

**Introduction to the symposium: Integrative Life-History of
Whole-Organism Performance**

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Review

Introduction to the symposium: Integrative Life-History of Whole-Organism Performance

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Abstract

A strong case can be made for whole-organism performance traits (i.e. dynamic, ecologically relevant traits whose expression is shaped by underlying morphological factors) as being the ultimate integrative traits. This is not only because they capture the output of multiple lower levels of biological organization, but also because they are directly relevant to individual fitness in multiple ecological contexts, and are in many cases important proximate determinants of survival and/or reproductive success. But although many ecological and evolutionary phenomena can be examined through the lens of performance (and vice-versa), performance research has been surprisingly slow to incorporate concepts from the large and important field of life-history evolution. Such a synthesis is important, because shifts in resource allocation strategies can have implications for these highly ecologically relevant, functional traits, whose expression may trade-off against fecundity, immune function, or longevity, amongst other key life-history traits. The papers in this symposium showcase many of the ways in which life-history strategies can have direct consequences for the expression, maintenance, and evolution of whole-organism performance (and at least one case where they may not). By approaching the issue of life-history trade-offs from a number of diverse perspectives, this symposium reveals the scope for future explicit integration of life-history techniques with those of whole-organism performance studies for a more complete understanding of multivariate phenotypic evolution.

Introduction

The study of whole-organism performance has a long and venerable history in integrative biology. Perhaps surprisingly though, it wasn't always as integrative as it currently is. Although Bartholomew (1958) realized almost 60 years ago that locomotor performance abilities provide a clear and measurable link between integrated physiological capacities and Darwinian fitness , it was another 25 years before Arnold (1983) formalized this link as the influential ecomorphological paradigm, giving researchers a statistical roadmap for linking organisms' morphology, performance, and ultimately fitness . At more or less the same time, researchers with interests in both animal function and evolution had begun to combine the two in creative ways, bringing to bear insights and approaches from each field on the other and pioneering the area of research that became known as evolutionary physiology (reviewed in Bennett and Huey 1990; Garland and Carter 1994; Feder et al. 2000). Much of the modern study of whole-organism performance has its roots in this vibrant and fertile period of intellectual expansion and integration, and the leaders of evolutionary physiology developed methods and conceptual frameworks for understanding the evolutionary ecology of performance in particular that remain ubiquitous and relevant today.

Evolutionary physiologists showed early and often (and many times subsequently) that performance traits are intimately involved in evolutionary processes. Studies focussing on the variation (e.g. Huey and Dunham 1987; Huey et al. 1990), heritability (e.g. Tsuji et al. 1989; Sorci et al. 1995), and selective aspects (e.g. Swallow et al. 1998; Le Galliard et al. 2004; Miles 2004; Husak et al. 2006) of whole-organism performance, as well as the broader comparative implications of performance evolution (Losos 1990; Irschick and Losos 1998; Collar and Wainwright 2006), appeared prominently in the literature. By the mid-to-late 2000s, the assimilation of performance studies under the broad umbrella of natural (reviewed in Irschick et al. 2007; Irschick et al. 2008) and sexual selection (reviewed in Lailvaux and Irschick 2006; Husak and Fox 2008) appeared complete (but see Husak and Lailvaux 2014; Husak 2016). However, there is at least one important field of evolutionary biology that historically has received far less attention from students of whole-organism performance research: life-history evolution.

Although certainly not ignored by performance researchers [and despite being identified previously as an important area for integration into evolutionary physiology (Feder et al. 2000)], work on life history has not featured as prominently in the whole-organism performance literature as one might expect given the centrality of life-history trade-offs in shaping the integrated organismal phenotype (Ghalambor et al. 2003; Oufiero and Garland 2007). This is curious, given that locomotor performance is a key component of one of the most important empirical life-history

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3 evolution studies ever conducted: the long-term study of Trinidadian guppies by David Reznick and
4 his many collaborators (Ghalambor et al. 2004; Reznick et al. 2004). This work, as well as an ever-
5 growing literature of other studies in taxa ranging from insects (Lailvaux et al. 2010; Okada et al.
6 2011; Reaney and Knell 2015) to lizards (Clobert et al. 2000; Lailvaux et al. 2012; Husak et al. 2015),
7 and birds (Veasey et al. 2001) (but less so mammals; Orr and Garland 2017), shows without question
8 that whole-organism performance traits are also life-history traits, and thus subject to trade-offs
9 with other traits with which performance shares a pool of acquired energetic resources (reviewed in
10 Lailvaux and Husak 2014) or that are otherwise linked to performance via mechanisms such as
11 hormonal pleiotropy (Flatt et al. 2005) or negative genetic correlations (Lande 1982; Sgro and
12 Hoffmann 2004).

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14 The recognition of whole-organism performance traits as life-history traits has several
15 important and, in our opinion, under-appreciated implications for how those traits will respond to
16 selection imposed either on performance itself, or on other traits that are linked directly or indirectly
17 to performance (Lailvaux and Husak 2014). While some of those implications can be addressed
18 ultimately through the application of methods suited to understanding multivariate evolutionary
19 trajectories (see Lailvaux et al. 2010; Husak et al. 2013 for examples), just as important are the
20 proximate mechanisms and consequences of trade-offs between performance and other
21 components of the integrated organismal phenotype, about which we still have a great deal to learn.
22 Indeed, many questions regarding the multivariate and plastic nature of performance remain
23 unanswered, such as why expected morphology->performance relationships and trade-offs are
24 sometimes not found; how environmental factors such as dietary quality and the social milieu affect
25 performance and life-history trade-offs through both ontogeny and adulthood (and ultimately
26 influence aging); which physiological pathways specifically are involved in performance trade-offs
27 with other life-history traits, as well as how phenotypic 'priorities' are mechanistically established;
28 and how can we predict which species and traits will be especially prone to life-history trade-offs
29 involving whole-organism performance?

