How does selection operate on whole-organism functional performance capacities? A review and synthesis

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ABSTRACT

Hypothesis: Natural and sexual selection should be stronger on whole-organism functional performance traits (sprinting, biting) than on correlated morphological variables.

Organisms: Lizards, snakes, turtles, frogs, and fish (review of past field and laboratory studies).

Field sites: Various (review of past field and laboratory studies).

Methods: We reviewed existing literature on the nature and intensity of natural and sexual selection on whole-organism performance traits. We answer some key questions in regards to how selection operates on performance, and whether selection is stronger on performance compared with morphological traits.

Results: We identified 23 studies that have quantified selection on performance. Natural and sexual selection were typically directional in nature, with a distinct preference for high rather than low values of performance. However, some studies uncovered no significant selection on performance, and there was also no evidence that selection was stronger on performance traits than morphological traits.

Keywords: ecology, evolution, locomotion, performance selection.

INTRODUCTION

Empirical studies of natural and sexual selection have proved invaluable in advancing our understanding of the evolutionary process (Arnold, 1983; Lande and Arnold, 1983; Endler, 1986; Kingsolver and Schemske, 1991; Brodie *et al.*, 1995; Kingsolver and Pfenning, 2007). Since its formulation, the concept of natural selection, and its close cousin, sexual selection, has stimulated numerous theoretical

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and empirical treatments (Kingsolver and Schemske, 1991; Kingsolver and Pfenning, 2007). Endler (1986) provided one of the first comprehensive overviews of field studies of natural selection. His review went a long way towards convincing researchers that natural selection in nature can be feasibly studied, and is, in many cases, surprisingly strong. Kingsolver *et al.* (2001) provided a 15-year update on field studies of natural selection published up until 1997 based on a comprehensive investigation of the strength of natural selection for various traits. Their extensive review found weaker selection on average than Endler (1986) did, and indicated that non-directional selection was typically weak (but see Hereford *et al.*, 2004). Thus, these two reviews have conclusively shown that (1) many researchers have successfully quantified natural selection in nature, and (2) the typical strength of selection in nature is not entirely understood (see Hereford *et al.*, 2004 as well), with some authors arguing for strong selection (Endler, 1986; Hereford *et al.*, 2004) and others arguing for relatively weak selection (Kingsolver *et al.*, 2001).

However, a close read of both Endler (1986) and Kingsolver *et al.* (2001) reveals key gaps in our understanding of natural selection. Despite hundreds of studies of natural and sexual selection, the total number of selection studies on whole-organism traits, such as behaviour or functional capacities (i.e. performance), was vanishingly small prior to 1997 (Kingsolver *et al.*, 2001). In this paper, we define whole-organism performance capacity as the ability of an animal to conduct an ecologically relevant task [e.g. sprint speed, bite force or locomotor endurance (see Lailvaux and Irschick, 2006)]. Our definition focuses on aspects of performance related to dynamic animal movements, as opposed to more 'passive' measures of performance, such as levels of immune function or reproductive output. Several pre-conditions exist for a 'performance' trait to be considered in our review. First, the task must be physically challenging, such as in the case of sprinting rapidly or locomotor endurance, both of which push the musculoskeletal system to its limits, although in different ways. Second, we focus on 'maximum performance' as opposed to submaximal performance (e.g. McElroy *et al.*, 2007). This combination is important because if animals are being pushed to their maximum capacity, and if the task itself is challenging, one is expected to observe variation among individuals that should be closely tied to variation in morphology, physiology, and fitness. By contrast, if the task itself is not physically challenging, or if animals are not pushed to their limits, then links between performance and fitness may be weak or non-existent. For example, one could measure the number of pages that a person reads per year, or the total amount of money that a person earns, but neither trait would shed much light on evolutionary issues such as those being discussed here. Third, we explicitly focus on performance traits emergent at the whole-organism level, as opposed to potential measures within an organism (e.g. enzyme reaction rate). We recognize that our definition is not the only valid one, but it is important for ensuring proper comparison among different kinds of studies. Any discussion of the definition of performance is also important if one is to review studies that link this trait to fitness. Fitness has been defined in many different ways in selection studies, including measures of survival, growth, and reproductive success, among others (see Janzen and Stern, 1998). Consequently, there is potential for overlap between measures of 'performance' and 'fitness', for example in the case of growth rate. Based on our definition of performance above, this is not a problem for our review, and the studies we reviewed (Table 1) used simple and widely accepted measures of fitness (survival, reproductive success, and in one study evasion success).

As defined, such performance traits reflect the interaction of several underlying physiological processes and are often important during ecological tasks relevant for natural and

sexual selection, such as competition for food, predator avoidance, territory defence, and mate choice (Huey and Stevenson, 1979; Garland and Losos, 1994; Irschick and Garland, 2001; Oufiero and Garland, 2007). Based on any definition of animal performance, more than 80% of the selection estimates available at the time of Kingsolver and colleagues' (2001) paper were for morphological traits and only a handful of studies presented data on selection on performance traits (e.g. Jayne and Bennett, 1990). However, several selection studies on behaviour and performance have been published in the past 10 years (e.g. Miles *et al.*, 2000; Warner and Andrews, 2002; Le Galliard *et al.*, 2004; Miles, 2004; Lappin and Husak, 2005; Walker *et al.*, 2005; Husak *et al.*, 2006; Kaplan and Phillips, 2006; Calsbeek and Irschick, 2007; Irschick and Meyers, 2007). In combination with older studies, these available results provide, we believe, a critical mass that merits review and synthesis. We note that a recent review highlighted new perspectives on how researchers can study natural and sexual selection on whole-organism performance capacity and on communities (Irschick *et al.*, 2007a). Our review diverges from that study, because whereas Irschick *et al.* (2007a) discussed a few case studies of selection on performance in detail, here we review all known studies, and statistically compare the strength of selection for performance traits versus morphological traits (following Kingsolver *et al.*, 2001).

