Evaluating performance costs of sexually selected traits

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Summary

1. Aspects of locomotor performance are thought to be important in a variety of natural contexts, including foraging and escaping from predators. The role of locomotor abilities in sexual selection is less well documented, but is probably of wide importance.

2. Sexual selection may exaggerate traits beyond their optimum with respect to biomechanical or physiological function, thus imposing 'costs' of various types. Locomotor performance, in conjunction with its lower-level determinants and its behavioural and ecological consequences, constitutes an ideal set of phenotypes with which to study such costs.

3. Organisms may possess traits that compensate for the negative effects of sexually selected traits on performance abilities. Ignoring these may lead to erroneous conclusions about the cost of a putatively sexually selected trait. At the same time, ignoring the effects of sexual selection on functionally important traits may lead us to underestimate their functional significance.

4. Many properties of organisms are affected by, or at least correlate with, overall body size, so this must be considered in any study of adaptation or sexual selection. For interspecific or interpopulation comparative studies, phylogeny must also be considered in statistical analyses.

5. We present a hypothetical data set that illustrates the perils of ignoring potential compensatory mechanisms when studying the costs of a sexually selected trait. We also discuss different ways of studying costs, including analyses of a single sex and of the differences between the sexes.

Key-words: behaviour, comparative method, locomotion, path analysis, performance, physiology

Introduction

Since Charles Darwin, sexual selection has been recognized as a factor that often seems to oppose adaptation via natural selection, and that can lead to the evolution of elaborate and even bizarre secondary sexual characteristics. Darwin (1859) coined the term 'sexual selection', and wrote that it 'depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring.' In 1871 he wrote: 'sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; while natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life.' (Darwin 1871). Although some researchers do not draw a distinction between natural and sexual selection, Darwin's conceptualization has nonetheless proven to be a very powerful paradigm for subsequent

and current research (Kirkpatrick 1987; Kotiaho 2001; Badyaev 2002; Stearns & Hoekstra 2005).

Elaborated secondary sexual characters result from two main types of sexual selection: intrasexual (e.g. male–male combat) and intersexual (or epigamic, e.g. female choice of males with particular characteristics). The opportunity for sexual selection is generally thought to be greater in males than in females, because the reproductive success of males is limited by access to females (as sperm production is typically cheap), whereas that of a female is limited by the number of offspring she can carry or raise, or by food, shelter or other such resources required for provisioning and care of offspring, either *in utero* or after hatching or birth (Trivers 1972; Stearns & Hoekstra 2005). Therefore, in general, we expect to find sexually selected traits in males more often than in females, and this expectation is supported by evidence for most groups of animals (reviewed by Bradbury & Andersson 1987; Andersson 1994). Birds provide many familiar examples of traits thought to have evolved via sexual selection, including complex songs, bright coloration and elaborate plumage morphologies such as the tail of
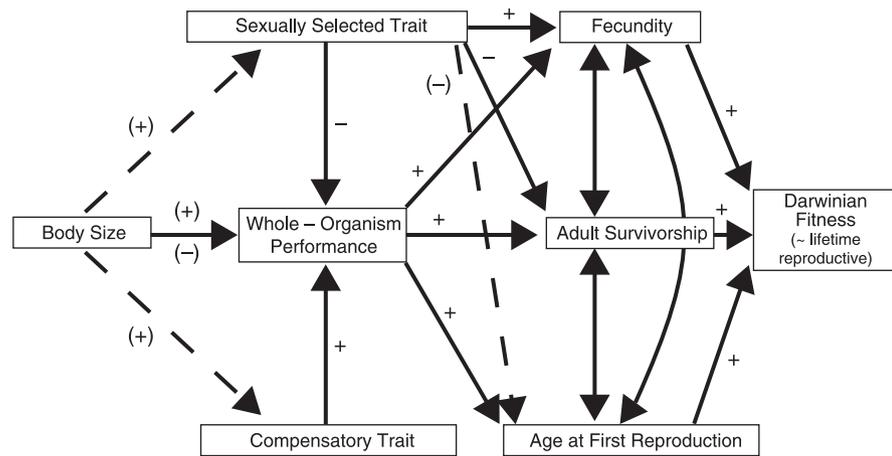
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Fig. 1. Path model discussed in the text. Arrows indicate direction of putative causality (for simplicity, terms to represent unexplained variation are omitted). Solid lines represent causal relationships that are almost certain to occur; dashed lines those that are less certain to occur and/or may vary in sign. Correlations between traits can be positive or negative and are represented by double-headed arrows (some possible correlations are omitted for simplicity). Compensatory trait refers to such subordinate traits as heart size, gill area or muscle fibre type that may have evolved to counter the detrimental effects of a sexually selected trait on an organism's performance (e.g. locomotor speed or stamina). +, Positive effect; –, negative effect; parentheses indicate that the sign of the relationship may differ from that shown. Sexually selected traits are assumed to have a negative effect on performance (see text), whereas compensatory traits by definition have a positive effect. Sexually selected traits evolve as a compromise between natural and sexual selection (and within the confines of genetic, developmental and physical constraints). Therefore, while they will have a net positive effect on at least one component of Darwinian fitness, such as fecundity (e.g. number of females obtained by a male), they typically have negative effects on other fitness components, such as adult survivorship or age at first reproduction (e.g. because they adversely affect growth rate). Conversely, performance is likely to have positive effects on all fitness components by increasing the ability to acquire mates, forage and avoid predation. Body size will often, but not always, be positively correlated with both sexually selected traits (e.g. tail length) and compensatory traits (e.g. heart size). Body size will often have a positive effect on some aspects of locomotor performance (e.g. stamina) but a negative effect on others (e.g. manoeuvrability). Here shown as a single box, performance actually comprises many elements, some of which may trade off because of biomechanical or physiological relations (e.g. speed *vs* stamina; see text). Different aspects of performance may be selectively important in different ecological settings. This conceptualization assumes that animals can be motivated to exhibit a maximal level of performance that can, at least in principle, be measured with some degree of accuracy. Not shown in the path model is the role of behaviour, which may often shield performance abilities from selection and/or allow compensation for low abilities (Garland *et al.* 1990a; Garland 1994a; Garland & Carter 1994; Garland & Losos 1994). Following Arnold (1983), paths to performance can be termed performance gradients; those to fitness can be termed fitness gradients.

male peacocks (Bradbury & Andersson 1987). Such traits are generally presumed to increase the male's reproductive success (Stearns & Hoekstra 2005), and have indeed been shown to do so in various empirical studies (Andersson 1986 on widowbirds). However, such traits as greatly elongated tail feathers may impose costs, for instance in terms of the ability to forage and to escape from predators. Any trait subject to sexual selection will also be subject to natural selection, and hence will not evolve without limits.

