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# THE LIFE HISTORY OF WHOLE-ORGANISM PERFORMANCE

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ABSTRACT

*For almost 40 years, studies of whole-organism performance have formed a cornerstone of evolutionary physiology. Although its utility as a heuristic guide is beyond question, and we have learned much about morphological evolution from its application, the ecomorphological paradigm has frequently been applied to performance evolution in ways that range from unsatisfactory to inappropriate. More importantly, the standard ecomorphological paradigm does not account for tradeoffs among performance and other traits, nor between performance traits that are mediated by resource allocation. A revised paradigm that includes such tradeoffs, and the possible ways that performance and fitness-enhancing traits might affect each other, could potentially revivify the study of phenotypic evolution and make important inroads into understanding the relationships between morphology and performance and between performance and Darwinian fitness. We describe such a paradigm, and discuss the various ways that performance and key life-history traits might interact with and affect each other. We emphasize both the proximate mechanisms potentially linking such traits, and the likely ultimate factors driving those linkages, as well as the evolutionary implications for the overall, multivariate phenotype. Finally, we highlight several research directions that will shed light on the evolution and ecology of whole-organism performance and related life-history traits.*

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## INTRODUCTION

LIFE-HISTORY evolution has played a prominent role in ecology since at least the 1970s, and includes the theoretical and empirical study of traits related to the evolution of life cycles, such as reproductive investment, age and timing of reproduction, and longevity (Stearns 1992; Charnov 1993). Although these traits are clearly important to Darwinian fitness, they typically are not the most proximate determinants of survival and reproductive success of individual animals. Instead, traits that confer advantages in foraging, escaping predators, and successfully mating are directly linked to individual fitness in an environment. These traits are encompassed by the concept of whole-organism performance, which can be broadly defined as any quantitative measure of how well an individual performs a dynamic, ecologically relevant task measured at the level of the organism, as opposed to lower levels of organization (cells, enzymes, etc.; Bennett and Huey 1990; Irschick and Garland 2001; Lailvaux and Irschick 2006; Husak et al. 2009b; Careau and Garland 2012). For almost 40 years, studies of whole-organism performance have formed a cornerstone of evolutionary and physiological ecology. This focus is due to the significance of performance traits as quantifiable and intuitive intermediaries between the organism and the environment, often being strong predictors of survival and reproductive success (Irschick et al. 2008). Furthermore, an animal's performance may affect multiple aspects of its overall Darwinian fitness and, consequently, any given performance trait may be subject to a wide variety of varying selection pressures, ranging from food acquisition (Vincent et al. 2005; Herrel et al. 2008) and predation (Snell et al. 1988; Husak 2006b; O'Steen et al. 2010) to male combat (Lailvaux et al. 2004; Lappin and Husak 2005), mate acquisition (reviewed in Lailvaux and Irschick 2006; Husak and Fox 2008), and even cannibalism (Wilcox and Lappin 2013). As such, an understanding of the factors shaping performance is critical for understanding how animals interact with, and are able to exist in, their environment. Life-history and performance traits are typically studied separately from each other yet they are similar in many ways, despite the disparate research foci of those who study them. Both types of traits depend on allocation of resources during an individual's lifetime, and both strongly impact fitness. Although whole-organism performance has taken center stage in its own literature (Irschick and Garland 2001; Irschick et al. 2008), we argue that it should be explicitly studied like any other phenotypic trait that must be "built" by an individual and may contribute to fitness—in other words, within the context of life history.

The causal relationships between Darwinian fitness and performance and between performance and the factors that influence it were encapsulated in Arnold's (1983) ecomorphological paradigm (Bartholomew 1958; Huey and Stevenson 1979; Bennett 1989; Huey 1989; Pough 1989), which stated that variation in morphology determines performance, which in turn determines variation in fitness (Figure 1A). This framework for quantitatively studying performance proved to be as fruitful as it was influential. However, in pursuing the ecomorphological paradigm, researchers have tended to approach these important relationships in an overly deterministic way, as well as to ignore other potentially important factors such as behavior (Garland and Carter 1994). From a strictly mechanistic perspective, and despite both the attention paid to performance and the variety of performance research conducted over the last several decades, there is still a great deal regarding the expression of whole-organism performance traits that we do not understand. Phenomena such as many-to-one mapping, whereby functional challenges have multiple morphological solutions, reveal unexpected flexibility in the morphology→performance gradient (e.g., Albertson et al. 2005; Wainwright et al. 2005; Collar and Wainwright 2006), and work on phenotypic compensation is similarly showing that selection may often operate on morphology in related lineages to overcome environmental challenges in functionally equivalent, yet mechanically