The most compelling reason for conducting a review of selection studies on performance is to address whether selection on performance is inherently stronger than selection on morphology. The issue of the 'pace' of evolutionary change is becoming increasingly prominent in the mind of scientists and the public (Hendry and Kinnison, 1999; Hendry *et al.*, 2006; Carroll *et al.*, 2007). More recently, researchers have adopted an experimental approach to this subject by using laboratory selection studies of select vertebrates [i.e. mice (Bronikowski *et al.*, 2006)] or rapidly breeding invertebrates [i.e. *Drosophilla* (Gibbs, 1999)] and microorganisms [e.g. bacteria (Bennett *et al.*, 1990)]. Depending on the circumstances (e.g. laboratory selection, selection in nature), selection can occur on the phenotype (e.g. if a researcher only allowed flies with long wings to survive), with correlated effects on other aspects of the phenotype or emergent functional properties, or on performance traits, such as in the case of fast lizards being favoured by natural selection because of their ability to flee predators. The key point is that multicollinearity among traits under selection is both common and expected (Mitchell-Olds and Shaw, 1987), and differentiating between direct and indirect selection is a significant challenge that requires a great deal of information on the natural history of the study organism. Therefore, how the intensity of selection on performance compares to morphological traits is an open question that may be heavily influenced by interrcorrelations among variables. Finally, it is also important to consider the possibility that, in some cases, selection may favour 'poor' performance, such as the case where the performance trait is energetically costly, or if it trades off with some other trait that is more important (i.e. such as a potential trade-off between speed and stamina).

Previous research has successfully used both heuristic path diagrams (Arnold, 1983) and statistical path analysis (for an overview, see Kingsolver and Schemske, 1991) to dissect interrelationships among different kinds of variables and their effects on fitness (for an instructive example, see Kaplan and Phillips, 2006). Heuristic path diagrams have been reformulated in many different ways, but we present Fig. 1 as a reasonable starting point for interpreting the results of this review. We adopt the path diagram used by Kaplan and Phillips (2006) that stresses the interrelationships among five factors: environment, development, morphology, performance, and fitness. They argue, and we agree, that environmental and developmental processes interact to produce phenotypes that selection can act upon. Selection itself can act on different factors within this diagram; for example, selection may remove defective phenotypes that
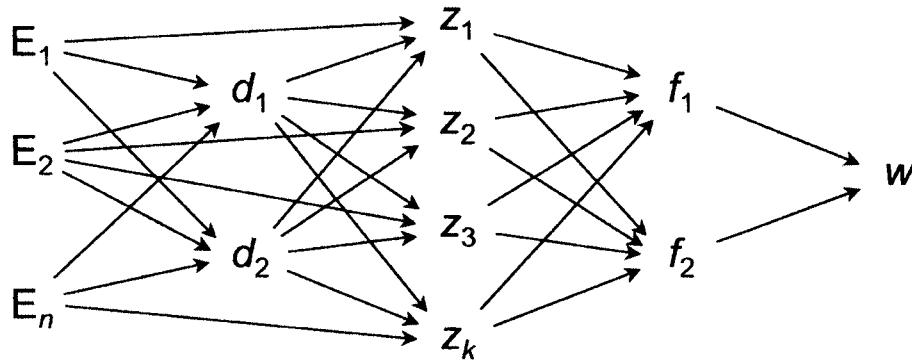
Fig. 1. A path diagram showing hypothetical interrelationships among five factors: the environment, development, morphology, performance, and fitness. Reproduced from Kaplan and Phillips (2006) with permission.

die because of developmental abnormalities, or selection might remove animals with inferior adult phenotypes that produce poor performance capacities. Missing from this diagram is the role of behaviour that other researchers (Garland and Losos, 1994) have emphasized. The importance of behaviour is two-fold. First, selection can occur on behaviour itself, such as an individual being picked off by a predator because of it continually going out into open areas, for example. Second, behaviour can alter the relationship between morphology and performance (Lauder and Reilly, 1996), making a path diagram far less easy to predict based on simple biomechanical relationships. Because the role of behaviour in selection studies is unclear, we use the path diagram of Kaplan and Phillips (2006) as a good starting point with the caveat that future studies should incorporate the role of behaviour.

   Any review of the strength of selection needs to take several factors into account. First, the intensity of selection on any trait (morphological and performance) is not likely to be constant either temporally or spatially. Fluctuating weather patterns, seasonal changes, and the impact of increasingly common ecological disturbances (e.g. hurricanes) imply that selection on any trait is rarely static (Grant, 1999). Some authors have argued that if selection is generally weak, and rarely stabilizing, then this provides evidence that the adaptive landscape may be constantly shifting, preventing traits from achieving stable adaptive configurations (Kingsolver and Pfenning, 2007). Whether such temporal changes differentially affect selection on performance or morphological traits is unclear, however. A second consideration is that traits as initially measured in selection studies (i.e. 'pre-selection' values) are frequently not static. In cases where the trait of interest is highly plastic – such as in plants (Schlichting, 1986) or in the tail fins of tadpoles (Van Buskirk and Relyea, 1998) – then understanding the type and magnitude of plasticity is crucial for predicting the long-term response to selection. Short-term plastic responses (e.g. enlarged muscle fibre size as a response to weight-lifting) are well known in humans, although this phenomenon may not always extend to animal taxa (see, for example, Gleeson, 1979). Finally, although selection can act upon traits, evolutionary change will not occur if the traits do not exhibit a genetic basis (i.e. are not heritable). Studies with garter snakes (Garland *et al.*, 1990) and *Sceloporus* lizards (Tsuji *et al.*, 1989) have shown significant heritabilities for performance traits (range of 0.30–0.36 for speed and stamina for *Sceloporus*, 0.58 for sprint speed for *Thamnophis* snakes), and

although other studies are needed, these data suggest that one can proceed with the view that significant selection on performance will likely yield evolutionary change.

Here, we take a synthetic view of selection on performance traits based on an overview of 23 selection studies published so far, and available to us (Table 1). The criterion for including these studies was that they measured natural or sexual selection for at least one performance trait. Our foremost goal is to provide a summary of the progress for selection studies on performance capacities and, as much as possible, a practical guide for researchers interested in studying selection on performance in nature. A second goal is to address four key questions that are likely to interest researchers:

1. Is selection on performance always directional?
2. Do sexual and natural selection operate in the same direction?
3. Does the strength of selection differ between morphology and performance?
4. Are plastic performance traits under selection?

