Hormonal regulation of whole-animal performance: Implications for selection

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Introduction

One of the fundamental questions in evolutionary biology is how natural selection and sexual selection mold phenotypes, and the resulting functional capacities of those phenotypes. Strong selection within animal populations is well-documented (Endler 1986; Brodie et al. 1995; Kingsolver et al. 2001) and recent reviews point toward 'whole-animal performance' as being central to understanding these patterns (Irschick et al. 2007, 2008). The last 20 years have witnessed an explosion of studies describing the evolutionary significance of performance traits such as running, biting, and swimming, yet the proximate mechanisms underlying such traits remain unclear for many animal species (Arnold 1983; Pough 1989; Garland and Losos 1994; Irschick et al. 2008). Moreover, as pointed out by recent authors (Blows 2007), fitness frequently is determined not by any one variable, but by a suite of interacting traits, including morphology, physiology, performance, and behavior. While many studies have focused on the musculoskeletal and energetic mechanisms underlying variation in performance of animals (Garland and Losos 1994; Biewener 2003), the hormonal regulation of performance traits has received less attention, despite the fact that hormones are known to exert profound effects on multiple aspects of morphology, physiology, and behavior, all of which affect most performance traits (Adkins-Reagan 2005).

A discussion of how hormones affect performance is important because it could shed light on how hormonal variation ultimately affects fitness. Understanding the role of hormones in influencing fitness is important because of criticisms that performance traits may not be the true targets of selection, but might be correlated, via the integrating effects of hormones, with other traits that are the "true" target of selection (reviewed by Garland et al. 1990; Husak and Fox 2008). This debate stems from a poor understanding of how hormones mediate performance traits, and how such traits in turn affect fitness. Interestingly, despite a general lack of discussion in the literature on animals, there exists an extensive literature concerned with how steroid hormones affect human performance (see Husak and Irschick 2009). Whereas humans attempt to enhance performance by using steroids for purposes related to sports (e.g., winning races and hitting more home-runs), performance traits in non human animals often make the difference between catching dinner or becoming dinner (Irschick et al. 2008). Therefore, by studying the effects of hormones on performance, we may gain general insights into the factors that influence organismal fitness, a burgeoning area of discussion in evolutionary biology (Kingsovler et al. 2001; Hereford et al. 2004).

A consideration of how hormones affect variation in morphology and performance opens up broader questions for how such traits evolve. For example, one important issue concerns whether traits such as morphology, performance, and behavior evolve more or less independently, or are tightly bound together in coadapted complexes. This issue has been debated at the level of hormonal control (Hau 2007; Ketterson et al. 2009) and has centered on two alternative hypotheses, namely evolutionary integration versus independence of receptors, target tissues,

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and level of circulating hormones (Hau 2007). This debate can be extended to studies examining hormones and performance traits, as there has been a rapid growth of studies over the past decade both of performance (Irschick et al. 2008) and hormones (Adkins-Reagan 2005). This relatively new abundance of knowledge suggests that we stand at a crossroads that may allow us to address several key questions. Does variation in hormonal systems mediate variation in performance within populations, or among species? Can we identify key hormones that are both conserved across taxa, and thus exert general effects on performance traits, or do effects differ dramatically across different taxa and performance traits? If there is selection on hormone-mediated performance traits, what are the evolutionary implications for the endocrine system and other traits linked to those hormones, and does the linkage result in tradeoffs?

The symposium papers in this issue address these, and other, vital questions by bringing together a diverse array of researchers who study a variety of animal taxa and use different approaches. Some of the contributions include discussion of traits classically referred to as 'performance' (Husak and Irschick 2009; Lorenz and Gäde 2009; HB John-Alder, RM Cox, GJ Haenel, and LC Smith, submitted for publication; Moore and Hopkins 2009), whereas others discuss traits typically referred to as 'behavior' (Ketterson et al. 2009; RF Oliveira, submitted for publication; Moore and Hopkins 2009; Leary 2009) or 'physiology' (McCormick 2009). Below, we discuss various meanings of the term "performance" and how it relates to these contributions. We argue that the seemingly disparate traits studied by these researchers, ranging from calling behavior of anuran amphibians to regulation of salt and water by anadromous fish, can all be studied in the broad context of how variation in the action of hormones affects performance.