Beginning with Fisher (1930 and earlier), several theories and models have been proposed for the evolutionary origin and subsequent maintenance or elaboration of putatively sexually selected traits (reviewed by Kirkpatrick 1987; Ryan & Keddy-Hector 1992; Schall & Staats 1997; Mead & Arnold 2004; see also Stearns & Hoekstra 2005). Despite many differences, all these ideas have at least one feature in common: the presence of elaborate sexually selected secondary characteristics, which appear to increase the reproductive success of the male (typically) while possibly compromising the bearer's survival or increasing its energy requirements. In principle, costs may be associated with any sexually selected trait (Møller

1989; Nicoletto 1991; Evans & Hatchwell 1992; Barbosa & Møller 1999; Park *et al.* 2000; Kotiaho 2001; Basolo & Alcaraz 2003).

One cost that has been proposed is lower ability to escape predation (Møller 1996), potentially through a reduction in locomotor performance. More generally, the morphology of an organism can affect its performance abilities, and thus aspects of its Darwinian fitness. Arnold (1983) introduced a paradigm that simultaneously highlighted the effects of subordinate phenotypes (e.g. morphological and biochemical variation) on an organism's performance abilities (e.g. in locomotion) and, in turn, the effects of the organism's performance abilities on components of Darwinian fitness. A diagram motivated by his paradigm is depicted in Fig. 1. Arnold's (1983) 'centrality of organismal performance paradigm' (Garland & Carter 1994) has been much discussed and elaborated since its introduction, and considerable theoretical and experimental work has examined effects of morphology on performance (Garland & Losos 1994; Plaut 2000; Ojanguren & Brana 2003; Billman & Pyron 2005; Blake *et al.* 2005). However, only a few studies have considered the costs of sexually selected traits in this framework (Ryan

1988; Møller 1989; Nicoletto 1991; Evans & Hatchwell 1992; Kotiaho 2001; Basolo & Alcaraz 2003; Evans 2004; Karino *et al*. 2006). For instance, birds (Thomas 1993) and fish (Beamish 1978; Webb 1984; Weihs 1989) exhibit sexually selected elongated tails and fins/feathers, along with an increase in body depth in some species (Ptacek 1998), that may decrease the efficiency of locomotion because they increase drag (cf. Pettersson & Hedenström 2000).

Barbosa & Møller (1999) used theoretical calculations to argue that longer tail feathers in male barn swallows (*Hirundo rustica*) increased flight drag and decreased foraging efficiency, yet they did not measure actual flight performance, as has been done in some bird biomechanical studies (Buchanan & Evans 2000; for review see Irschick & Garland 2001). Similarly, several studies have examined the costs of sexually selected traits in poeciliid fish. For example, Nicoletto (1991) examined the relationship between critical swimming speed and tail morphology in a feral population of guppies (*Poecilia reticulata*) from New Mexico. Although he did not find any relationship between tail shape and critical swimming speed, he also did not find a significant difference in the areas of the three tail types he examined. In a study of swordtails (*Xiphophorus montezumae*), another member of the Poeciliidae, Basolo & Alcaraz (2003) found a higher rate of oxygen consumption, both routinely and during courtship, in males with intact swords compared with those that had their swords surgically removed. Finally, a recent study of variation among six populations of *Gambusia* found that C-start performance (Domenici & Blake 1997) was positively associated with standard length and negatively associated with gonopodium length in a multiple regression, leading the authors to conclude that 'relatively large gonopodia seem to incur a cost of reduced burst-swimming speed' (Langerhans *et al*. 2005). Therefore some evidence indicates that sexually selected traits actually can impose a performance cost. On the other hand, Royle *et al*. (2006) found that male *Xiphophorus helleri* with the relatively longest swords had the highest C-start performance, which suggests the possibility of one or more compensatory traits that may have covaried with sword length (see below; Fig. 1).

Because whole-organism performance is not solely determined by any one trait, natural selection may cause alterations of other traits to counteract the negative effects of a sexually selected trait, and such traits can be termed 'compensatory traits' (Fig. 1; Kirkpatrick 1987; Møller 1996; Jennions *et al*. 2001). According to Kirkpatrick (1987, pp. 49–50), 'Compensatory modifications of the males to cope with the demands of the preference, such as increased aerobic scope and enlarged musculature, will often evolve.' For example, *Gambusia affinis* from populations with predators appear to have evolved body shapes that increase their maximum burst-swimming speed (Langerhans *et al*. 2004).

LOCOMOTOR PERFORMANCE IN RELATION TO COSTS IMPOSED BY SEXUALLY SELECTED TRAITS

From the perspective of Fig. 1, locomotor performance comprises an excellent set of phenotypes to study the costs of sexual selection. First, most behaviours involve locomotion (Garland 1994a, 1994b; Garland & Losos 1994; Blake 2004), including escaping predators, capturing prey and fighting (Briffa & Sneddon 2007); therefore a decrease in locomotor ability (performance capacity) is likely to have fairly direct effects on the Darwinian fitness of the individual. This assumes that animals actually use their maximal abilities in some important situations (for review see Irschick & Garland 2001). Indeed, several studies have now provided empirical evidence of natural selection acting on locomotor abilities (Miles *et al*. 2000; Sinervo *et al*. 2000; Le Galliard *et al*. 2004; Husak 2006 and references therein). Second, for many organisms some aspects of locomotor performance are relatively easy to quantify in the laboratory (e.g. for fish: Beamish 1978; Webb 1984; Domenici & Blake 1997; Plaut 2001; Nelson *et al*. 2002; Blake 2004; Lauder & Drucker 2004). Third, aspects of morphology and physiology can have direct effects on performance abilities (Beamish 1978; Arnold 1983; Garland & Losos 1994; Plaut 2000; Blake *et al*. 2005), and sexual selection can exaggerate a trait beyond its optimum with respect to its effect on locomotor function, thus causing a decrease in performance ability. Fourth, given our fairly good understanding of the mechanisms underlying variation in locomotor performance, at least for some groups of animals, it is possible to imagine various traits that might compensate for the adverse effects of a sexually selected trait (Evans & Thomas 1992; Balmford *et al*. 1994; Møller 1996). Finally, it is possible that individual variation in locomotor abilities may reflect overall health or vigour, and hence be a subject of sexual selection (see Introduction; Garland *et al*. 1990b; Chappell *et al*. 1997; Robson & Miles 2000; Husak *et al*. 2006; Kotiaho & Puurtinen 2007).

