Sprint speed did not correlate with circulating testosterone or corticosterone concentrations, ruling out the hypothesis that sexual selection is targeting some other hormone-mediated trait and seemingly favouring high sprint speed capacity (Husak *et al.*, 2006a). Furthermore, among adult collared lizards, high sprint speed does not increase the probability of survival (Husak, 2006a, 2006b), ruling out the alternative hypothesis that faster males sire more offspring simply because they survive better than slower rivals. To determine *how* being faster helps males sire more offspring, Husak *et al.* (in press) examined patterns of maternity and paternity within the population to show that the females that faster males defended had lower proportions of offspring sired by other males (i.e. 'extra-pair fertilizations'). However, faster males did not have higher proportions of offspring sired by females that they did not overlap, meaning that high speeds did not give fast males an advantage at sneaking copulations from females they did not defend. These studies, taken together, show the utility and power of testing alternative hypotheses simultaneously to understand how selection operates on performance.

LOCOMOTION AND MALE COMPETITION

The potential importance of locomotor performance during male interactions was first revealed by the finding of a link between locomotor performance and social dominance

in staged laboratory encounters. In several lizard species, males with better maximal locomotor performance won more dyadic encounters on average (Garland *et al.*, 1990; Robson and Miles, 2000; Perry *et al.*, 2004), but not always (López and Martín, 2002; Huyghe *et al.*, 2005). The finding that locomotor performance predicted dominance suggested that maximal locomotor abilities could be subject to sexual selection, but these studies raised numerous new questions and alternative explanations. First, extrapolation from staged laboratory contests to natural social organizations is unclear. Second, winning may not be associated with better locomotor performance *per se*, but instead with some other trait that is correlated with locomotor performance, such as androgen hormone concentrations, display behaviour, or other performance trait (reviewed in Husak *et al.*, 2006a; Miles *et al.*, 2007) (see also below). Third, if better locomotor ability was directly responsible for winning contests, it remained ambiguous *how* being a better locomotor performer translated to contest success (Lailvaux and Irschick, 2006a).

Locomotor endurance in particular is associated with success in male competition (reviewed in Lailvaux and Irschick, 2006a). The dominant orange morph of male side-blotched lizards (*Uta stansburiana*) have higher endurance capacity than yellow and blue morphs, though the yellow ‘sneakers’ and blue ‘mate-guarding’ morphs do not differ in endurance (Sinervo *et al.*, 2000). The latter observation is interesting, as the two adopt very different behavioural strategies to attain a fitness advantage over the others (female mimicry and cuckoldry in the former and mate guarding in the latter). It would be instructive to know what, if any, locomotor traits are important to these two morphs for mating success. Territorial male Pecos pupfish (*Cyprinodon pecosensis*) have higher endurance capacity than non-territorial males (Kodric-Brown and Nicoletto, 1993), suggesting that better locomotor performers may have a mating success advantage.

Scramble competition for mates is a widespread mating strategy in the animal kingdom (Ghiselin, 1974; Andersson, 1994). In this mating strategy, greater endurance capacity is likely favoured in searching males. Among invertebrates, examples are known in tarantulas (Shillington and Peterson, 2002), butterflies (Wickman, 1992; but see Kemp *et al.*, 2006), spiders (Moya-Laraño *et al.*, 2002, 2007a; Brandt and Andrade, 2007a), and beetles (Moya-Laraño *et al.*, 2007b). Among vertebrates, examples are known in mammals (Stockley *et al.*, 1996), snakes (Duvall and Beaupre, 1998; Shine *et al.*, 2005), and horned lizards (Zamudio, 1998; Stark *et al.*, 2005). Selection on endurance capacity may be more intense where the density of searching males is lower and females are widely dispersed (Shine *et al.*, 2005). During scramble competition, average searching speed or endurance (i.e. stamina; all largely aerobic processes) is likely more important than maximal sprinting speed (a largely anaerobic process) for finding the most mates (Moya-Laraño *et al.*, 2007b). These examples highlight the importance of determining which type of locomotor performance is likely used to increase mating success.