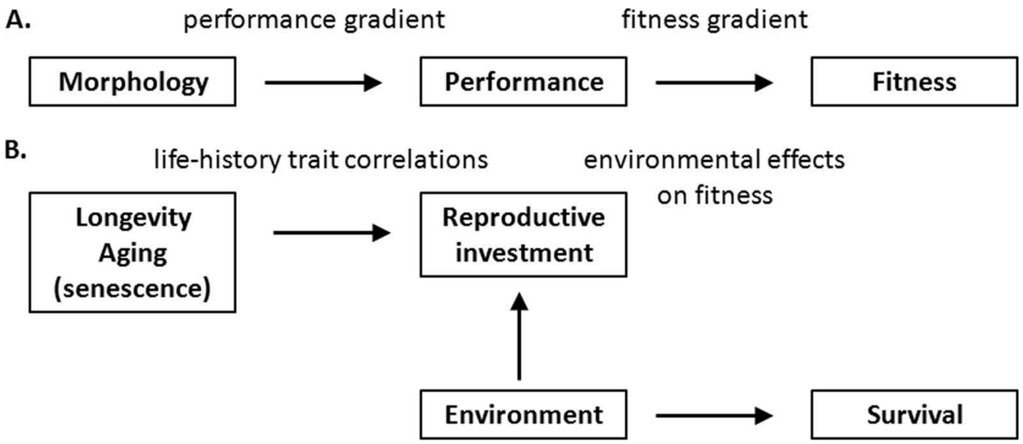

FIGURE 1. CONCEPTUAL SIMILARITIES BETWEEN THE ECOMORPHOLOGICAL PARADIGM AND LIFE-HISTORY STUDIES

(A) The selection gradient on morphological traits can be divided into a performance gradient, where variation in morphology explains variation in performance, and a fitness gradient, where variation in performance explains variation in fitness among individuals in a population. (B) In studies of life-history traits, two main approaches are to study links among traits and to study how the environments influence reproduction and survival.

disparate, ways (Husak et al. 2013). A growing literature also shows that performance can be plastic and subject to modification from a variety of both intrinsic and environmental factors that typically are not considered in studies of performance. Indeed, there is increasing evidence to show that the morphology→performance gradient can be altered or disrupted under certain conditions (e.g., Irschick et al. 2006; Langerhans et al. 2007). From a more adaptationist perspective, we are also learning that the relationship between performance and Darwinian fitness is itself subject to modification, depending on the selective context in question. The emerging view is that performance may in some cases be just one of a multivariate suite of traits that might influence fitness, and these traits interact or trade off with each other in ways that are not apparent from univariate viewpoints (Hall et al. 2010b; Lailvaux et al. 2010; Table 1). A current challenge is to understand the form and intensity of total selection on performance within the context of the whole organism (Hunt et al. 2009), as was originally intended by Arnold (1983), rather than examining only specific, individual selective contexts and single traits piecemeal as has been the case to date (Wilson and Nussey 2010; Lailvaux and Kasumovic 2011; McGuigan et al. 2011).

Despite the inarguable importance of the ecomorphological paradigm to the establishment and development of the evolution and ecology of whole-organism performance, even a brief survey of current performance research suggests that much of this newer work is constrained by selective use of Arnold's (1983) framework more than it is enhanced by it. However, an important caveat regarding the state of modern performance research is that the ecomorphological paradigm has frequently been applied to performance evolution in ways that range from unsatisfactory to inappropriate—in fact, Arnold (1983) proposed a clear way forward for evaluating morphology, performance, and fitness in an integrative manner, yet only a handful of studies have completed the entire ecomorphological gradient, from morphology to overall fitness, within a single species (e.g., Langerhans 2009; see also Wilson et al. 2010b). But just as important from a conceptual viewpoint, the ecomorphological paradigm in its original form does not account

TABLE 1

*Revisions and extensions to Arnold's ecomorphological paradigm*

| Reference | Contribution |
|---|---|
| Bartholomew 1958; Huey and Stevenson 1979; Bennett 1989; Pough 1989 | Development of the concept of whole-organism performance |
| Arnold 1983 | Development of statistical framework for ecomorphological paradigm |
| Arnold 1988; Moore and Hopkins 2009; Careau and Garland 2012 | Incorporated energetics into ecomorphological paradigm |
| Garland and Losos 1994 | Incorporated behavior into ecomorphological paradigm between performance and fitness |
| Irschick and Garland 2001; Irschick 2003 | Incorporated "ecological performance" into ecomorphological paradigm between morphology and performance *and/or* performance and fitness |
| Ghalambor et al. 2003 | Incorporated life-history traits into ecomorphological paradigm |
| Miles et al. 2007 | Incorporated hormones into ecomorphological paradigm |
| Husak et al. 2009b | Distinguished "dynamic" from "regulatory" performance traits |

Summary of studies that explicitly developed and extended portions of the classic ecomorphological paradigm (Figure 1A) and additional links between whole-organism performance and life-history traits (Figure 3). This list is not exhaustive, nor does it include every study that has influenced the development of these topics.

for life-history tradeoffs among performance and other traits that might impact on Darwinian fitness, nor between performance traits that are mediated by resource allocation. The physiology of such tradeoffs remains little understood (Zera and Harshman 2001; Ricklefs and Wikelski 2002), but are likely to have crucial and sometimes counterintuitive effects on both performance components of the phenotype and ultimately on fitness (Garland 2014). A revised and extended paradigm that includes such tradeoffs, and that takes into account the myriad possible ways that fitness might be affected by them, has the potential to revivify the study of performance and make important inroads into understanding the relationships between morphology and performance and between performance and Darwinian fitness. Ultimately, this synthetic approach will allow a more comprehensive view of how phenotypes evolve—i.e., as suites of traits that positively and negatively impact other suites of traits.