In principle, sexual selection could give rise to potential handicaps related to locomotor abilities in any group of organisms. Hummingbirds, for example, rely on flying ability to a great extent in their daily activities, including foraging and territorial interactions. Sexual dimorphism exists in many species, including male plumage characteristics that are thought to have been sexually selected. Sex differences in morphology and flight performance have been documented (Chai *et al*. 1996), but we are not aware of any studies claiming that the sexually selected traits impose a penalty in terms of flight performance or energetic costs.

Among the vertebrates, fish and lizards have received the greatest attention in terms of measuring locomotor performance. Here we focus on fish, with particular reference to the genus *Xiphophorus* (swordtails and platyfish in the family Poeciliidae), which includes

about 20 live-bearing, freshwater species. This emphasis reflects our ongoing studies with this group and also the fact that it has been relatively well studied in terms of sexual selection, morphology and performance. Several modes of swimming in fish have the potential to be affected by a sexually selected trait. These swimming modes capture an array of locomotor capabilities, and informative performance traits can be measured for each. A common measure of a fish's swimming performance is its 'escape response', often characterized by a 'C-start' in response to an external stimulus, such as dropping an object into its tank (Domenici & Blake 1997). This mode of swimming is important for evading predators (Walker *et al.* 2005) and is characterized as an 'unsteady' swimming state. Therefore, if exaggerated morphologies hinder a fish's ability to escape, such as by increasing the drag, this may have direct effects on its survival. More recently, studies have measured a fish's sprinting abilities down a 'dragstrip', similar to studies of sprinting in terrestrial vertebrates (Nelson *et al.* 2002). This mode of swimming would come after the escape response as the fish continues to evade the predator after the initial attack (or when pursuing prey). Similarly, exaggerated morphologies may hinder this performance, leading to a decrease in survival or foraging success. A third type of performance, often measured as an indicator of a fish's health and aerobic capacity, is critical swimming speed (U_{crit}) (Kolok 1999; Reidy *et al.* 2000; Plaut 2001). This performance can be classified as 'steady' swimming, is similar to endurance measures in terrestrial vertebrates, and is characterized by more aerobic respiration (Reidy *et al.* 2000). Exaggerated morphologies may reduce swimming efficiency and increase cost, and thus decrease U_{crit}. In addition to U_{crit}, the endurance of a fish can also be examined. This mode of swimming is similar to endurance trials in terrestrial vertebrates (Garland 1984, 1993, 1994a, 1994b; Djawdan 1993; Garland & Losos 1994; Cullum 1998; Perry *et al.* 2004), and can be defined as the time a fish can swim continually against a prescribed velocity (Beamish 1978; Plaut 2001). Similarly to their effect on U_{crit}, sexually selected traits have the potential to reduce swimming efficiency or increase the cost, and thus reduce endurance at a given swimming speed.

In addition to the various modes of swimming in fish, maximum oxygen consumption ($V_{O_{2max}}$) can be measured during steady-state swimming of gradually increasing intensity directly to determine whole-animal aerobic capacity (Gordon *et al.* 1989; Plaut & Gordon 1994; Chappell & Odell 2004). All else being equal, a higher $V_{O_{2max}}$ will correlate directly with a higher U_{crit}. Therefore, if an exaggerated morphology caused by sexual selection had an adverse effect on swimming efficiency, and hence lowered U_{crit}, then an increase in $V_{O_{2max}}$ would be one way that a fish might compensate, increasing U_{crit} up to 'normal' levels.

Some aspects of locomotor performance may trade off due to biomechanical, biochemical or physiological relations (Vanhooydonck & Van Damme 2001; Vanhooydonck *et al.* 2001; Van Damme *et al.* 2002; Blake 2004). For example, many studies and reviews of locomotor performance have recognized that an individual usually cannot perform well under both aerobic and anaerobic modes (Garland & Losos 1994; Reidy *et al.* 2000; Ojanguren & Brana 2003; but cf. Garland 1988; Chappell & Odell 2004). This is due to the amount of different muscle fibre types within the individual. If an individual is a good sprinter, then it will typically have relatively more white muscle at the cost of red muscle, making it relatively poor at endurance (Mosse & Hudson 1977; Jayne & Lauder 1994; Gibb & Dickson 2002; Syme *et al.* 2005). Therefore it is best to examine an array of performance measures to obtain a comprehensive picture of the effect that a sexually selected trait may have on performance (Figure 1).

It is also important to acknowledge that different aspects of locomotor performance may be favoured in different ecological contexts. For example, many members of the Poeciliidae inhabit areas both with and without predators (Reznick *et al.* 1996; Basolo & Wagner 2004; Langerhans *et al.* 2004; Langerhans *et al.* 2005), and recent evidence suggests that the fish from high-predator environments may be evading predators through an increase in C-start (Langerhans *et al.* 2005; Walker *et al.* 2005; cf. Chappell & Odell 2004). If only one performance is measured, such as critical swimming speed (Ryan 1988; Nicoletto 1991), then a significant effect might not be found because this might not be the aspect of performance that is most relevant with respect to predation. Instead, selection might be acting on another swimming mode such as C-start. On the other hand, recent studies have shown that interpopulation variation in U_{crit} correlates with stream velocity or habitat type (stream *vs* lake) (McGuigan *et al.* 2003; Nelson *et al.* 2003), although C-start was not measured in these studies. Thus it is theoretically possible that a sexually selected trait might impose a cost on some aspect of performance that was not important from the standpoint of natural selection in a given set of ecological conditions. In the wild, it is also possible that behavioural mechanisms can compensate for performance deficiencies (Garland *et al.* 1990a; Garland 1994a; Garland & Carter 1994; Garland & Losos 1994; Jennions *et al.* 2001), thus shielding performance abilities from natural selection, but this 'behaviour as a filter' hypothesis is beyond the scope of the present paper (Clobert *et al.* 2000; Robson & Miles 2000; Husak *et al.* 2006).