Most research linking locomotor performance and potential mating success has focused on terrestrial species and a few aquatic species (see above). However, there are suggestions that better aerial locomotor performers may attain higher mating success via superiority in male contests or territorial defence. For example, more agile midges (*Chironomus plumosus*) were more successful at mating with females in mating swarms because they were better able to manoeuvre around rival males to reach the females (Crompton *et al.*, 2003). Male gliding lizards (genus *Draco*) are highly territorial and chase each other through the air to evict rivals from territories (Mori and Hikida, 1992, 1993, 1994; Shine *et al.*, 1998). Males that are more ‘agile’ gliders, or have better manoeuvrability, presumably have an advantage over poorer gliders in territorial disputes (see Shine *et al.*, 1998, and references therein). Similar hypotheses have been

proposed for raptorial birds (Blomqvist *et al.*, 1997; but see Kruger, 2005). Indeed, the predominance of female-biased sexual size dimorphism in these groups is what led to the hypothesis that more ‘agile’ or ‘manoeuvrable’ males should be better defenders of territories and females (see also Swaddle *et al.*, 2000). Biomechanical considerations reveal that smaller size may make a male more manoeuvrable or agile (Norberg, 1990), thus gaining an advantage over rivals in a complex three-dimensional environment. Similar to aerial species, better locomotor ability has been proposed to explain small male size in spiders that must climb while searching for mates (Moya-Laraño *et al.*, 2002, 2007a; but see Brandt and Andrade, 2007a, 2007b). Here, small male size is advantageous when facing the challenges imposed by moving against gravity in search of mates.

LOCOMOTION AND FEMALE CHOICE

Mate choice and mating biases, usually females choosing among males, can impose strong sexual selection pressures on the sex being chosen, and can lead to the evolution of extraordinary ornaments and display behaviour (Darwin, 1871; Andersson, 1994). Indeed, such ornaments may impose costs to the bearers (Andersson, 1994; Kotiaho, 2001), including decreased locomotor capacity (reviewed in Oufiero and Garland, 2007; Vanhooydonck *et al.*, 2007). Nonetheless, females may benefit from mate choice by direct benefits via resources acquired from the chosen mate(s) or indirect benefits through offspring viability via ‘good genes’ or ‘sexy sons’ (Kirkpatrick and Ryan, 1991; Andersson, 1994; Kokko, 1998; Kokko *et al.*, 2003; Kotiaho and Puurtinen, 2007).

From a performance perspective, the indirect benefits of ‘good genes’ inherited from superior fathers would be better performance in a female’s offspring (Evans *et al.*, 2004; Lailvaux and Irschick, 2006b). However, few studies have shown female preference for better locomotor performers. In the seed beetle *Stator limbatus*, females obtain indirect benefits from mating with larger males because male size is heritable and larger males invest in larger ejaculates, which enhance female fecundity (Moya-Laraño and Fox, 2006; Fox *et al.*, 2007). Despite this preference, smaller males are better scramblers (i.e. better locomotor performers) and have a competitive advantage over larger males (Moya-Laraño *et al.*, 2007b). Clearly, trade-offs such as these warrant more research into the interactive effects of multiple sexually selected traits, and a multivariate approach will help to disentangle the fitness effects of each (Blows and Brooks, 2003; Blows *et al.*, 2003). Female guppies (*Poecilia reticulata*) preferred male ornaments that are correlated with swimming performance (Nicoletto, 1991, 1993), despite the fact that offspring of superior and inferior fathers did not differ in locomotor performance (Nicoletto, 1995). Female choice of more agile males during aerial displays appears to be common in bustards (Raihini *et al.*, 2006) and species of seabirds where females are the larger sex (Serrano-Meneses and Székely, 2006). On the other hand, female green anoles (*Anolis carolinensis*) do not prefer males with superior locomotor performance (Lailvaux and Irschick, 2006b), even though natural selection tends to favour faster hatchling lizards in other species (Warner and Andrews, 2002; Miles, 2004; Husak, 2006a). Empirical evidence for indirect benefits of mate choice are sparse (reviewed in Kotiaho and Puurtinen, 2007), but whole-organism performance traits may be a good place to look for them.