In this review we adopt a conceptual approach to considering the various and reciprocal ways in which several important life-history factors and the expression of various whole-organism performance traits might impact each other and their relationships with overall fitness. Our review is necessarily selective, and focuses only on those life-history traits that have some demonstrated or likely links with whole-organism performance. The relatively limited scope of this review is for two reasons: first, life history is a large and multifaceted research area that does not lend itself to concise and comprehensive review; and, second, we hope that by approaching the topic in a way that identifies the most important areas for interface between life history and whole-organism performance, we will inspire future researchers to tackle the many fascinating questions that these various areas, when combined, pose. However, it should be clear that all of the life-history factors discussed in this review, as well as various other potential factors which we do not consider here, such as temperature, the life-history implications of which have recently been reviewed elsewhere (Angilletta 2009), can and will interact with each other to shape the form and expression of whole-organism performance traits; indeed, the term "whole organism" exemplifies the concept that performance captures and integrates numerous aspects of individual variation in morphology, physiology, and behavior. This notion that whole-organism performance is embedded within a complex phenotype (Ghalambor et al. 2003) is therefore at the very heart of life-history tradeoffs, and an important theme of this review. We focus this paper on both the proximate and ultimate connections between life history and performance. We review how whole-organism performance traits may be affected by resource acquisition and are susceptible to life-history tradeoffs through resource allocation. We then discuss mechanistic links between life-history traits and performance traits, arguing that there is no real distinction in how and why resources could be allocated to these seemingly different types of traits. Finally, we discuss how tradeoffs can influence the evolution of the multivariate phenotype, concluding with a synthesis and suggestions for future research.

## Life-History Tradeoffs

Life-history theory attempts to explain how disparate yet related characteristics of organisms are shaped by selection to achieve reproductive success (Stearns 2000). Central to this idea is the notion of tradeoffs, which represent the costs (in the currency of Darwinian fitness) paid when a beneficial change in one trait is connected with an unfavorable change in another (Stearns 1989). At its most basic, life-history evolution can be approached from two perspectives, namely how different traits are connected to each other and how the environment affects organismal survival and reproduction (Stearns 2000). These two perspectives mirror the morphology→performance and performance→fitness gradients of the ecomorphological paradigm, respectively (Arnold 1983; Figure 1B), in that they consider how relevant traits covary both with each other and with key selective pressures. Despite these clear parallels, however, the study of whole-organism performance from the viewpoint of life history (and vice versa) has been incomplete; indeed, for something that has good reason to be considered the ultimate integrative trait, the extent to which whole-organism performance has failed to be integrated with the many important components of life-history evolution is surprising (but see Huey et al. 1990; Ghalambor et al. 2004; Careau and Garland 2012). Part of the reason may be attributed to the emphasis in ecomorphology, deeply rooted in the concepts of functional morphology, of the deterministic relationship between morphology and performance (Wainwright and Reilly 1994; Irschick and Henningsen 2009). However, a major lesson from life-history theory that is described mathematically by the "Y-model" of resource allocation (James 1974; van Noordwijk and de Jong 1986) is that investment of acquired energetic resources in a particular trait denies those same resources being allocated to a different trait (Figure 2A). This limitation constitutes the basis for life-history tradeoffs (Tomkins et al. 2004). For example, the common tradeoff between survival and fecundity is thought to result from differential allocation of resources to traits promoting survival and reproduction (Figure 2A). Whole-animal performance traits, which often directly affect survival, require allocation of resources toward building rigid mechanical structures (e.g., bone, cartilage, exoskeletons), soft tissue (e.g., muscle, circulatory and respiratory structures), and metabolic machinery (e.g., ATP, enzymes, proteins) that can represent a large investment of resources at one or multiple points during the lifetime of an individual (Figure 2B).