Below, we develop a hypothetical multispecies data set with which to illustrate some ways to analyse the costs of a sexually selected trait. We use the fish genus *Xiphophorus* as a model, and simulate the effects that the sexually selected 'sword' has on endurance. We also include ventricle (heart) mass as a potential compensatory trait. Finally, we analyse the data in two ways: (1) by comparing males across species, and (2) by comparing the difference between males and females

across species. For our example, the two analyses lead to similar results and demonstrate that when an important compensatory trait is left out of the model, the sexually selected trait may appear to have a positive effect on performance.

STUDY SYSTEM THAT MOTIVATED OUR HYPOTHETICAL EXAMPLE

Within the genus *Xiphophorus*, the predominant sexually selected trait is an elongation of the lower margin of the caudal fin (the sword), which is exhibited only by males. Recent phylogenies indicate that the sword has evolved more than once in *Xiphophorus* (the sister lineage *Priapella* lacks swords; Marcus & McCune 1999; Morris *et al*. 2001). Apparently the sword has evolved in relation to a pre-existing female preference (Basolo 1990, 1995), but is also used during male–male interactions (Bissazza 1993). Evidence indicates that females prefer males with swords, even within species that lack swords. Within the genus, there is a mixture of mating tactics including forced copulation (gonopodial thrusting) and courtship displays. Species exhibiting the sword will display in front of the female with unpaired fins spread and show a stereotyped swimming display that varies among species (Bisazza 1993). Therefore it seems clear that the sword is a sexually selected trait and may impose a cost.

Preliminary work on the cost of swords has yielded mixed results. Ryan (1988) examined swimming endurance of male *X. nigrensis* and found no effect of natural variation in sword length in wild-caught and F_1 laboratory-reared individuals. Moreover, he did not include measures of other traits such as heart mass, gill area or tissue aerobic capacity that might vary and override (at least partially) any effect of sword length. Basolo & Wagner (2004) found that *X. helleri* from habitats with predators had a body morphology significantly different from conspecifics from predator-free environments, including shorter swords, which suggests that swords may adversely affect escape abilities. However, recent evidence on *X. helleri* suggests that sword length may have a positive effect on C-start performance (Royle *et al*. 2006). Finally, in *X. montezumae*, Basolo & Alcaraz (2003) demonstrated a cost

in routine oxygen consumption of males with swords as compared both with males that had their swords surgically removed, and with females.

CREATION AND ANALYSIS OF COMPARATIVE DATA SET

As an example, if the left half of Fig. 1 we model the effect on endurance of an elongation of the lower margin of the caudal fin (sword) of *Xiphophorus* individuals. We performed path analyses using AMOS ver. 5 (http://amosdevelopment.com). We include body size in the analyses because of its expected positive effect on endurance capabilities, because heart (ventricle) size should covary strongly with body size, and because some sexually selected traits may also covary with body size. Ventricle mass (Odell et al. 2003) is included as a compensatory mechanism to counteract the negative effects of the sword on endurance. Although we have argued above that it is best to examine an array of locomotor capabilities, as well as multiple compensatory mechanisms, this simplified model serves to illustrate the potential effects of a sexually selected trait on performance, as well as compensatory mechanisms that might have co-adapted to overcome the cost.

As a frame of reference, we began with the data on male and female standard length for 61 species of North American minnows from Pyron (1996). We then excluded species with a length <20 or >190 mm to make the overall size range more similar to that found within *Xiphophorus*, leaving 57 species. As a group, Pyron's (1996) minnows are not sexually dimorphic in standard length, so we multiplied female standard lengths by 1·2 to mimic the situation in *Xiphophorus* (most species of poeciliids are sexually dimorphic, with males being the smaller sex; Bisazza (1993)). To create swords, we computed a random variable with an exponential distribution (SPSS shape parameter = 3). From this, we set values smaller than 0·1 to zero (because some *Xiphophorus* have no swords) and values larger than 1·15 to 1·15 (because some swordtails have swords that are slightly longer than standard length). We then computed sword length as the resulting value multiplied by male standard length. A plot of sword *vs* body length is shown in Fig. 2. We then
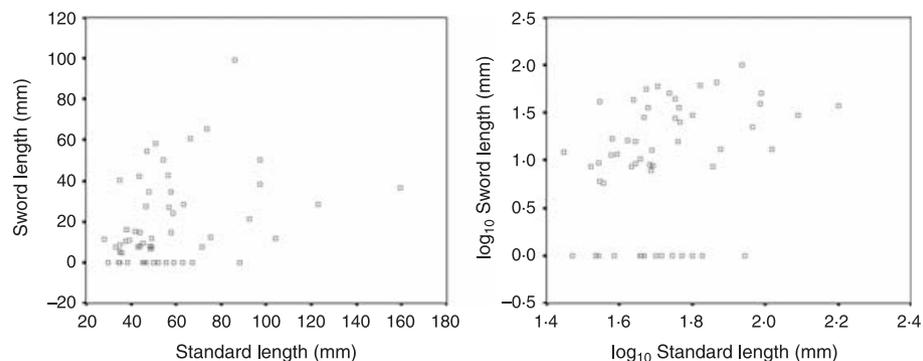
Fig. 2. Hypothetical data for sword length (mm) in relation to standard length (mm) for males of 57 species of fish.
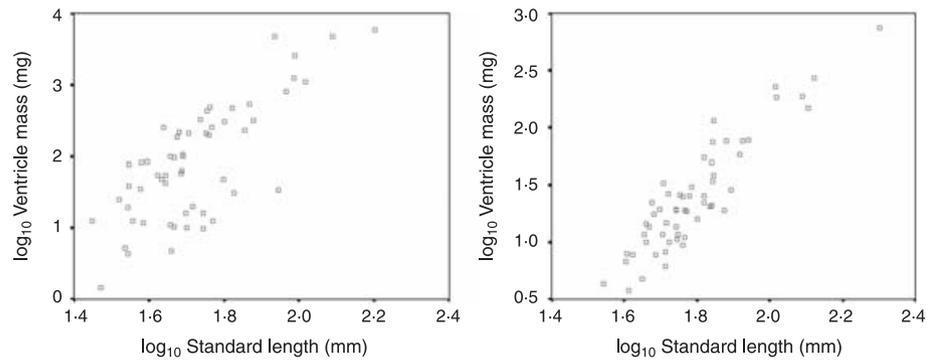
Fig. 3. Hypothetical data for $\log_{10}$ ventricle mass (mg) in relation to $\log_{10}$ standard length (mm) for 57 species of fish. Note that males (left) show greater variation in ventricle mass because it was computed partly as a function of sword length, which only (some) males possess.
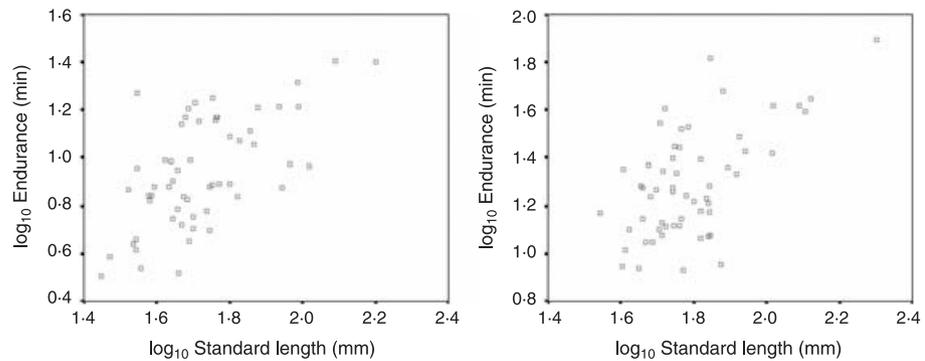