The first and third questions are particularly interesting in the light of recent reviews examining the 'pace' of evolution in modern times (Hendry and Kinnison, 1999; Kingsolver *et al.*, 2001; Carroll *et al.*, 2007). However, quantifying the pace of selection across different studies is challenging because of differences in the taxa studied, sample sizes, and the time period and fitness components over which selection is measured. Other researchers have successfully used either the unit of Darwins (Hendry and Kinnison, 1999) or standardized selection coefficients as measures of selection (Kingsolver *et al.*, 2001). Here, we were only able to compare standardized measures of the strength and direction of selection for studies that have already published these values (following Kingsolver *et al.*, 2001). We compiled estimates of variance-standardized linear and quadratic selection gradients (Hereford *et al.*, 2004) for all performance traits and fitness components available to us (Table 1). The linear gradients (β) measure the change in relative fitness for a change of one standard deviation of the trait mean and allows comparison of the strength of directional selection (Lande and Arnold, 1983; Kingsolver *et al.*, 2001). The quadratic gradients (γ) measure the curvature of the selection surface and enable comparison of the shape of selection (i.e. disruptive versus stabilizing selection). Of the 23 studies reviewed, we obtained 47 estimates of β terms and 32 estimates of γ terms, a significant step forward relative to the previous review (Kingsolver *et al.*, 2001).

SUMMARY OF PROGRESS FOR SELECTION STUDIES

Mark–recapture studies of natural populations

The most common method to assess selection is to conduct mark–recapture studies on individuals in the field. Researchers initially mark a sample of individuals from a population, and then re-sample the population at a later date (e.g. 6 months, a year). Survivors are then compared against the non-survivors for some trait of interest (e.g. morphology, performance trait). One could also combine mark–recapture with genetic studies of paternity to establish another measure of fitness [reproductive success (see Husak *et al.*, 2006)]. One advantage to the mark–recapture method is the natural setting under which selection is quantified. Understanding how selection operates on organismal traits in a natural setting is invaluable, especially for studying how annual or seasonal variation in environmental conditions (e.g. rainfall) affects fitness (Brodie *et al.*, 1995). Some challenges

Table 1. List of studies of natural and sexual selection on performance in reptiles, fish, and amphibians

Locomotor trait	Species	N	Setting	Age class	Duration	Fitness measure	Linear	Quadratic	Ref.
							Selection gradients		
Swimming speed	*Chelydra serpentina*	121	Enclosure study	Hatchlings	1 year	Survival	0.809	0.719	(1)
Endurance capacity	*Lacerta vivipara*	67	Enclosure study	Adult males	1 year	Siring success	0.122	−0.016*	(2)
Endurance capacity	*Lacerta vivipara*	88	Enclosure study	Adult males	1 year	Survival	−0.073	0.006*	(2)
Endurance capacity	*Lacerta vivipara*	59	Enclosure study	Yearlings	1 year	Survival	0.280	0.007*	(2)
Endurance capacity	*Lacerta vivipara*	441	Enclosure study	Hatchlings	1 year	Survival	0.127	−0.023*	(3)
Swimming speed	*Nerodia sipedon*	711	Enclosure study	Hatchlings	3 months	Survival	S (+)	NA	(4)
Swimming speed	*Nerodia sipedon*	513	Enclosure study	Hatchlings	6 months	Survival	S (+)	NA	(4)
Swimming speed	*Pseudacris regilla*		Laboratory study	Tadpole larvae		Evasion success	S	NA	(5)
Swimming speed	*Poecilia reticulata*	55	Laboratory study	Adults	Minutes	Evasion success	N.s.	NA	(6)
Sprint speed	*Bombina orientalis*	940	Enclosure study	Hatchlings	1 day	Survival	0.185	NA	(7)
Sprint speed	*Bombina orientalis*	632	Enclosure study	Hatchlings	1 day	Survival	0.104	NA	(7)
Endurance capacity	*Uta stransburiana*	35	Field experiment	Adult females	1–3 months	Survival	0.270	−0.004	(8)
Sprint speed	*Sceloporus undulatus*	220	Field experiment	Hatchlings	6 weeks	Survival	0.177*	−0.059*	(9)
Sprint speed	*Sceloporus undulatus*	220	Field experiment	Hatchlings	12 weeks	Survival	0.154*	−0.085*	(9)
Sprint speed	*Sceloporus undulatus*	220	Field experiment	Hatchlings	10 months	Survival	0.149*	−0.069*	(9)
Endurance capacity	*Lacerta vivipara*	610	Field study	Hatchlings	1 year	Survival	N.s.	N.A.	(10)
Endurance capacity	*Sceloporus merriami*	NA	Field study	Adults	1–10 months	Survival	N.s.	N.A.	(11a)
Endurance capacity	*Sceloporus merriami*	NA	Field study	Adults	1–10 months	Survival	N.s.	N.A.	(11a)
Endurance capacity	*Sceloporus occidentalis*	296	Field study	Hatchlings	6 weeks	Survival	N.s.	N.A.	(11b)
Endurance capacity	*Thamnophis sirtalis*	113	Field study	Adults	1 year	Survival	0.110	n.s.	(12)
Endurance capacity	*Thamnophis sirtalis*	275	Field study	Hatchlings	1 year	Survival	0.093	n.s.	(12)
Endurance capacity	*Thamnophis sirtalis*	86	Field study	Hatchlings	1 year	Survival	0.067	n.s.	(12)
Endurance capacity	*Thamnophis sirtalis*	250	Field study	Yearlings	1 year	Survival	0.001	n.s.	(12)
Endurance capacity	*Anolis sagrei*	147	Field study	Adult males	4 months	Survival	0.120*	0.030*	(13)
Endurance capacity	*Anolis sagrei*	80	Field study	Adult males	4 months	Survival	0.060*	−0.050*	(13)
Endurance capacity	*Anolis sagrei*	90	Field study	Adult males	4 months	Survival	−0.040*	0.090*	(13)
Endurance capacity	*Anolis sagrei*	166	Field study	Adult females	4 months	Survival	0.080*	0.040*	(14)
Distance capacity	*Thamnophis sirtalis*	113	Field study	Adults	1 year	Survival	0.128	n.s.	(12)
Distance capacity	*Thamnophis sirtalis*	275	Field study	Hatchlings	1 year	Survival	0.094	n.s.	(12)