One intriguing example of potential female choice for male locomotor performance is in raptorial birds, most of which display female-biased sexual size dimorphism (see above). Many investigators have proposed that males are smaller so that they are more agile for capturing more types of prey, which they then feed to the females and young (Reynolds, 1972; Hakkarainen *et al.*, 1996). In this case, females may prefer more agile males because of direct

benefits (better food delivered to her from him), as well as indirect benefits (better locomotor abilities passed on to her offspring) provided by the male (Olsen and Olsen, 1987; Hakkarainen *et al.*, 1996). Future studies should seek to measure flight performance directly in addition to morphological proxies of it (e.g. wing size/shape or body size).

If females are to choose better locomotor performers, they must be able to assess male performance. One possibility is that male displays directly reflect locomotor performance. For example, the famously elaborate displays of manakins that involve numerous complex locomotor patterns (Prum, 1990, 1998), as well as the displays of other birds (Prum, 1997), may directly reflect male endurance capacity and/or speed (e.g. Brandt, 2003). On the other hand, instead of a display that is constrained by locomotor performance, males may have an ornament that signals performance capacity, such as in the case of endurance differences that exist between male colour morphs in side-blotched lizards (Sinervo *et al.*, 2000) and pupfish (Kodric-Brown and Nicoletto, 1993). Another possibility is that females assess male performance capacity by ‘eavesdropping’ on male interactions and associating with winners (reviewed in Wong and Candolin, 2005). This scenario assumes that winners are better performers, which may be the case in many taxa (see above). In our example of collared lizards, it is possible that because of the high visibility and close proximity of individuals in their habitat, females may assess male quality during interactions between males. All of the hypotheses in this section are speculative, but they are plausible and warrant further investigation.

FUTURE DIRECTIONS

We recommend several avenues for future research to improve our understanding of how sexual selection might operate on locomotor performance and the morphological traits underlying it. We note that even though we discuss sexual selection on locomotor performance specifically, our general framework is applicable to numerous performance traits (Irschick *et al.*, 2007). Rather than lament about difficulties associated with studying locomotor performance or be pessimistic about the intractability of performance–fitness studies, we point out challenges to try to spark the ingenuity and creativity of researchers. Adequately addressing the issues discussed in this review will require a multidisciplinary approach by researchers who study a wide variety of animal species.

Terrestrial locomotor performance has dominated the performance literature, especially as measured in squamate reptiles (e.g. Garland and Losos, 1994; Irschick and Garland, 2001; Delcomyn, 2004), though aquatic locomotion has also received considerable attention (reviewed in Domenici and Blake, 1997; Webb, 2004; Walker *et al.*, 2005; Oufiero and Garland, 2007). Endurance capacity is a well-studied trait, but we encourage researchers to quantify how endurance is used in nature (see Garland, 1999; Miles *et al.*, 2007). Perhaps the most promising, and challenging, style of locomotion for future study is aerial performance. Measuring aerial manoeuvrability and agility in a repeatable, standardized way that reflects maximal performance may prove difficult. Terrestrial manoeuvrability was successfully quantified in lizards using a pinboard obstacle course (Vanhooydonk and Van Damme, 2003) and non-linear ‘race-tracks’ (Higham *et al.*, 2001). Similar designs are easily imagined for aquatic species (Webb *et al.*, 1996; Weihs, 2002; Maresh *et al.*, 2003; Webb, 2004). For gliding and flying species, the use of specifically designed enclosures may hold promise. Of central importance will be preventing aerial species from landing on and attempting to cling to surfaces of obstacles (i.e. walls or poles) before maximal performance is achieved. Obstacle courses through which individuals fly through appropriately spaced structures may be good for quantifying manoeuvrability, as was done with bats (Stockwell,