Fig. 4. Hypothetical data for $\log_{10}$ swimming endurance (min) in relation to $\log_{10}$ standard length (mm) for 57 species of fish (males on left, females on right). Note different *y*-axis ranges; on average, males have lower endurance than females for a given body size (Fig. 5).

$\log_{10}$-transformed both female and male standard length, and sword length was transformed as $\log_{10}$(sword + 1) because females lack swords.

To model a trait that might compensate for the negative effects of sword length on swimming endurance, we computed $\log_{10}$ ventricle mass (Odell *et al.* 2003) as:

$$-4 + (3 \times \log_{10} \text{standard length}) + (0 \cdot 8 \times \log_{10} \text{sword length}).$$

We then added random noise (separately by sex) to this value by drawing values from a normal distribution with mean 0 and SD 0·2. Figure 3 shows a plot of the ventricle mass data. $\log_{10}$ swimming endurance was computed as:

$$0 \cdot 5 + (1 \times \log_{10} \text{standard length}) + (0 \cdot 5 \times \log_{10} \text{ventricle mass}) + \text{noise}$$

where noise was a random normal variable with standard deviation of 0·15 (separately by sex). Finally, for males, we modelled a detrimental effect of sword length by adding the term $-0 \cdot 3 \times [\log_{10}(\text{sword length} + 1)]$. The relation between endurance and standard length is shown in Fig. 4.

Figure 5 shows the hypothetical data for $\log_{10}$ swimming endurance (minutes) of males and females. The
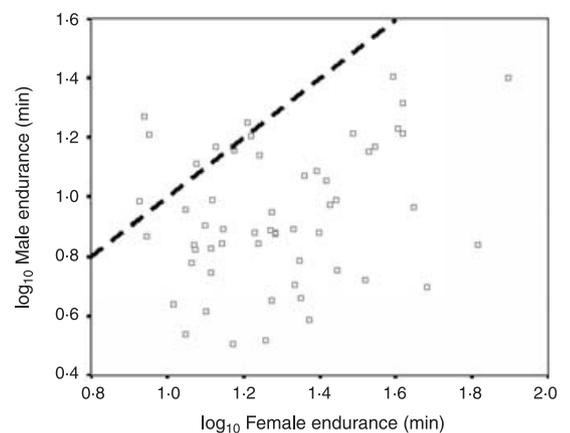

Fig. 5. Hypothetical data for $\log_{10}$ swimming endurance (min) of males and females for 57 species of fish. Dashed line indicates equal endurance; thus on average females have greater endurance, which reflects their larger body size and absence of swords, which negatively affect endurance in males that possess them (see text).

values are somewhat positively correlated (Pearson's $r = 0 \cdot 258$, two-tailed $P = 0 \cdot 053$), but the main pattern in the data is that females generally have substantially greater endurance (paired $t = 9 \cdot 56$, $P = 2 \times 10^{-13}$), with the mean $\log_{10}$ endurances being 1·2916 (females) *vs* 0·9420 (males), or 19·6 *vs* 8·7 min on the arithmetic

Male

Sword Length
Standard Length
Swimming Endurance
Ventricle Mass

+0·294 P = 0·021
−0·447 P < 0·001
−0·216 P = 0·021
+0·758 P < 0·001
+1·015 P < 0·001

+0·294 P = 0·021
+0·302 P = 0·003
+0·530 P < 0·001

	Ventr.	Sword	Endur.
Length	0·758**	0·294*	0·619**
Ventr.		0·811**	0·716**
Sword			0·458**