Trait	Species	n	Setting	Age class	Duration	Fitness component	Linear	Quadratic	Ref.
Distance capacity	*Thamnophis sirtalis*	86	Field study	Hatchlings	1 year	Survival	0.012	N.s.	(12)
Distance capacity	*Thamnophis sirtalis*	250	Field study	Yearlings	1 year	Survival	0.104	N.s.	(12)
Distance capacity	*Thamnophis ordinoides*	646	Field study	Hatchlings	1 year	Survival	−0.059	−0.122	(15)
Sprint speed escaping	*Crotaphytus collaris*	60	Field study	Adults	1 year	Survival	0.383	−0.341*	(16)
Sprint speed foraging	*Crotaphytus collaris*	60	Field study	Adults	1 year	Survival	0.063	−0.102*	(16)
Sprint sensitivity	*Anolis sagrei*	147	Field study	Adult males	4 months	Survival	0.030	0.001	(13)
Sprint sensitivity	*Anolis sagrei*	80	Field study	Adult males	4 months	Survival	−0.010	−0.040	(13)
Sprint sensitivity	*Anolis sagrei*	90	Field study	Adult males	4 months	Survival	0.030	−0.007	(13)
Sprint speed	*Thamnophis sirtalis*	86	Field study	Hatchlings	1 year	Survival	0.071	N.s.	(12)
Sprint speed	*Thamnophis sirtalis*	275	Field study	Hatchlings	1 year	Survival	−0.154	N.s.	(12)
Sprint speed	*Thamnophis sirtalis*	113	Field study	Adults	1 year	Survival	0.265	N.s.	(12)
Sprint speed	*Thamnophis sirtalis*	250	Field study	Yearlings	1 year	Survival	0.122	N.s.	(12)
Sprint speed	*Thamnophis ordinoides*	646	Field study	Hatchlings	1 year	Survival	0.119	−0.055	(15)
Sprint speed	*Sceloporus occidentalis*	296	Field study	Hatchlings	6 weeks	Survival	N.s.	N.A.	(11b)
Sprint speed	*Crotaphytus collaris*	19	Field study	Adult males	1 year	Siring success	0.640	0.022*	(17)
Sprint speed	*Crotaphytus collaris*	64	Field study	Hatchlings	1 year	Survival	0.270	−0.023*	(18)
Sprint speed	*Urosaurus ornatus*	45	Field study	Hatchlings	1 year	Survival	0.110	0.190	(19)
Sprint speed	*Urosaurus ornatus*	43	Field study	Adult females	4 months	Survival	−0.161*	−0.138*	(20)
Sprint speed	*Urosaurus ornatus*	57	Field study	Adult males	4 months	Survival	0.428*	−0.378*	(20)
Sprint speed	*Anolis sagrei*	147	Field study	Adult males	4 months	Survival	−0.090*	0.030*	(13)
Sprint speed	*Anolis sagrei*	80	Field study	Adult males	4 months	Survival	−0.160*	−0.020*	(13)
Sprint speed	*Anolis sagrei*	90	Field study	Adult males	4 months	Survival	−0.090*	0.230*	(13)
Sprint speed	*Anolis sagrei*	166	Field study	Adult females	4 months	Survival	−0.130*	0.050*	(14)
Sprint speed	*Chelydra serpentina*	112	Field study	Hatchlings	3 days	Survival	−0.001	N.A.	(21)
Movement rate	*Lacerta agilis*	28	Field study	Adult males	1 week	# offspring	0.069	N.A.	(22)
Bite force	*Urosaurus ornatus*	43	Field study	Adult females	4 months	Survival	−0.518*	−0.225*	(20)
Bite force	*Urosaurus ornatus*	57	Field study	Adult males	4 months	Survival	0.284*	0.240*	(20)

Note: For each selection analysis, we report on the locomotor trait examined, study species, sample size, setting, age class examined, study duration, and fitness component examined. We also report, where feasible, the standardized linear and quadratic selection gradients. N.s., not significant; S, significant; N.s., not available.

References: (1) Janzen (1995); (2) Le Galliard and Ferrière (2008); (3) Le Galliard *et al.* (2004); (4) Kissner and Weatherhead (2005); (5) Watkins (1996); (6) Walker *et al.* (2005); (7) Kaplan and Phillips (2006); (8) Miles *et al.* (2000); (9) Warner and Andrews (2002); (10) Clobert *et al.* (2000); (11a) A. Dunham (personal communication, in Bennett and Huey, 1990); (11b) R.B. Huey (personal communication, in Bennett and Huey, 1990); (12) Jayne and Bennett (1990); (13) Calsbeek and Irschick (2007); (14) Calsbeek (2008); (15) Brodie (1992); (16) Husak (2006a); (17) Husak *et al.* (2006); (18) Husak (2006b); (19) Miles (2004); (20) Irschick and Meyers (2007); (21) Janzen (1993); (22) Olsson *et al.* (2000).

*Kindly communicated by the first author based on statistical data presented in the reference.

include the likelihood of multicollinearity among study variables [especially when using regression analyses among large sets of variables in natural settings (Mitchell-Olds and Shaw, 1987)], the need for large sample sizes for proper statistical analyses (Janzen and Stern, 1998), and the large amount of time that must be devoted to effectively mark the majority of the study population. This method is also subject to an insidious trade-off. Statistical analyses of selection, such as logistic regression (Janzen and Stern, 1998), require relatively large sample sizes to achieve reasonable power (Hersch and Phillips, 2004), and therefore large populations are desirable. However, this aim is opposed by the need for comprehensive marking of individuals, which is best accomplished in small, closed populations, such as might occur on an island, which severely limits emigration and immigration (see Kingsolver, 1999).