2001). Measures of aerial agility or manoeuvrability in undisturbed free flight (e.g. Swallow *et al.*, 2000; Crompton *et al.*, 2003) are appropriate for some questions, but they may not represent maximal capabilities. The evolutionary implications of selection on such traits deserve further theoretical consideration (Husak, 2006a; Husak and Fox, 2006).

In an ideal research programme that seeks to determine the adaptive significance of a trait or suite of traits, manipulation of the trait(s) is necessary to determine causality. It seems reasonable to decrease locomotor performance (by adding weights, etc.), but increasing it will require ingenuity. Hormone manipulations are undesirable, as they typically entail too many other phenotypic changes due to pleiotropy, preventing a clear test of the fitness effects of only increased performance (Miles *et al.*, 2007). Our hope is that future researchers will ingeniously, and humanely, experiment with performance manipulations. Studies that use 'phenotypic engineering' (e.g. Ketterson *et al.*, 1996; Ketterson and Nolan, 1999) may be useful, but researchers should be mindful of what traits are altered with such manipulations. If manipulations of only a single trait are not possible, then combining broader-effect manipulations (e.g. phenotypic engineering) with subsequent multivariate methods to estimate the form and strength of multivariate selection on each piece of a suite of traits (e.g. Brodie *et al.*, 1995; Blows and Brooks, 2003; Blows *et al.*, 2003) is advised.

A pervasive assumption in ecomorphological studies is that relative performance is invariant over time (reviewed in Irschick *et al.*, 2006; see also Irschick *et al.*, 2008). Natural selection operates on heritable variation in phenotypic traits. Thus, studies that seek to demonstrate selection on performance traits should demonstrate heritability of the trait. Maximal sprint speed is heritable in the broad sense in several lizard species (Garland, 1988; Tsuji *et al.*, 1989; Bennett and Huey, 1990; Warner and Andrews, 2002; but see Sorci *et al.*, 1995), whereas the heritability of endurance capacity is equivocal (Robson, 2000; Austin and Shaffer, 1992). The heritability of other locomotor traits is poorly known. Multiple mechanisms may lead to intra-individual variance in performance. First, relative performance may change during ontogeny such that 'good performers' in a population at a young age may not be so later in life (Austin and Shaffer, 1992; Watkins, 1997). Such ontogenetic changes are understudied and deserve future attention. Second, performance may change within an activity season [bite-force performance (Irschick *et al.*, 2006; Irschick and Meyers, 2007)]. However, such seasonal changes appear less common in locomotor performance traits studied to date (Austin and Shaffer, 1992; Husak *et al.*, 2006a; Irschick and Meyers, 2007). The proximate mechanisms that lead to intra-individual variation in performance, as well as the evolutionary implications of such variation, also are poorly understood and present a promising avenue of research.

The role of locomotor performance in female choice is another exciting area of future research. There is speculation that whole-organism performance traits may represent good measures of male 'quality' that are assessable by females (reviewed in Lailvaux and Irschick, 2006a), yet empirical tests are lacking. If females do exhibit active choice of, or mating biases towards, high-performance males, then what are the benefits? While direct benefits of associating with better locomotor performers are plausible (e.g. because they are better at obtaining food for females), the real benefit of studying performance in a female choice context is the possibility that they may help in our understanding of indirect benefits to females. Since some locomotor performance traits are heritable in the broad-sense, locomotor superiority of offspring can be an indirect benefit. Quantitative genetic studies of locomotor performance, combined with field microevolutionary studies (e.g. Husak *et al.*, 2006a), may shed light on how the genes of superior performers fare over multiple generations.

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