Male – Female

+0·090 P = 0·500
−0·451 P < 0·001
−0·126 P = 0·086
+0·385 P = 0·002
+0·786 P < 0·001

+0·090 P = 0·500
+0·281 P = 0·026
+0·182 P = 0·1486

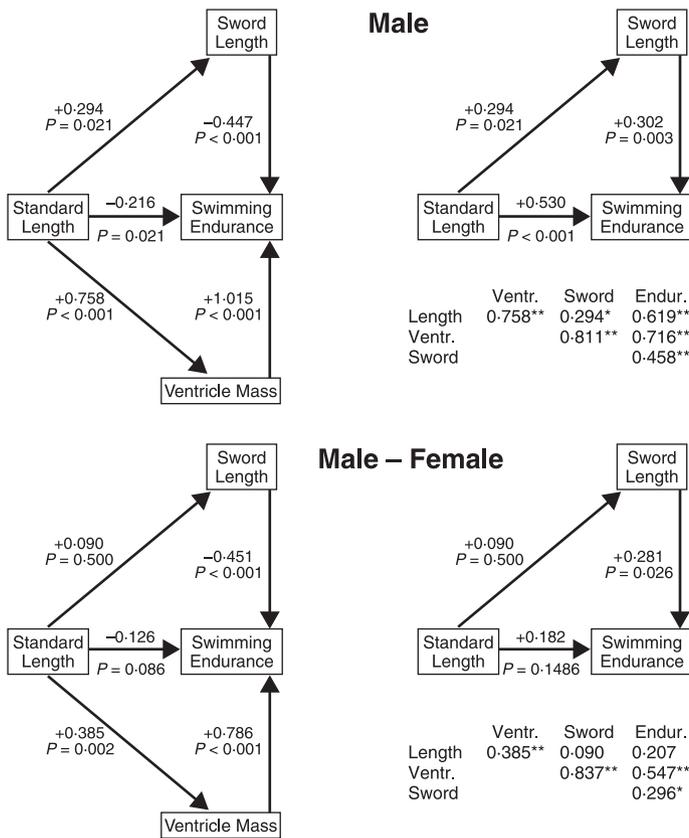|	Ventr.	Sword	Endur.
Length	0·385**	0·090	0·207
Ventr.		0·837**	0·547**
Sword			0·296*

Fig. 6. Path models examining the relationships of body size, sword length (a sexually selected trait), ventricle mass (a compensatory trait), and swimming endurance in males only (top panel) and using the male–female difference for each trait (bottom panel). Data analysed are shown in Figs 2–5. Also included are path models with ventricle mass removed. Tables of pairwise Pearson correlations are given for each analysis (*, two-tailed $P < 0·05$, **, $P < 0·01$). Both analyses show that when the compensatory trait is excluded, sword length appears (erroneously) to have a statistically significant positive effect on swimming endurance. This result is also obtained when examining the simple correlation tables. However, when the full models that include ventricle mass are analysed, sword length appears (correctly, given how the data set was created; see text) to have a negative effect on swimming endurance.

scale. Given that many species of males have swords, one might be tempted to infer that the lower average endurance of males is caused by the handicapping effect of those swords. However, males are also smaller in log standard length, and that alone might cause the difference in endurance. Although the overall comparison of males with females is ambiguous, analyses of differences between the sexes can be used (see below).

If we focus only on males, as only they possess swords in this example, then the following path analyses for $\log_{10}$ endurance demonstrate the problem of not considering a compensatory trait, ventricle size. If only body size and sword size are included in the model, then the path analysis (Fig. 6, top right) indicates that swords actually have a statistically significant positive effect on endurance. However, when ventricle size is included, the negative effect of sword length becomes clear (Fig. 6, top left). As judged by the magnitude of the standardized partial regression coefficients (β = a

path coefficient), ventricle mass is a stronger predictor of log endurance than is log sword length. Note, however, that ventricle mass and sword length are strongly correlated ($r = 0·811$; Fig. 6, top), which could cause problems of multicollinearity (Slinker & Glantz 1985). Another possible indication of multicollinearity in the present data set is the fact that the full path models (left side of Fig. 6) indicate a negative effect of standard length on endurance, whereas the effect built into the simulations was actually positive. (This may also be partly an effect of the complicated relationship between sword length and standard length, as shown in Fig. 2) Several statistical approaches can be used to deal with such strong intercorrelations between independent variables (Garland 1984; Slinker & Glantz 1985). If possible, however, the best strategy is to sample additional species whose multivariate phenotype tends to reduce the strength of intercorrelations.

As discussed above, another way to analyse this type of data is by computing differences between the sexes for each species. The rationale for this is that females may be nearer to the optimum for any particular trait, as dictated by natural selection. Thus male characteristics, such as performance or a trait that might handicap performance, can be compared with those of females, which would often lack the putative handicap, or at least express it at a reduced magnitude. Like Promislow *et al.* (1992), we computed differences in log-transformed values (log male – log female endurance; log male – log female standard length; log male – log female ventricle mass). For sword length, we can simply use log(male value + 1) because all females lacked swords in this hypothetical data set. A path model (Fig. 6, bottom left) indicates that the difference in endurance between males and females is significantly positively related to the difference in ventricle size, and negatively related to the difference in sword size. And, as above, if we do not include the difference in ventricle size, then we get the misleading result that the difference in sword length is a positive predictor of the difference in endurance (Fig. 6, bottom right).

Discussion

Our simulated data set demonstrates the interplay among various traits that have the potential to influence locomotor abilities, as well as demonstrating the use of different types of analyses to examine costs. It also illustrates that compensatory traits can mask the negative effects (costs) of a sexually selected trait. This can occur when we analyse only the sex that possesses the putatively costly trait (e.g. swords in males of the fish genus *Xiphophorus*), as well as when considering the difference in traits between the sexes (e.g. log male value – log female value). Indeed, our hypothetical data set illustrates that, in either type of analysis, the putatively costly trait can even appear to have a positive effect on an organism's performance if a compensatory trait is not included in the analysis (Fig. 6).

Here we present a simple case considering a single performance measure, a single sexually selected trait that handicaps that performance, a single compensatory trait (ventricle mass), and body size. However, multiple performance measures, handicaps and compensatory traits can be included in path analyses (Fig. 10·5 in Garland & Losos 1994; Bauwens *et al*. 1995; Petraitis *et al*. 1996; Miles *et al*. 2000; Armbruster *et al*. 2002; Caumul & Polly 2005; Angilletta *et al*. 2006). If this were a real data set, then phylogenetically based statistical methods would need to be used (Abouheif & Fairbairn 1997; Prum 1997; Ryan & Rand 1999, Armbruster *et al*. 2002; Aparicio *et al*. 2003; Blomberg *et al*. 2003; Cox *et al*. 2003; Billman & Pyron 2005; Caumul & Polly 2005; Garland *et al*. 2005; Ives *et al*. 2007).

EXISTING STUDIES OF COMPENSATORY TRAITS

Previous studies examining the cost of a secondary sexual characteristic have produced mixed results. Although some have documented a clear cost to components of Darwinian fitness (Ryan *et al*. 1982; Garcia *et al*. 1994), others have found no effect of the trait (Ryan 1988; Chappell *et al*. 1995), or even a positive effect of the trait on performance (Royle *et al*. 2006) or on components of Darwinian fitness (Petrie 1994). Although these studies examine an array of potential costs, the discrepancies may arise because compensatory mechanisms were not taken into account.