One of the first published comprehensive field studies of natural selection on performance was that of Jayne and Bennett (1990), who marked a large sample of juvenile garter snakes (>500 individuals) born from gravid females captured in nature. Jayne and Bennett (1990) measured maximum sprint speed and endurance on juvenile garter snakes and their analysis demonstrated that selection varies between years, as selection favoured high sprint speeds in one year, but not in the other. Furthermore, there was some evidence of stabilizing selection on endurance in sub-adult snakes. In a recent series of studies, Husak and colleagues (Husak, 2006b; Husak *et al.*, 2006) completed mark–recapture studies of collared lizards (*Crotaphytus collaris*). They were able to test the adaptive significance of two performance variables (bite force and sprint speed), associated morphological variables (head shape and hindlimb length), and hormone concentrations (testosterone). By both marking adult males and females, and also acquiring genetic data from juveniles and their likely parents, they determined whether enhanced performance resulted in higher reproductive success. Adult males with high bite forces and sprint speeds had greater reproductive success, but were not more likely to survive to the following year (Husak, 2006b; Husak *et al.*, 2006). Faster hatchlings, however, had a survival advantage over slower individuals. Thus, they detected ontogenetic differences in the strength of selection on a performance trait. However, there was no significant link between testosterone concentrations and performance, or between hormone concentrations and reproductive success and survival.

Other field studies have shown strong support for directional natural selection favouring high performance. Recent work on the lizard *Urosaurus ornatus* by both Miles (2004) and Irschick and Meyers (2007) found positive directional selection for high sprint speeds on the probability of survival in juveniles and adult males, respectively. There was also a weak stabilizing trend on sprint speed in the study by Irschick and Meyers (2007). Warner and Andrews (2002) reported similar significant support for selection favouring high sprint speeds in juvenile *Sceloporus undulatus* lizards. Finally, a recent study revealed some of the complexities of selection on performance. Calsbeek and Irschick (2007) measured habitat use, morphology, and sprint speed on both broad and narrow dowels in male juvenile *Anolis sagrei* lizards on several small Bahamian islands, and then examined survival to maturity. Their analysis revealed two fitness peaks, one corresponding to lizards that had low sprint sensitivity (sprinted relatively equally well on broad and narrow dowels), occupied narrow perches, and had short hindlimbs, and the other for lizards with high sprint sensitivity, occupied broad perches, and had long hindlimbs. This result is eerily familiar to macro-evolutionary patterns across different Caribbean *Anolis* species [e.g. twig versus trunk specialists (Losos, 1994)], hinting at a microevolutionary mechanism for broader patterns of island anole diversity.

One of the few examples of significant stabilizing selection comes from a mark–recapture study on the lizard *Uta stansburiana* by Miles *et al.* (2000), who found evidence for quadratic selection on endurance capacity in female lizards. Experimental removal of follicles before ovulation caused a lower reproductive burden and increased endurance performances in female lizards. The experimental increase in endurance capacity relaxed some of the mortality costs of reproduction except for the very high performance females (Miles *et al.*, 2000).

Finally, several mark–recapture studies found no evidence for significant selection on locomotor performance. In two separate studies, Janzen (1993, 1995) reported non-significant selection on sprint speed and swimming speed, respectively, in hatchling snapping turtles (*Chelydra serpentina*). Ray Huey and colleagues found no evidence for significant selection on maximum sprint speed and endurance capacity in the lizards *Sceloporus occidentalis* and *Sceloporus merriami* (R. Huey, personal communication). Clobert *et al.* (2000) found no evidence for selection on endurance capacity in hatchling common lizards (*Lacerta vivipara*) that were measured directly after birth and released into nature, although later analyses (Le Galliard and Ferrière, 2008) showed some evidence for directional selection against low endurance in juvenile *L. vivipara* in semi-natural enclosures. Brodie (1992) found no significant selection on sprint speed in hatchling garter snakes (*Thamnophis ordinoides*) despite a large sample size (Table 1). Finally, in the lizard *Lacerta agilis*, there was no evidence of selection on movement rate (Olsson *et al.*, 2000). Although unusual among the other studies here, movement rate is a useful variable that may provide an index of aerobic capacity in reptiles.

Semi-natural experiments

Natural mark–recapture field studies do not represent the only means of studying the effects of variation in fitness arising as a consequence of performance variation. An interesting approach consists of semi-natural experimental arenas that represent 'halfway houses' between controlled environments and natural habitats. Such experiments typically consist of large enclosed arenas in which a sample of animals can be easily marked and recaptured, and in which key predators can also be placed. Small aquatic organisms such as fish and tadpoles represent particularly fitting systems for this approach, as these animals often occur naturally in small, enclosed ponds. An advantage of this semi-natural approach is the ability to manipulate and measure the target population at higher levels of detail compared with in the field. In the field, for most species, scientists are able to mark only a subset of the population of interest, and continual immigration and emigration are a constant source of concern (Kingsolver, 1999). By comparison, in semi-natural experiments, scientists can realistically mark every individual being used, while measuring performance and morphology on them as well. Even more interestingly, one can also measure the performance of the predator itself, therefore providing a complete index of how performance affects fitness in both predators and prey.

Several studies have successfully used this approach. Walker *et al.* (2005) quantified selection on fast-start performance in guppies (*Poecilia reticulata*) arising as a result of predation by a fish predator. They tested the hypothesis that faster fast-start escape responses in small fish result in higher fitness when the predator is a larger fish. Their data support this hypothesis, and also indicate that the direction of the escape response is a crucial component of a successful escape response for a fish. Watkins (1996) used a similar approach to determine whether selection favours fast-start swim speeds in tadpoles using

garter snakes (*Thamnophis*) as a predator. Similar to Walker *et al.* (2005), faster tadpoles were more successful in escaping the snake predator than slower tadpoles. O'Steen *et al.* (2002) revealed an interesting twist on a selection study by determining whether populations of Trinidadian guppies (*Poecilia reticulata*) introduced to low- and high-predation regimes in Trinidad 26–36 generations prior to the study had evolved to match their local surroundings in terms of their escape responses and performance. Consistent with predictions, they found that guppies introduced into a high-predation pond from a low-predation pond were more likely to survive encounters with a natural predator (a chiclid fish) than guppies that had been introduced into a low-predation pond. While not a selection study in the traditional sense, this paper reveals the end product of the selection process, and shows how performance capacity can evolve rapidly to match predation conditions. In enclosure experiments with the watersnake *Nerodia sipedon*, Kissner and Weatherhead (2005) showed that snakes with high sprint speeds were significantly more likely to survive overwintering than slower snakes; however, because of the nature of the enclosures (that likely excluded most predators), the reason for this result is unclear.