Application of the tradeoff principle to the morphology→performance link, for instance, reveals that the intuitive biomechanical relationship between the design of a morphological structure, such as a limb, and the performance of that structure is not fixed and can be modified by a variety of factors, including the amount, type, or quality of skeletal muscle involved in movement (James et al. 2005). Recent studies of dishonest signaling also show that morphology may be a poor predictor of performance, particularly in the case of invertebrates where muscle is hidden from view inside an exoskeleton (Backwell et al. 2000; Lailvaux et al. 2009), and there is evidence to suggest that within some animal species individuals take advantage of these deceptive signals in order to further their own fitness (e.g., Wilson et al. 2007, 2009; Bywater and Wilson 2012). Such dishonesty is almost certainly manifest as tradeoffs in some other trait, either as an increased allocation toward a related trait or compensation for some of the costs accrued through lower actual performance in those contexts where such performance is required (see Husak and Swallow 2011 for discussion of compensation for functional costs in a sexual selection framework). As of the time of writing, such compensatory tradeoffs are seldom considered or tested for in functional

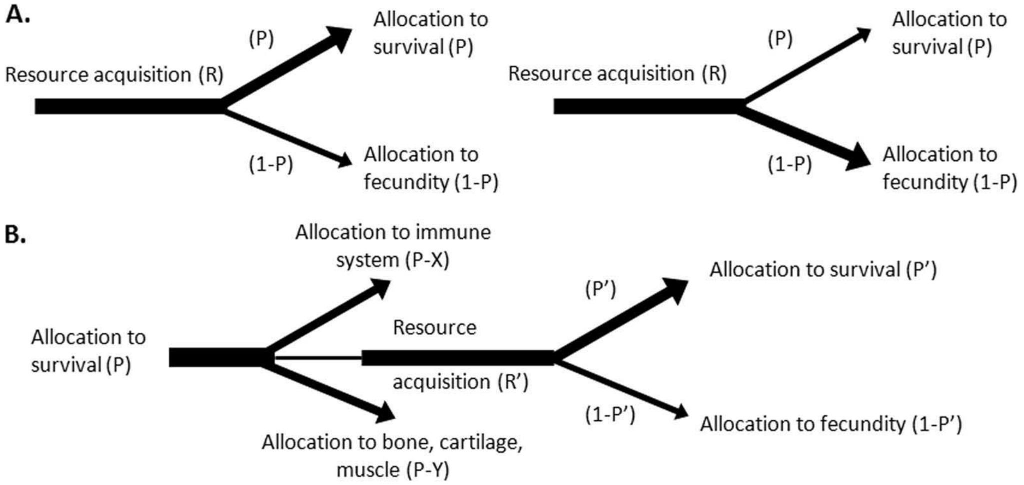

FIGURE 2. LIFE-HISTORY TRADEOFFS

(A) Classic Y-model illustrating the mechanism for a near-ubiquitous life-history tradeoff between survival and fecundity via differential allocation of resources to each when resource acquisition is similar. The width of the arrow represents the relative proportion of resource availability and allocation. (B) A modified Y-model showing allocation of resources to survival (P) via investment in immunity (P-X) and tissues important to whole-animal performance (P-Y). The model also shows how allocation of resources to survival via performance can lead to further acquisition of resources, which can later be allocated to future survival (P') or fecundity (1-P').

systems. Nonetheless, the lesson from dishonest signaling is that individuals may subvert and distort the intuitive and deterministic morphology→performance gradient, and the mechanisms by which dishonest individuals do so are firmly grounded in life history and life-history tradeoffs. Although cloaked by deception, such mechanisms, once revealed, hold great promise for understanding life-history effects on whole-organism performance in other contexts as well.

## PERFORMANCE AND RESOURCE ACQUISITION

Because resource allocation is the basis for life-history tradeoffs, investigations of life history tend to focus on the mechanisms underlying differential allocation. But before resources can be allocated, they must first be acquired. The amount and type of accrued energetic resources can have important consequences for life-history tradeoffs. Within the traditional acquisition/allocation life-history model, the effect of acquiring more resources is relatively straightforward—more resources means more energy available for investment in fitness-enhancing tasks, and if the acquired resource pool is great enough, then certain genetically determined phenotypic tradeoffs may be alleviated or eliminated altogether (van Noordwijk and de Jong 1986; Houle 1991). Accordingly, experimental food supplementation can increase allocation to a variety of life-history traits, including growth, reproduction, and immune function (Boutin 1990; Norris and Evans 2000). On the flipside, reducing or limiting the available resource pool through techniques such as dietary restriction is often a useful method for exposing resource allocation priorities (Glazier 1999; but see Sgrò and Hoffmann 2004) because traits that compete for a limited resource pool cannot be simultaneously optimized.

