

Studying the evolution of whole-organism performance capacity: sex, selection, and haiku – an introduction

Substantial attention has been devoted towards understanding how morphological traits evolve in a microevolutionary context (Charlesworth, B., Lande, R., and Slatkin, M., 1982, *Evolution*, **36**: 474–498; Endler, J., 1986, *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press; Kingsolver *et al.*, 2001, *Am. Nat.*, **157**: 245–261). While we agree that such attention is warranted, we aim to divert your attention towards another topic, namely the microevolution of whole-organism performance capacity. The articles in this special collection present more detail on definitions of performance capacity, but we define it here as the quantitative measure of the ability of an organism to conduct an ecologically relevant task. Classic examples include sprint speed, bite force, and locomotor endurance, among other measures (Irschick, D.J., and Garland, T., Jr., 2001, *Annu. Rev. Ecol. Syst.*, **32**: 367–396).

The most burning issue that motivated this special collection was how the forces of natural and sexual selection operate on performance traits, in contrast to morphology. Because performance as defined here is measured at the whole-organism level, variation in performance arises from variation from many other traits, such as aspects of physiology and morphological shape. Therefore, visualizing selection on performance is potentially trickier than for morphology because one is immediately drawn to the potential for interrelationships: does selection favour high performance, good morphological attributes, or both? Some of the papers in this special collection address this topic head-on, and suggest a high degree of intercorrelation between morphology and performance, as well as with behaviour (Le Galliard and Ferriere, this issue). Another paper shows that the strength of selection appears not to differ between morphological and performance traits (Irschick, Meyers, Husak, and Le Galliard, this issue). These findings remind the reader of the complex nature of co-evolved aspects of the phenotype and genotype (Cheverud, J., 1982, *Evolution*, **36**: 499–516), and also imply that selection studies should aim to move towards more comprehensive measures of the entire phenotype and emergent functional and behavioural properties. A review of selection studies (Irschick *et al.*, this issue) reveals another interesting finding – selection on performance, much like morphology, is rarely stabilizing or disruptive. Nearly half of the 23 selection studies reviewed were directional, with a distinct favouring of high performance. One intriguing possibility is that selection may favour different combinations of morphology and performance in different years, as environmental conditions change (Calsbeek, this issue), leading to directional selection within a season and a more static pattern of evolution over ecological time. Sadly, as this special collection highlights, we lack the long-term studies of performance to test this intriguing possibility.

One of the most exciting developments over the past 10 years has been an increased appreciation for the dual and potentially conflicting role of sexual and natural selection (Le Galliard and Ferriere, this issue). In some of the papers in this special collection, there is evidence that the two forces act in unison, meaning that high-quality males (at least in the

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case of lizards) can have their cake and eat it, too. Enhanced locomotor performance in collared lizards, for example, seems to result in both enhanced survival and reproductive success – potentially by enabling male lizards to both effectively elude predators and out-compete rival males (Husak and Fox, this issue). As the use of genetic paternity techniques becomes less expensive and technically easier, we expect more studies that examine both survival and reproductive success simultaneously. Finally, one should not ignore the relevance of sexual dimorphism in performance capacity; it is a delicious buffet for evolutionary biologists to sample from (Van Damme, Entin, Vanhooydonck, and Herrel, this issue). Dimorphism in performance capacity, beyond differences in body size between the sexes, implies differential selection for different ecological tasks in females and males, which diverges from the traditional focus on sexual size dimorphism (Blanckenhorn, W.U., 2005, *Ethology*, **111**: 977–1016).

Another relevant issue for this collection of papers is understanding the evolutionary dynamics of performance beyond simple fitness studies. Kingsolver and Huey (this issue) argue that three simple rules may dictate many aspects about how performance evolves. These three provocative rules are easily understood by memorizing an artfully worded haiku: ‘Bigger is better, and hotter makes you smaller, hotter is better’. Although organismal biologists have generally eschewed ‘rules’ or ‘laws’ that are common in other fields, these three rules are bolstered by significant amounts of data, although more studies are needed. Their usefulness derives from their ability to make long-term predictions for how evolution will proceed in a twenty-first century of dramatic environmental change (Carroll, S.P., Hendry, A.P., Reznick, D.N., and Fox, C.W., 2007, *Funct., Ecol.*, **21**: 387–393). For example, the ‘hotter is better’ hypothesis goes against simple ideas that organisms will evolve to match local environmental conditions. Instead, this rule implies the existence of strong constraints on physiology and resultant performance, and these rules may canalize phenotypic and biochemical adaptation. These rules also reinforce the view of a close connection between environmental conditions, performance, and growth patterns. The role of temperature on growth rate (and resultant size of offspring) in organisms also suggests that the ability of organisms to adapt to changing environments may be more canalized than one might have originally expected.

All of the studies in this special collection provide new launching pads for researchers to jump off, and we point towards one particular avenue. Based on a review of selection studies (Irschick *et al.*, this issue), we believe that the time is ripe for researchers to embark on new ways of understanding how selection operates within natural populations. The sheer volume of morphology–fitness studies reviewed by Endler (1986) and Kingsolver *et al.* (2001) questions the value of gathering similar data over the next decade or so. Improved wireless and mobile technology – especially video technology – means that researchers can increasingly take the ‘lab into the field’ (Dangles, O., Casas, J., and Coolen, I., 2006, *J. Exp. Biol.*, **209**: 393–398), enabling researchers to measure more easily those performance and behavioural traits that heretofore would have required taking animals into artificial laboratory settings. We hope that integrative selection studies that simultaneously examine morphology, performance, and even behaviour may yield a radically different view of how populations do (or do not) adapt to a changing world. We look forward to a new era of microevolutionary studies!

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