What is performance and why is it important?

The concept of animal performance as a target of selection has been around for at least half a century (Bartholomew 1958; Huey and Stevenson 1979; Arnold 1983; Irschick and Garland 2001) and has enduring appeal because of the intuitive notion that the "race will go to the swift," suggesting higher fitness for superior performers (Jayne and Bennett 1990). However, it was Arnold's (1983) seminal paper describing a statistical framework for studying the evolution of morphological and physiological traits that ushered in a new era of quantitative studies of performance (Bennett 1987; Pough 1989; Bennet and Huey 1990; Garland and Losos 1994). Arnold's (1983) view was that by studying performance traits, one could empirically study the microevolutionary process of adaptation; this heuristic view has also been expanded to interspecific studies (Emerson and Arnold 1989).

Before proceeding, we define "performance" in the context of this symposium. First, we agree with the classic view that performance is a quantitative measure of how well an organism accomplishes some ecologically relevant task (Huey and Stevenson 1979; Arnold 1983; Bennett 1987; Pough 1989; Bennett and Huey 1990; Garland and Losos 1994; Irschick and Garland 2001; Irschick 2003; Irschick et al. 2008). Second, we emphasize that performance tasks are holistic manifestations of the entire organism, as opposed to measures of suborganismal processes, e.g., how well an enzyme catalyzes reactions. However, even when considering both of these aspects of performance, there remains room for interpretation, and in the context of hormonal control, we suggest a broadening of traditional measures of performance. If one adheres to the view that performance is a metric of how well an animal accomplishes a task, then we can consider two primary categories: (1) dynamic performance and (2) regulatory performance. Dynamic performance traits measure movements of the whole body, or parts of the body, and constitute most common measures such as sprint speed, endurance, and bite force. In contrast, regulatory performance traits measure how well organisms regulate physiological processes of the whole body, or withstand environmental conditions. Regulatory performance traits include such measures as regulation of salt and water (McCormick 2009), thermoregulation or thermal tolerance, growth, digestive capacity, immune response, and production of gametes. Thus, many regulatory performance traits may be thought of as essential components of maintaining homeostasis in organisms (Romero et al. 2009). Although dynamic and regulatory performance traits are different in many ways, they each represent an integrated measure of how well organisms accomplish some vital task, and are therefore relevant to organismal fitness.

Whereas there has been only modest discussion of how hormones affect performance, there is an extensive literature on how hormones affect behavior, and prior treatments have made a distinction between "behavior" and "performance." For example, Pough (1989) distinguished performance, which is typically measured by physiological ecologists, from behavior, but there are no explicit criteria to differentiate the two. Garland and Losos (1994) distinguished between "maximal performance," which is what an animal can do when pushed to its limits, and "behavior," which is what an animal actually does when faced with behavioral options. We adopt the view that many behavioral traits, as measured by behavioral ecologists, are quantitative measures of how well individuals accomplish a particular task. Thus, our proposed broader view of performance includes common examples of "maximal performance" such as maximal sprint speed, maximal capacity for endurance, maximal bite force, and maximal acceleration, as well as common examples of "behavior" such as rate of foraging, rate of display, and rate of feeding offspring. Relevant to this symposium, the underlying hormonal regulation of different types of performance is likely to be different, but this has received little formal attention. We hope that our broader view of performance traits can provide a more general view of studying organismal evolution.

Performance studies: a role for hormones?