Recent studies have shown that simple dietary restriction can have profound effects on a number of important life-history traits, including whole-organism performance, in species such as fish (Martínez et al. 2002; Fu et al. 2011), lizards (Le Galliard et al. 2004;

Lailvaux et al. 2012), beetles (Knell and Simmons 2010), and mice (Ingram et al. 1987). These effects tend generally to manifest themselves as a reduction in whole-organism performance in calorie-restricted individuals (but see Royle et al. 2006, who showed that caloric restriction during ontogeny can be compensated for during later life stages), and are generally explicable from a proximate physiological perspective. Muscle in particular is expensive, requiring net protein synthesis, and thus positive protein balance, to produce and maintain (Marden 1989; Marden et al. 1998; Tipton and Wolfe 2001). Consequently, maintaining muscle mass necessary for certain performance traits in the face of a low-resource environment is challenging. In addition, low-resource environments can affect different muscle types and performance capacities differently (Knell and Simmons 2010); in cod (*Gadus morhua*), for example, the metabolic capacities and breakdown of white glycolytic fibers were more affected than red oxidative fibers by starvation (Martínez et al. 2003), yet burst swimming speed did not decrease significantly more than critical swimming speed ($U_{crit}$, which is frequently used as a measure of prolonged swimming performance) in this same species (Martínez et al. 2004). These findings suggest that white fibers are more active in $U_{crit}$ than was previously suspected, and highlight the importance of understanding the metabolic pathways and muscle mechanics underlying key performance measures (Seebacher et al. 2012); similarly, exertion or distance capacity (i.e., where an animal is chased until exhaustion, and the total distance run is measured), the terrestrial equivalent of $U_{crit}$ is commonly considered a measure of locomotor endurance in lizards and other animal species despite being both functionally and ecologically distinct from endurance measured on a treadmill. Indeed, distance capacity has been shown to be more closely related to anaerobic metabolism than to $VO_{2max}$ in the lizard *Ctenosaura similis* (Garland 1984), suggesting that exertion and endurance are in fact likely to exhibit little overlap.

In contrast with simple caloric restriction, the effects of altering the type of resources consumed on performance capacities are not well understood. Studies of humans have clearly shown that exercise effects are themselves affected by nutrition (Atherton and Smith 2012) and different performance activities utilize different substrates. For example, prolonged aerobic activity is associated with an increased proportion of fat and decreased proportion of carbohydrates used as fuel (although at moderate to high aerobic intensities fatty acid and muscle triglyceride oxidation is limiting, and muscle glycogen and blood glucose oxidation consequently increase; Coyle 1995), whereas weight training likely utilizes more carbohydrates to power burst performance (Roy et al. 1998). Nevertheless, relatively few studies have considered the effect of metabolic substrate manipulation on whole-organism performance capacities (see Macaluso et al. 2013 and references therein). For example, Coyle et al. (2001) showed that low-fat diets alter aspects of fat oxidation in endurance cyclists, but did not test for an effect on cycling performance, whereas Oostenbrug et al. (1997) found no effect of fish oil supplementation on cycling endurance (but see Hoppeler et al. 1999, who found that endurance running performance may be enhanced in humans following acclimation to a high-fat diet). In particular, no studies to our knowledge in nonhuman animals have taken advantage of the geometric framework of diet, which conceptualizes animal diets as multidimensional "nutrient space" where each dimension or axis represents a different nutrient (Simpson and Raubenheimer 1993; Raubenheimer and Simpson 1999), to investigate whether divergent performance pathways require different nutrient substrates (i.e., fats, proteins, and carbohydrates) during either development or throughout adult maintenance of performance. The differential use of, and requirements for, specific nutrients and, hence, the existence of various functional nutrition "targets," might be predicted based on physiological concerns such as the composition of the muscle fibers involved in executing various performance tasks (Marden 1989; but see Sinclair et al.

2011, who showed that insects in different states of "condition" utilize different substrates to fuel metabolism). If different performance traits require, or are enhanced by, specific nutrients and diets to support the expression of those traits, then consideration of performance and related traits through the lens of nutrition could shed light on their functional and evolutionary ecology at multiple levels of organization, as well as impact how humans, for example, might maximize specific performance goals or training effects (Atherton and Smith 2012).

The presence of energy-rich macronutrients in diets could also be important because they might ameliorate costs to key life-history traits, including performance, thereby altering tradeoffs in the same way as would increasing the amount of acquired resources, albeit more efficiently. Indeed, extreme variation among individuals in diet composition would greatly decrease the usefulness of the Y-model of resource allocation, since caloric quantity may be less important than diet quality for allocation to performance (and subsequently other traits). Finally, some animals might exhibit specialized adaptations to preserve stores of important specific nutrients; for example, within 50 minutes of depleting its glycogen stores during rapid simulated predator escape, the desert-dwelling mouse *Pseudomys nanus ferculinus* is able to completely resynthesize those stores from other sources without ingesting carbohydrates or any other food (Bräu et al. 1999).