Le Galliard *et al.* (2004) conducted a study in which they examined selection on locomotor endurance in common lizards (*Lacerta vivipara*) inhabiting large enclosures. Their goal was to simultaneously examine growth and survival as lizards matured to become adults under different food regimes. They found that lizards with initially poor endurance could become better performers over time by feeding more (i.e. compensation). Selection disfavoured lizards that had low endurance values at birth, but the nature of this selection was not static, as the performance values of individuals changed over time, particularly in relation to food levels. In a complementary study, Le Galliard and Ferrière (2008) present new data that confirm directional selection acting on yearling lizards for endurance capacity, although there was no significant selection in adult males. We note that not all studies have shown that food levels experienced during early growth ultimately affect performance (for an example with fish, see Royle *et al.*, 2006).

Finally, in a particularly elegant study, Kaplan and Phillips (2006) examined interrelationships among environmental conditions (e.g. temperature), development, morphology, and performance (sprint speed in tadpoles) in the toad *Bombina orientalis* in controlled enclosures. The authors examined interactions between the environmental context in which tadpoles and their mothers were raised, their ultimate morphology, and their ability to survive predation events from predatory tadpoles of another species. Kaplan and Phillips (2006) found that increases in incubation temperature increased tail length, thereby increasing speed, and ultimately the likelihood of survival. However, interactions were complicated among different aspects of temperature, morphology, performance, and fitness and the authors suggest that, in some cases, increased maternal investment can negatively affect offspring across a range of environmental conditions.

Two related studies that did not directly measure selection on performance, but did measure selection on a morphological trait (vertebral number) that relates directly to performance (burst speed), merit mention. Swain (1992a) showed that burst speed in the stickleback fish *Gasterosteus aculeatus* was positively related to the ratio of abdominal to caudal vertebrae (VR). Swain (1992a) also provided some evidence of selection on vertebral phenotypes in nature that seemed to indicate a favouring of only the fastest fish. Moreover, in laboratory predation trials with sunfish, Swain (1992b) showed that the direction of selection was size-dependent; as body length of the sticklebacks increased, the 'optimal' VR ratio declined, and there was evidence for both direct and indirect selection that acted

in opposing directions for certain larval lengths. This finding suggests that vertebral diversity may be maintained by opposing kinds of selection that act differently at different fish body sizes.

FOUR QUESTIONS OF INTEREST

Is selection on performance always directional?

Although rarely stated implicitly, most researchers believe that any selection on performance should be both positive and directional. Indeed, at first glance, the alternatives seem difficult to justify. Stabilizing selection implies that selection favours neither particularly good nor bad performance. Negative directional selection implies a favouring of particularly bad performance, which has, to our knowledge, never been tested for specifically, although one could envision scenarios in which it could happen. However, reviews of selection studies have cautioned against such overly simplistic views (e.g. Kingsolver and Pfenning, 2007). For example, the potential for disruptive selection, in which there are distinct performance peaks, merits some serious consideration, especially given the well-documented presence of discrete male 'morphs', such as are commonly found across animal taxa (Gross, 1996). Moreover, trade-offs between different traits (morphological, performance, or both) suggests that at least a reasonable number of performance traits should experience stabilizing selection.

Despite these considerations, an inspection of available studies confirms that directional selection is a common trend for performance traits. Of the 23 studies reviewed here, 12 demonstrate directional selection ($\approx 50\%$). Only one study (Miles *et al.*, 2000) reported significant stabilizing selection on performance, namely endurance capacity in females of the lizard *Uta stansburiana*, although other studies have reported trends in this direction (Jayne and Bennett, 1990; Irschick and Meyers, 2007). Only one of the studies we reviewed showed any evidence of disruptive selection, which involved a complex form of correlational selection on performance and morphology (see also Calsbeek, 2008). Calsbeek and Irschick (2007) found two distinct fitness peaks for the lizard *A. sagrei*. Lizards that had long hindlimbs, poor sprinting ability on narrow dowels, and habitat preference for broad perches were favoured on one peak. Lizards with short hindlimbs, good sprinting performances on narrow dowels, and habitat preference for narrow perches were favoured on the other peak. We note that this example can be viewed as strong directional selection within each of these two groups.

One of the reasons for a lack of disruptive selection may be a lack of fitness–performance data related to feeding, in which individuals within populations often consume divergent prey items (e.g. hard vs. soft prey). Indeed, Smith (1993) showed two fitness peaks in an African seed-eating bird, each corresponding to a distinct beak depth. However, while he did not demonstrate selection on seed-crushing ability directly, he did demonstrate that the larger-beaked finch could crush harder seeds than the smaller-beaked finch, indirectly providing evidence for disruptive selection on performance. Working with crossbill finches in North America, Benkman (2003) showed a similar pattern for large-beaked and small-beaked birds. In this latter case, the two beak morphs corresponded to birds with different feeding 'efficiencies' based on their ability to process different seed types.

However, one should not ignore studies that detected no significant selection on performance. Of the 23 reviewed studies, six (Bennett and Huey, 1990; Brodie, 1992; Janzen, 1993, 1995;

Clobert *et al.*, 2000; Olsson *et al.*, 2000) found no evidence for selection on any of the performance traits they examined and several of the estimates of selection gradients reported in other studies were also not significant (Table 1). When one adds these estimates together, the median selection gradient is 0.093 for linear terms (β) and −0.018 for quadratic terms (γ). The distribution of β is asymmetrical about zero, with as much as 75% positive estimates, and the null-hypothesis that positive directional selection is as common as negative directional selection is therefore strongly rejected (*t*-test, $t_{47} = 3.30$, $P = 0.002$). In contrast, the distribution of γ is symmetrical about zero, suggesting that stabilizing selection is not more common than disruptive selection. Thus, the available data suggest: (1) a trend towards directional selection on performance traits in nature; (2) directional selection typically favours high rather than low performance; and (3) quadratic selection is typically weak.

Do sexual and natural selection operate in the same direction?