The idea of compensatory mechanisms decreasing the costs of sexually selected traits is not a novel one. Møller (1996) suggested several types of 'cost-reducing' traits in relation to the production and maintenance of a sexually selected character, including mechanisms that are 'produced in advance of or simultaneously with the sex trait which reduce the cost of the character.' Balmford *et al*.'s. (1994) comparative study of birds suggests that greater wingspans have evolved to reduce the cost of tails elongated by sexual selection. Similarly, Pettersson & Hedenström (2000) demonstrated theoretically that, in fish, adjustments in standard metabolic rate can compensate for hydrodynamic disadvantages (e.g. high drag from elongated tails) under certain food conditions.

Some evidence suggests that sexual selection may favour males with higher locomotor abilities and/or aerobic capacities, which would affect endurance. This has been suggested for lizards in general (Garland 1993; Cullum 1998), for *Varanus gilleni* (Bickler & Anderson 1986) and for helodermatid lizards, in which males have higher body size-adjusted maximal oxygen consumption (Beck *et al*. 1995). It was also suggested for junglefowl (Chappell *et al*. 1996), but empirical studies have yielded ambiguous results (Chappell *et al*. 1997, 1999). Because body size often correlates positively with locomotor endurance (Garland 1994b), increases in body size might result from sexual selec-

tion if such selection favours high endurance. Thus larger males in some species may indicate that sexual selection has favoured high endurance. So many traits correlate with body size that it is tenuous to single out endurance in the absence of direct evidence that sexual selection is acting on endurance (cf. Anderson & Vitt 1990). Stronger evidence would be provided by demonstrating that males show higher endurance than females after adjusting statistically for correlations with body size. Existing empirical studies are mixed regarding this possibility in lizards (Garland & Else 1987; Cullum 1998; Dohm *et al*. 1998). Three correlational studies of lizards have examined individual variation in laboratory-measured locomotor performance in relation to social dominance in experimental arenas, and all found evidence to support a relationship. In *Sceloporus occidentalis*, dominance was positively related to speed but not stamina (Garland *et al*. 1990b). In *Urosaurus ornatus*, dominance was positively related to both speed and stamina (Robson & Miles 2000). In *Anolis cristatellus*, dominance was positively related to endurance and to the rate of assertion displays in the field, but not to speed (Perry *et al*. 2004). Evidence suggesting that endurance may be subject to sexual selection in lizards also comes from field studies of *Uta stansburiana* (Miles *et al*. 2000; Sinervo *et al*. 2000 and references therein). Most recently, Husak *et al*. (2006) found that the maximal sprint speed of territorial, adult male collared lizards (measured in the laboratory) was a positive predictor of the number of offspring sired in the field.

ALTERNATIVE WAYS TO STUDY COSTS OF SEXUALLY SELECTED TRAITS

The assumed costs of sexually selected traits have been examined in various ways. Kotiaho (2001, p. 366) stated that 'to count as an evolutionarily significant cost, an increase in the magnitude of sexual traits has to either increase mortality or decrease reproductive success.' We agree with that point, but would add, consistent with Arnold (1983; Fig. 1), that it can also be interesting and informative to study costs of sexually selected traits on an organism's performance abilities (performance gradients), whether or not the performance ability has an important effect on Darwinian fitness.

In any case, Kotiaho's (2001) definition does not specify any particular baseline for comparison. One possibility is to compare individuals of the same sex and population. Individuals with higher values for the putatively costly trait (independent variable) should show lower values for performance traits and/or for components of Darwinian fitness. For example, some studies have demonstrated that males within a species with higher values for the putatively sexually selected trait have a decrease in overnight body mass (Thomas 2002), locomotor abilities (Langerhans *et al*. 2005; Karino *et al*. 2006) and survival (Ryan *et al*. 1982;

Garcia *et al*. 1994; but cf. Petrie 1994; for a review of such correlational studies see Kotiaho 2001). Additionally, some studies of individual variation have involved experimental manipulations, such as lengthening or shortening of tails. These studies have further demonstrated costs within the same sex and species (foraging efficiency: Møller 1989; Evans & Thomas 1992; oxygen consumption: Basolo & Alcaraz 2003; number of matings: Andersson 1986; survival: Møller & de Lope 1994; Kotiaho 2000).

Among populations (or among species), a similar approach can be taken. For example, mean values can be computed for the sexually selected trait and either locomotor performance or actual fitness components, such as average survivorship or litter size. For instance, Promislow and colleagues examined the survival cost of sexual size dimorphism among species of mammals (Promislow 1992) and birds (Promislow *et al*. 1992). They found that the degree of male-biased adult mortality was positively correlated with the degree of sexual size dimorphism. Additionally, this approach can be used to investigate compensatory mechanisms among species. For example, Balmford *et al*. (1994) found that, among 57 species of birds, those that exhibited longer tail feathers, potentially through the result of sexual selection, also exhibited greater wingspans, which they suggested had evolved to reduce the cost of the secondary sexual character. As noted above, such comparative studies require phylogenetically based statistical methods.

Alternatively, the effects of an assumed costly trait in males could be compared with its effects in females of the same species, with the general perspective that values of the trait in females are nearer to the optimum set by prevailing natural selection (Lande 1980). Most morphometric traits have strong positive genetic correlations between the sexes (Lande 1980; Falconer & Mackay 1996; Møller 1996; Badyaev 2002). Therefore the absence of a putatively sexually selected trait in females suggests that natural selection is acting against it in that sex. Some sexually selected traits are sex-limited, females lacking them entirely, as in some bird songs, or the swords of *Xiphophorus* species. In that case, we obviously cannot study the effects of the trait in females within a given population. However, we can study several populations and/or species that vary in the degree of the trait in the male, compute mean values for each population or species, and then determine whether the difference in the sexually selected trait (mean male value − mean female value) is associated with the difference in locomotor performance or survival. Note that sexual dimorphism in body size is most commonly studied as a ratio of male/female size (Balmford *et al*. 1994; see recent discussion by Cox *et al*. 2003), but that cannot be done for a trait that is absent in females. In our hypothetical example, analysis of differences between male and female traits yielded similar results. In both cases, the sword has a positive effect when ventricle mass is not included

in the model, but the negative effect of the sword is observed when ventricle mass is included (Fig. 6).