If the effects of variation in the amount and type of acquired resources on performance traits are poorly understood, the existence of life-history tradeoffs that might be associated with such variation is almost entirely unexplored (Naya et al. 2007). Previous studies employing the nutritional geometry approach in a model species for the study of life-history tradeoffs, the cricket *Teleogryllus commodus*, have shown striking effects of diet on reproductive investment (Maklakov et al. 2009). For example, both male lifespan and reproductive investment in the form of calling effort are maximized on a high carbohydrate, low-protein diet, and both of these traits also genetically covary negatively with locomotor performance in this same species (Lailvaux et al. 2010). However, a recent study using similar artificial diets to test the effects of altering the ratios of carbohydrate:fat:protein on jump performance in *T. commodus* found no direct effect of diet on jumping ability in either males or females (Lailvaux et al. 2011). Thus far, no other studies to our knowledge have attempted to examine performance within the context of diet and life-history tradeoffs, and no general patterns can therefore be discerned. Despite the potential shortcomings of artificial diets, particularly for obligate food specialists such as many insects (Chown and Nicolson 2004), the use of such diets for both determining and varying intake targets (defined as the optimal balance and amount of nutrients required for postingestive processes to occur at minimal fitness costs) in different life-history contexts and on different performance traits is of interest in terms of understanding the relationship between performance and the nutritional targets and substrates that support whole-organism performance expression. Furthermore, there is currently ample scope for examining tradeoffs between animal function and reproduction using diet as an intermediary. Finally, and from a slightly different perspective, the acquisition of resources is itself often dependent on an individual's performance abilities (e.g., Vincent et al. 2005; Van Wassenbergh et al. 2006; Montuelle et al. 2008), thus potentially creating variation among individuals in subsequent resource allocation opportunities and decisions. Consequently, the relationship between performance and diet in some species may be complex.

## Performance and Allocation Tradeoffs

Like many other life-history traits, whole-organism performance capacities are susceptible to tradeoffs with others, depending on the amount of acquired resources available. However, only rarely are such tradeoffs identified or tested for. Below we discuss several important life-history traits and contexts with demonstrated or suspected links to whole-organism performance capacities, and briefly consider the ways in which performance may

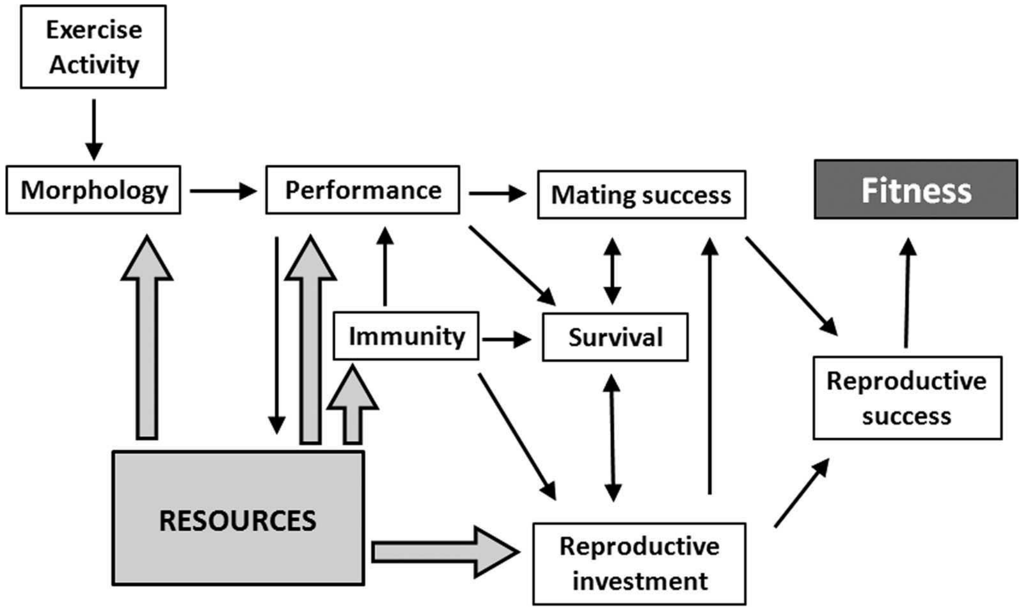

Figure 3. A General Hypothesis Illustrating How the Ecomorphological Paradigm Might Interface With Several Key Life-History Traits Via Resource Allocation

Relationships are inferred from studies cited within the main text. In no case have all of these traits been linked definitively within a single species; thus, the direction and, in some cases, existence of specific relationships are lacking current empirical support. Furthermore, males and females will almost certainly exhibit different sets of tradeoffs in various species. Future studies will refine and clarify many of the relationships posited here.

trade off with each. Figure 3 illustrates these connections schematically. Resource availability can directly impact the classic morphology-performance-fitness paradigm via the building of morphology and the availability of specific nutrients for performance, all of which can lead to individual variation in morphology and performance, depending on resource acquisition and allocation. We make no distinction in this figure between resource quantity and quality for simplicity, but we argue above that diet quality may impact life-history traits (including performance) in a number of ways. Survival and reproduction may trade off directly via decreased allocation to somatic maintenance in favor of increased reproductive investment (e.g., Hunt et al. 2004a; but see Cox et al. 2014), or the tradeoff may exist due to differential allocation to reproduction and traits such as performance and immunity that directly influence survival in other ways. As stated above, performance may also be directly important to resource acquisition; thus, we have included a link to reflect this possibility as well. Finally, exercise, or activity, depending on definitions, may influence morphology, which then may have a multitude of cascading effects on fitness.