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31 We organized this symposium as a proactive attempt to stimulate thinking on these and
32 related questions involving performance life-history. To this end, we invited a diverse group of
33 scientists employing a variety of approaches, systems, and study organisms to consider topics
34 spanning all aspects of both the ecomorphological paradigm and life-history evolution. In the first,
35 Lailvaux and Husak (2017) conduct comparative analyses across 72 mammal taxa to test whether
36 mammal species that spend relatively more energetic resources on reproduction – i.e. those on the
37 “fast” end of the “slow-fast” life-history continuum – are forced to spend relatively less on
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locomotion. Predicting such trade-offs, however, requires often fine-grained understanding of the costs of both performance and life-history traits that performance might potentially trade-off against. Husak and Lailvaux (2017) consider ways of assessing these costs, and show using a comparative life-history dataset on phrynosomatid lizards that costs can differ significantly among different performance traits. They also borrow from animal signalling theory to define different types of costs that performance may incur, including development costs (incurred before the performance trait is used), production costs (incurred while the performance trait is being used), and maintenance costs (incurred after development, but not while in use). Measuring costs at such a fine scale may allow better prediction and detection of trade-offs. Smith and French (2017) illustrate this point well by showing that how individuals invest in traits is rarely simple or straightforward. Many assume that immune responses and the energy invested to produce them should always be maximized, but this is not necessarily the case. Other traits, such as performance, may better enhance survival and fitness in certain conditions than maintaining the ability to produce the greatest possible immune response. Bonneaud et al. (2017) build on this theme by arguing that more tolerant individuals in a population - that is, those that minimize negative effects of pathogens - may be able to avoid some costs associated with the infection. This is a different scenario than considering simple investment strategies, and instead illuminates the importance of considering attributes of both the host individuals and the pathogens.

Various types of performance traits may themselves trade-off amongst each other, yet detecting trade-offs among the multivariate performance phenotype is a challenge. Careau and Wilson (2017) use a simulation approach to show that the sampling distributions of maximum performance traits are such that among-individual trade-offs in such traits are often masked by within-individual variation; however, those trade-offs can be recovered through the use of multivariate mixed-models (MMMs). This study demonstrates the utility of MMMs for understanding performance trade-offs and echoes earlier calls to move away from measuring only maximum performance (Adolph and Hardin 2007; Adolph and Pickering 2008). Staying with the theme of relationships among suites of traits, Dantzer and Swanson (2017) review the concept of *hormonal pleiotropy* (whereby a given hormone affects, and thus links, multiple traits) and consider how the nature of the pleiotropic relationship might constrain or facilitate the evolution of each of those phenotypes. To do so, they construct a simple quantitative genetic model and predict the conditions under which the selection and the response to selection might be equivalent or at odds based on genetic correlations between hormones, performance traits, and life-history traits drawn from the literature. Hormones are also the focus of Kilvitis et al. (2017), who argue that epigenetically-mediated plasticity in the regulation of glucocorticoids could adaptively regulate

performance during expansion into novel environments. Epigenetics represents a novel frontier for both performance and life-history, and the *epigenetic potential* defined in this paper is an exciting and relevant concept in this regard.

Although range expansion is one option available to many animal taxa, certain species are constrained in their mobility. For those with relatively immobile juvenile stages in particular, shifting resource allocation in response to environmental cues is often a useful strategy. However, Jaumann & Snell-Rood (2017) show that the caterpillars of cabbage white butterflies do not respond to increased conspecific juvenile or adult density, and exhibit neither increased fecundity nor higher levels of conspecific avoidance behaviour under higher density conditions. This suggestion that life-history strategies can in some cases be relatively inflexible is an important counterpoint to adaptationist research programs, and a reminder of the constraints on both proximate and ultimate drivers of evolutionary trajectories.

The variety of topics considered in the symposium challenges what one might consider to be a performance trait. Orr and Garland (2017) argue that researchers have been relatively limited in their view of performance, focusing primarily on dynamic performance traits, such as sprinting and biting, but have paid much less attention to other types of performance. Lactation performance and sperm performance traits are likely important to fitness in a variety of taxa, and both traits are energetically costly. Thus, investigators need to think more broadly about the multivariate performance phenotype, but also more creatively and inclusively about what is considered under the purview of “performance”. Finally, Addis et al (2017) promote a similar perspective on “non-traditional” performance traits, and conduct a rigorous investigation into intraspecific variation in life-history strategies in *Thamnophis elegans* garter snakes. This study shows that insulin like-growth factor-1 (IGF-1) likely mediates the intraspecific link between ecomorphology and life-history, and thus connects earlier work on the interspecific IGF-1-facilitated mammalian fast-slow life-history continuum (e.g. Swanson and Dantzer 2014) directly to the classic ecomorphological paradigm in an ectotherm species. That connection is made explicit through the estimation of selection differentials.

The diversity of approaches and topics highlighted here illustrate both the scope of an integrated performance/life-history perspective on animal function, and the breadth of opportunities for applying that perspective to the end goal of developing a comprehensive understanding of phenotypic evolution. Such an understanding can be achieved only by embracing an integrative and multivariate view of organismal function, and these papers collectively constitute an exciting implementation of this approach.

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