The above-mentioned approaches are complicated by several biological and statistical issues. Morphology, performance and components of Darwinian fitness are often correlated with body size, and body size is often sexually dimorphic. Therefore body size will generally need to be considered in any study of a sexually selected trait. The causes of body size dimorphism are numerous (see reviews by Fairbairn 1997; Cox *et al*. 2003), and body size itself is often thought to be the subject of fairly intense sexual selection. One classic example is pinnipeds, in which interspecific variation in male/female size is strongly positively correlated with harem size (Alexander *et al*. 1979; other examples of comparative analyses of size dimorphism in vertebrates include a rare common-garden study by Dewsbury *et al*. 1980; Oakes 1992; Emerson 1994; Pyron 1996; Cox *et al*. 2003). Given that body size affects almost all an organism's properties, including visibility and fighting ability (Briffa & Sneddon 2007), it is often difficult to know whether selection has acted on size *per se* or on some correlated trait. Moreover, one 'easy' way for selection to change a trait, such as fecundity or locomotor endurance (Garland 1994b), may be just to change body size.

However, the study of sexual dimorphism in body size itself as an indicator of sexual selection is problematic because the appropriate null model is not necessarily that the sexes should be equal in size. Male and female size are likely to be strongly positively genetically correlated within populations (see review by Badyaev 2002), which should tend to inhibit sexual divergence in body size (Lande 1980), but both empirical and theoretical studies suggest that this will not always be a strong constraint on the evolution of sexual dimorphism (Reeve & Fairbairn 1996, 2001). In addition, assuming that the positive genetic correlation between male and female size is not too strong a constraint, sex differences in size would be expected, for three obvious reasons. First, given their very different roles in reproduction and associated behavioural ecology, one might generally expect different sex-specific optima from the standpoint of natural selection alone. Second, differences in reproductive activities are likely to lead to differences in energy expenditure, which would, in turn, affect growth rate and thus adult body size (Anderson & Vitt 1990). Third, differences in the hormonal milieu may lead to sex differences in growth and differentiation of various organs, behaviour (including general activity levels), energy expenditure and partitioning, and hence body size at most ages (Cox *et al*. 2005). Thus any difference in body size cannot be taken as clear evidence of past sexual selection. This line of reasoning is similar to arguments that have been used to point out limitations of comparative studies involving only two species (Garland & Adolph 1994). As reviewed by Badyaev (2002), an important area for future research is detailed studies of

sex-specific regulatory mechanisms that allow sex-specific expression of genes that are shared between the sexes. Most genes that underlie sexual size dimorphism are not on the sex chromosomes, so sex-specific regulatory mechanisms must account for most size dimorphism.

The study of secondary sexual characters (genetically determined sex characteristics that are not directly connected with the act of reproduction and/or characteristics that have been shaped by sexual selection) as indicators of sexual selection suffers less from such problems, for several reasons. First, differences in energy expenditure would not lead as directly to sex differences in secondary sexual characters, compared with growth rate and hence body size. Second, the significance of many secondary sex characteristics (e.g. human male facial hair) with respect to natural selection seems far lower than for body size, which affects, or at least is correlated with, innumerable other traits. Therefore, by default, sex differences in secondary sexual characters are more likely to be the result of sexual selection. Third, the evolution of sex differences in secondary characters should be relatively easy because most are controlled primarily by the gonadal steroids via tissue-specific differences in responsiveness.

Measures of an organism's performance, such as locomotor endurance, may be affected by both body size and secondary sexual characters (Fig. 1), as well as the hormonal milieu (Sinervo *et al.* 2000, 2007). All else being equal, body size is likely to have a positive effect on endurance-type activities (Garland 1984, 1994b), but a negative effect on acceleration and manoeuvrability. It has been suggested that the 'reversed' sexual size dimorphism (males smaller than females) in some groups of birds probably evolved in response to female choice for acrobatic display elements (Prum 1997). Similarly, habitat height is negatively correlated with male/female size in spiders, consistent with the hypothesis that smaller males are favoured in species in which males must climb to reach females located in high habitats (Moya-Laraño *et al.* 2002). As discussed above, many secondary sexual characters (e.g. elongated tail feathers of birds) would be expected to have a negative effect on most measures of locomotor performance. However, such effects may not be apparent if organisms have evolved compensatory mechanisms to overcome the handicap (Balmford *et al.* 1994; Møller 1996). Thus locomotor performance poses an interesting topic of study for those interested in sexual selection and its consequences. If a putatively sexually selected trait covaries with body size, then this correlation needs to be accommodated (Fig. 6). If the trait under consideration scales isometrically with body size, then a simple ratio of trait/size can be used (Balmford *et al.* 1994).

Concluding remarks

We encourage future studies to take an integrative, multilevel and functionally informed approach to the study of sexual selection, physiology and performance. We also encourage those who work on sexual selection to take a more pluralistic view and acknowledge in their research programmes that all traits may also be subject to natural selection (see King 1989 on snake tail lengths), even some of the classic examples of sexually selected traits, such as bird tail feathers (Buchanan & Evans 2000; Aparicio *et al.* 2003). At the same time, we would caution adaptationists that even our most cherished examples may have been shaped by sexual selection to a greater extent than we have imagined. For example, Simmons & Scheepers (1996) have argued that the elongated neck of giraffes evolved primarily in response to sexual selection, rather than natural selection related to feeding at high levels, as is traditionally presented in text books. Much work remains to be done in sorting out the relative importance of natural selection, sexual selection and genetic drift; phenotypic plasticity; how pleiotropic gene action may constrain or facilitate the rate and direction of multivariate, hierarchical evolution; and how fundamental biochemical and biophysical properties may constrain the possible 'morphospace' into which organisms can evolve. Equilibria set by the balance between natural and sexual selection – within the confines determined by genetic architecture, developmental and physiological mechanisms – will be dynamic as environmental and demographic conditions change, thus causing temporal changes in the selective regime, and evolution of the genetic architecture itself.

Acknowledgements

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