## IMMUNITY

Immune systems are costly to use and maintain (Lochmiller and Deerenberg 2000; Hasselquist and Nilsson 2012), and constitute a large expenditure of an individual's acquired resource pool (Råberg et al. 2000; Martin et al. 2003). Consequently, a large literature has accumulated investigating life-history tradeoffs between individual immunity and other important fitness-enhancing aspects of the organismal phenotype (see Jacot et al. 2004; Uller et al. 2006; Reaney and Knell 2010; Cotter et al. 2011 for some recent examples). Previous studies have clearly shown that immune activity has a direct effect on many aspects of whole-organism physiological function, and yet the impact of infection and the immune response on whole-organism performance itself has seldom been explored. Schall (1982) demonstrated that *Plasmodium*-infected *Sceloporus occidentalis* lizards experienced a significant drop in locomotor stamina compared to uninfected individuals (although maximum sprint speed was unaffected by malarial infection). More recently, Mages and Dill (2010) showed that juvenile salmon (*Oncorhynchus gorbuscha*) infected with female *Lepeophtheirus salmonis* sea lice exhibited reduced swimming endurance compared with uninfected controls, especially at higher lice loads. Chatfield et al. (2013) experimentally infected *Lithobates pipiens* frogs with chytrid fungus (*Batrachochytrium dendrobatidis*), and found that only following eight weeks of infection did jump velocity significantly decrease in treatment animals, raising the possibility that performance effects of short-term and chronic infection might be distinct. Indeed, Nebel et al. (2013) found no effect of acute phase immune response on prolonged flight performance in western sandpipers (*Calidris mauri*). In addition to a likely effect of immune activation on performance, there is evidence from a variety of taxa that immune function is itself compromised by performance. Reduced immune function during strenuous exercise has been reported in human athletes (Smith et al. 2011; Walsh et al. 2011), and infection is considered to be an important feature of "overtraining" in endurance runners (reviewed in Noakes 2003). Similarly, Nebel et al. (2012) reported a negative effect on immune function following endurance flight in starlings (*Sturnus vulgaris*).

These findings raise a number of questions regarding the mechanisms by which infection and whole-organism performance may (or may not) affect each other. In this respect, it is especially important to bear in mind that life-history tradeoffs are frequently mediated by individual condition, and that the pool of energetic resources available to an individual might profoundly impact any realized tradeoffs with immunity (Sheldon and Verhulst 1996) via intermediate effects on traits such as fecundity (Gwynn et al. 2005). For example, Meylan et al. (2013) showed that immune system activation in pregnant *Zootoca vivipara* lizards resulted in complex tradeoffs among a suite of life-history traits, including endurance and reproductive investment, that were primarily dependent on individual condition, strongly hinting at resource allocation decisions as the mechanism driving those tradeoffs. By contrast, a more direct effect of infection on performance cannot be ruled out in other studies based on current evidence showing that immune activation can cause tissue damage via increased oxidative stress (e.g., Bertrand et al. 2006; see also Umberger et al. 2013, who showed that muscle infection with a parasitic nematode impairs swimming velocity in small southern flounders, *Paralichthys lethostigma*).

In addition to condition, immunity has also been shown to interact directly with testosterone (T; e.g., Veiga et al. 1998; Muehlenbein and Bribiescas 2005), which has long been considered an immunosuppressant (Folstad and Karter 1992; Wedekind and Folstad 1994), although not always in straightforward ways (Braude et al. 1999; Fuxjager et al. 2011). Given the clear link between testosterone and whole-organism performance, and the likely link between performance and immunity (see above), multiple mechanisms could potentially modulate the relationship between immunity and performance. In light of recent connections drawn between whole-organism performance and sexually selected behavior, especially in males (reviewed in Lailvaux and Irschick 2006; Husak and Fox 2008), immunity is a likely candidate trait that might serve as an important intermediary affecting allocation and testosterone-driven tradeoffs between secondary sexual signals and performance. Indeed, immunity (or immunocompetence) and sexual selection have been closely intertwined ever since the classic and controversial hypothesis of parasite-mediated sexual selection was proposed by Hamilton and Zuk (1982), wherein "bright males" are hypothesized to have greater immune function.