Our premise that hormones should be studied as a means of understanding performance is straightforward; because hormones exert systemic effects on multiple aspects of morphology, physiology, and behavior, there is good reason to believe that they will also exert effects on performance traits. In fact, we already know a certain amount about how some hormones influence humans' athletic performance. Exogenous testosterone can significantly increase overall strength of humans (reviewed by Hartgens and Kuipers 2004; Husak and Irschick 2009) but the relationship between increased strength and other aspects of performance (e.g., agility) are less well-studied. At first blush, one might consider hormones as a "morphological" trait underlying performance when framing a research question within Arnold's (1983) statistical framework of studying microevolution. However, hormones may directly influence morphology, behavior, and performance, complicating causal pathways. Hormones may, in some cases, serve as the proximate mechanisms that link morphology, performance, and behavior, as suggested by John-Alder, Cox, Haenel, Smith (submitted for publication) in this issue. However, this may not be a universal phenomenon, as behavioral decisions and the social environment can directly affect endocrine systems (reviewed by Oliveira, submitted for publication), which may in turn impact other aspects of the phenotype, including performance. Future work will clarify these possibilities, but we emphasize that one may need to study aspects of endocrine systems to understand the "black box" behind variation in performance.

Several common themes regarding hormonal regulation of performance emerged from our symposium. First, relationships among hormones, morphology, physiology, performance, and fitness are complex. Ketterson et al. (2009) discuss whether there is integration of hormonally controlled performance traits or, instead, whether they are independent, with aspects of endocrine systems, and the traits they mediate, evolving separately. Husak and Irschick (2009) explain how the effects of testosterone in humans are often discordant with effects that have been detected in non human species. In discussing the endocrine control of the migration of salmon and of their performance in seawater, McCormick (2009) proposes that the magnitude of temporal and/or spatial shifts in selection pressure over an animal's life may allow prediction of whether or not it is advantageous for hormones to regulate performance. The second emergent theme is that performance traits, and the endocrine systems that mediate them, should be considered not only by examining single hormones or performance traits, but also by considering multiple, intercorrelated aspects of the phenotype. Moore and Hopkins (2009) and Lorenz and Gäde (2009) suggest an energetic approach to studying links among hormones, morphology, performance, and fitness. This approach is appealing because energy is the common currency that underlies many tradeoffs among phenotypic traits, including hormones and performance. The third theme is that hormonal regulation of performance is not a simple one-way street, in which hormones affect performance, but not vice versa. Using fish as a model system, Oliveira (submitted for publication) shows how behavioral decisions in different social environments are influenced by hormonal mechanisms, with those decisions then feeding back to cause subsequent changes in the endocrine system. Drawing from work on anuran amphibians, Leary (2009) emphasizes that we must consider both senders and receivers in a signaling system that is under hormonal control so that we may better understand how variation in endocrine systems is maintained in a population.

Future directions

We can point toward several promising research areas that build upon the investigations outlined in this symposium. First, and most obviously, collaborations between functional morphologists, behavioral ecologists, and endocrinologists are necessary for successful implementation of any hormone-performance study. Second, we believe studies of hormones both on humans and on non human animals have much to learn from one another. For example, recent studies with humans show that exogenous testosterone, in combination with exercise, produces a dramatic improvement in overall strength, especially when individuals are maintained on a high-protein diet. The role of both exercise and diet has been perhaps undervalued in hormonal studies on non human animals, although for understandable reasons. Unlike humans, different animal species show differing effects of exercise on performance, in some cases a positive effect, in other cases, no effect, suggesting the need for further study on the interactive effects of hormones, diet, and exercise on performance. As a third line of research, we suggest that long-term demographic and behavioral studies with hormones are clearly needed (Ketterson et al. 2009). For example, long-term studies can address differences between acute versus chronic exposure to hormones. Whereas some studies have revealed benefits accrued over short periods of time (e.g., role of testosterone in influencing reproductive success in the short term), others have revealed negative, longer term consequences (e.g., reduced immune function, increased energy expenditure). However, how such hormonal effects are manifested over the lifetime of an organism is poorly understood for most animal species, in large part because of the difficulty of long-term manipulation and/or monitoring of hormone levels (which also poses valid ethical concerns). Finally, studies that investigate multiple hormones and their interactive effects on morphology, physiology, and performance simultaneously would be welcome (Moore and Hopkins 2009), as most studies have focused on the effects of only one or two at a time.

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