Most of the debate regarding selection on performance has centred around whether animals with high performance values are more likely to survive across sampling intervals (Table 1). This perspective is based on the notion that high performance, especially locomotor performance, is important for eluding predators and capturing prey, and therefore defining fitness as likelihood of survival is intuitively obvious. However, high performance also presents some potential benefits in a sexual selection context (Irschick *et al.*, 2007b; Husak and Fox, 2008). High performance could be important for social interactions, such as endurance capacity or bite force when male rivals fight (Lappin and Husak, 2005). Sprint speed and endurance capacity may also be involved in territory defence and mate search by males (Sinervo *et al.*, 2000). In polygynous species, male dominance is typically directly associated with mating success (i.e. greater numbers of mating partners), and therefore performance traits that enhance male dominance are also likely to increase total fitness. However, strong sexual selection can also impose costs in terms of survivorship (for a recent perspective, see Oufiero and Garland, 2007).

For at least one species (collared lizards, *Crotaphytus collaris*), the available data indicate that sexual and natural selection act in unison, at least for one breeding season. Collared lizards are highly polygynous, and high bite forces dictate territory acquisition, and therefore access to reproductive females (Lappin and Husak, 2005; Husak *et al.*, 2006). In these lizards, males with high sprint speeds also tend to have high bite forces, thus there is no apparent trade-off between sprint speed and bite force. This result is not entirely surprising in light of research showing strong links between sexual signal size and performance in lizards (Lailvaux and Irschick, 2006) and suggests that high-quality males may enjoy the best of both worlds: high survival rates and high reproductive success. Unpublished data for the anole *A. sagrei* shows that male lizards with large sexual signals (dewlaps) also do not suffer a survival decrement compared with males with small sexual signals, which is consistent with the view that high-quality males do not suffer increased mortality (J. Wood, unpublished data). However, more data examining the roles of both sexual and natural selection for whole-organism performance are needed for a much wider range of species before any firm generalizations can be drawn (Husak and Fox, 2008; Le Galliard and Ferrière, 2008).

Does the strength of selection differ between morphology and performance?

An oft-cited axiom in functional morphology is that morphological variation should translate directly into variation in performance capacity. There is also good reason to believe, from a theoretical perspective, that the intensity of selection should be stronger on performance than on morphology, as selection is expected to act on the former directly but only indirectly on the latter. However, some researchers have pointed out strong disequilibrium between morphology and performance, or between performance and fitness. For example, behaviour can alter the relationship between morphology and performance and represents an important source of variation in fitness, especially under natural conditions (Irschick, 2003). Therefore, we do not always expect a strict relationship between morphology, performance, and fitness among individuals or species (Irschick *et al.*, 2005).

One approximate way to address the issue of the relative strength of selection on morphology and performance traits is to compare the mean strength of direct selection for performance traits with the mean strength of direct selection for morphological traits. To this aim, we retrieved 275 estimates of standardized linear selection gradients for morphological traits in vertebrate taxa using the database from Kingsolver *et al.* (2001). Furthermore, since the direction of selection is not informative for morphological traits, we calculated the absolute value $|\beta|$ to estimate the strength of selection. The median $|\beta|$ was 0.120 for performance traits compared with 0.140 for morphological traits in our database (Table 1). There was no evidence for stronger directional selection on performance than on morphology (Kruskal-Wallis rank sum test, $KW = 0.45$, $P = 0.50$).

A more subtle way to address this issue is to use multivariate or path analyses of selection on both performance and morphological traits for a given species (Arnold, 1983; Kingsolver and Schemske, 1991). This procedure allows the uncoupling of direct selection on morphology from indirect selection on morphology explained by performance traits. If selection on morphology results mainly from the effects of morphology on performance, direct selection on morphology should be weak relative to indirect selection through performance traits. Unfortunately these statistical methods have not been used or reported systematically, and we have limited data for a quantitative analysis. However, a simple comparison of three studies shows conflicting patterns ranging from small to large direct selection on morphology (Table 2). Taken together, our findings suggest that there is no strong evidence that selection on performance is stronger than selection on morphology. Although we cannot offer a simple explanation for this finding, we suggest that the often tight intercorrelation among morphological and performance variables may explain the similar findings for the two kinds of variables. We urge field workers to collect more data on multivariate selection on morphology and performance to disentangle the effects of selection on each kind of trait independent of intercorrelated variables.

Are plastic performance traits under selection?

Most researchers examining selection assume some level of invariance in performance or morphology across the period over which selection is studied, although this is rarely explicitly stated (for discussion, see Walker, 2007). However, some of the most intriguing case studies of selection involve dramatic ontogenetic changes in the study organisms across the period over which selection was studied. The majority of selection studies ignore the effect of such changes by only considering selection on initial values (i.e. measuring who lives and dies

Table 2. Results of three multivariate selection studies for morphology and performance traits

Study species	Fitness component	Traits	Selection (β)	Phenotypic correlation
Selection on morphology is fully explained by indirect selection through a performance trait				
Crotaphytus collaris	Siring success	Hind limb length	0.164	
		Sprint speed	0.643**	$r = 0.63$**
Selection on morphology is partly explained by indirect selection through a performance trait				
Lacerta vivipara	Juvenile survival	Body size	0.150**	
		Endurance	0.120*	$r = 0.20$*
Selection on morphology is not explained by indirect selection through a performance trait				
Thamnophis sirtalis fitchi	Juvenile survival	Body size	0.148*	0.148*
		Sprint speed	−0.132	$r = 0.55$**
		Endurance	0.129	$r = 0.29$**

Note: For each of the three studies, we give the study species, fitness component examined, studied traits, standardized direct selection gradients, and phenotypic correlation between the morphology traits and the performance traits. Results are from Husak *et al.* (2006), Le Galliard *et al.* (2004), and Jayne and Bennett (1990), respectively.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

based on initially measured values). Some of the studies reviewed here suggest that focusing purely on initial values may be misleading. Indeed, we argue that researchers should re-measure the traits of interest (morphology, performance) both before and after selection. This issue is particularly relevant when examining selection across different seasons, as a large body of work has demonstrated seasonal changes in morphological and functional traits (Garland and Else, 1987; Deviche and Gulledge, 2000; Tramontin and Brenowitz, 2000; Irschick and Meyers, 2007). Some plastic changes occur as a means of compensation for initially poor performance. In the context of selection, compensation refers to compensatory morphological and/or performance changes across different stages of growth (see Le Galliard *et al.*, 2004). Compensation and plasticity intersect most obviously in adult animals, in which the pace of growth has slowed and plastic changes are most easily measured.

Recent work with lacertid lizards (*Lacerta vivipara*) provides evidence for compensatory change in performance during growth (Le Galliard *et al.*, 2004). Young lizards that had initially poor endurance could improve their endurance on a high-food diet and 'catch up' to initially good performers. By comparison, under more limited food conditions, poor and good performers maintained their rank order as they matured. This finding implies that during periods of high resource abundance, there may be ample opportunity for performance values to change markedly over relatively short periods of time. On the other hand, in an environment with limited resources, the relative rank order of individuals (in terms of 'performance') may be more canalized, and there may be little opportunity for compensation. Thus, selection should be more static in the low-food than in the high-food environment.

Another example of compensatory change in performance and morphology comes from a study on two performance traits (bite force, sprint speed) and associated morphological variables (head shape, limb length) from the breeding season to the fall in the lizard

Urosaurus ornatus (Irschick and Meyers, 2007). In this system, bite force and head shape are seasonally plastic. The head sizes of lizards change seasonally in proportion to their initial (breeding season) state. Individuals with large heads in the breeding season shrink their heads (up to 10% in width) in a matter of months (from May/June to September/October). Those individuals also decrease their bite force, whereas individuals with small heads actually increase their head sizes and bite forces. Interestingly, there was no significant selection on bite force or head shape in either male or female *U. ornatus*, and the rapid plastic changes in morphology and performance may have dampened the force of selection on performance. However, if one examines the very best values of bite force for different individuals, selection favoured high 'personal best' values, but not high initial values. Because the changes in morphology and performance are occurring relatively rapidly (over weeks and months), this phenomenon of 'shifting values' may mean that relatively 'poor' performers are not doomed to remain at a low level their entire lives. In comparison, a relatively static morphological variable, hindlimb length, and its biomechanical partner (sprint speed) experienced positive directional selection in male lizards; fast male lizards were more likely to survive than slow male lizards from the breeding to the non-breeding season.

FUTURE DIRECTIONS

We are pleased to note that in the last 5–6 years there has been tremendous progress towards understanding how selection operates on whole-organism performance traits. This still small but emerging literature will continue to complement the ever-burgeoning body of selection work on morphological traits. Our primary recommendation is to encourage researchers to continue making fundamental progress in how selection operates on performance. We encourage researchers to study a broader range of taxa, as the vast majority of the studies cited here come from lizards, snakes, turtles, amphibians, and fish. Data on mammals, invertebrates (a particularly good potential model system for examining selection on performance), and birds would be especially welcome.

Beyond this line of encouragement, we can point towards five areas that merit more attention. First, as noted by others (Kingsolver and Pfenning, 2007), there is a need for long-term studies of selection, and this statement is especially important for performance traits. Selection studies can offer the promise of simple and clear results (e.g. selection favours high sprint speed), but a historical perspective can show a more complex picture. Selection rarely operates at the same direction and intensity, even over human lifespans (Grant, 1999). In an era of increasingly rapid global climate changes, rapid evolution may become a hallmark of the twenty-first century (Carroll *et al.*, 2007). Yet, research on the interplay between selection, climate change, and whole-organism performance has barely been tapped. Some recent work shows strong environmental susceptibility in selection on performance for *Anolis* lizards (R. Calsbeek, unpublished data). Year-to-year fluctuations in rainfall can greatly impact the total amount of vegetation on Bahamian islands, which in turn affects selection on habitat, morphology, and performance. Another example comes from studies of desert lizards, which experience dramatic annual variation in rainfall, thereby potentially affecting the relative abundance of predators (e.g. snakes) (Sinervo and DeNardo, 1996). Although not yet shown directly, this annual variation is almost certain to affect the relative intensity of selection on performance traits in desert lizards, offering outstanding opportunities for future research.

Second, performance traits are unlikely to evolve in isolation from other features of the phenotype. How does selection operate on suites of traits (Blows, 2007), such as performance, morphology, habitat use, and behaviour? Subtle interactions among these traits may reveal heretofore undocumented cases of disruptive and stabilizing selection that are generally rare in selection studies (Calsbeek and Irschick, 2007). Moreover, such data may reveal the 'topography' of the ever-shifting adaptive landscape within animal populations. Consider an example of an insectivorous animal that crushes insect prey with its jaws. Bite force is generated by both head muscles and the overall size and shape of the jaw, yet we know very little about which aspect of the phenotype would be likely to change if selection favoured high bite forces, such as during periods when only hard prey are abundant. Selection may favour unique combinations of jaw shape and musculature that might not be typically predicted based on an analysis of bite force alone. Furthermore, the integrated jaw complex may also undergo complex changes in relation to bite force as the environment changes towards more 'flush' conditions in which more kinds of prey become available, and selection on high bite forces is relaxed.

Third, improved technological advances allow researchers literally to take the 'laboratory' into the field, blurring traditional lines between 'laboratory studies' and 'field studies'. The advent of field-portable high-speed cameras, accelerometers, and other portable devices for measuring physiological responses now enable researchers to measures performance in natural settings. These developments are especially important in light of recent work showing complex patterns of ecological locomotor performance compared with laboratory (maximal) performance (Irschick and Losos, 1998; Irschick *et al.*, 2005; Husak and Fox, 2006).

Fourth, a re-inspection of the path diagram in Fig. 1 shows that most of the studies reviewed here have focused on the last two relationships (morphology → performance → fitness); few studies have examined the role of environmental or developmental variation in inducing ranges of phenotypes for selection to act upon (for a notable exception, see Kaplan and Phillips, 2006), particularly in the context of performance. In an era of increasing worldwide temperatures, it would be especially useful to understand the selective consequences of varying incubation temperatures on performance and fitness across a wider range of organisms (Janzen, 1995).

Finally, an expansion of comparative approaches to selection is long overdue. The only constraint (albeit a significant one) preventing researchers from examining multiple species is time and resources. However, comparative approaches offer the best way to test whether microevolutionary forces operating within communities can explain macroevolutionary patterns (Charlesworth *et al.*, 1982). Community approaches to selection are rapidly taking hold in studies of plant ecology (Whitam *et al.*, 2006), yet we lack a similar mindset for animal systems. Because of the large amount of work involved in studying selection on multiple species, researchers working on different taxa should consider combining forces to ensure that selection is measured in the same manner in different species, thereby generating comparative databases for microevolutionary responses within different species.

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