When resource availability is manipulated, such tradeoffs can become evident. In *Sceloporus graciosus* lizards, males given supplementary testosterone and supplementary food had increased immune function compared to control lizards with and without supplementary T that did not receive supplemental food (Ruiz et al. 2010). This suggests that display behavior and immune function can be increased when resources are not limited for allocation to each. Given the ubiquity of parasites and disease in nature (Schulenburg et al. 2009; Martin et al. 2011), if performance, immunity, and sexually selected signals trade off against each other, as we have every reason to believe that they might, then the costs of immunity are an important component of performance life history that cannot be ignored. Progress in this area will depend upon investigators determining which aspects of immune function are more likely to trade off than others, based on immune challenges that their species of interest are likely to encounter in nature (Lochmiller and Deerenberg 2000; Demas et al. 2011), and on formulating specific predictions about how altered resource allocation might affect tradeoffs between performance and certain aspects of immune function.

## SEX, REPRODUCTIVE INVESTMENT, AND SEXUAL SELECTION

Males and females acquire fitness in different ways, and consequently optima for life-history traits associated with fitness are often sex-specific in many species (Bonduriansky et al. 2008; Maklakov and Lummaa 2013). Males, for example, have long been expected to adopt a "live fast, die young" reproductive strategy that discounts survival, and by implication those traits closely associated with survival, in favor of reproduction (although there are many documented exceptions; Vinogradov 1998). Differential allocation of resources by the sexes toward key traits such as reproductive investment therefore generates much of the variance in life history observed within a species, as both theory and data suggest that males and females resolve life-history tradeoffs in different ways; but whereas sexual dimorphism in reproductive behavior and ecology have been well-studied, sex-based differences in physiological capacities underlying such behavior, as well as their respective priorities in terms of resource allocation, are less common.

The differing costs of reproduction in males and females lie at the heart of many sex differences in life history (Wedell et al. 2006), and this is no less true of performance traits. For example, males are frequently superior performers to females even after controlling for differences in body size, particularly with regard to traits that afford an advantage over rivals during male-male combat (e.g., bite force in some territorial lizard species; Huyghe et al. 2005; Lappin and Husak 2005; Lailvaux and Irschick 2007b; Husak et al. 2009c), likely because variation in mating success also tends to be greater in males relative to females, and sexual selection pressure on mate acquisition and related traits is therefore also generally greater in males. A growing literature is demonstrating both phenotypic and genetic links between secondary sexual traits and male functional capacities, the central notion being that males may signal relevant performance capacities to rival males or, more controversially, to potential mates (Lailvaux and Irschick 2006; Irschick et al. 2007). The correlated nature of performance and secondary sexual signals has enormous implications for performance evolution and expression because it constitutes a second link between performance and fitness (the other being survival) that may be subject to modification by selective factors that affect not only performance, but sexual traits connected with performance as well. Selection on male secondary sexual traits could therefore result in correlated change in male performance capacities, or vice versa, depending on the nature of the relationship (Lailvaux et al. 2010). Even if sexual signals do not specifically signal performance, selection on exaggerated traits that share resources with morphological structures that determine performance can alter the shape, size, or function of those structures (Emlen 2001). Indeed, sexual signals frequently incur a variety of energetic costs, the repercussions of which may be manifest as altered metabolic or physiological trait expression (reviewed in Garratt and Brooks 2012), and exaggerated morphological signals could also impose functional and energetic costs on the whole organism. These putative, and possibly reciprocal, performance costs to sexual trait expression (Oufiero and Garland 2007), as well as possible morphological and functional compensation for such costs, are an active and exciting area of current performance research (Husak and Swallow 2011; McCullough et al. 2012).

From a female perspective, selection on male morphological and performance traits could displace those same traits in females from the female selective optimum because males and females share most of a genome. Unresolved intralocus sexual conflict has been shown to affect both the sex-specific phenotypic and genetic variances and evolutionary trajectories (Hall et al. 2010a) in a variety of taxa, and has been understudied in terms of whole-organism performance (but see Long and Rice 2007). In some cases, the above notion of compensation could feed into intralocus sexual conflict, and indeed selection may act to compensate for functional conflicts in each sex (Husak and Swallow 2011; Cameron et al. 2013). In contrast to the above situation where selection on females compensates for male traits, selection can act specifically on female morphology to ameliorate the locomotor costs of bearing eggs or young (Veasey et al. 2001), resulting in suboptimal locomotor morphology which, if expressed in males, impinges on male performance ability. In other cases, compensatory selection for reproductive costs can even be for improved performance in females relative to males. For example, collared lizards (*Crotaphytus collaris*) are extremely dimorphic in body size and limb shape, with males being larger and with longer relative limbs (McCoy et al. 1994). Despite this, there is no detectable sex difference in maximal sprint speed capacity, which is hypothesized to be due to the much larger relative heads of males (Peterson and Husak 2006). However, a life-history perspective offers an alternative hypothesis: since gravidity reduces sprint speed in females in this species (Husak 2006a), it is plausible that there is selection on females for high maximal capacity so that they can maintain “adequate” speeds while gravid, though slower absolutely, to escape predators (Husak 2006c; but see Shine 2003; Iraeta et al. 2010). Lack of apparent sex differences in performance (e.g., Van Damme et al. 2008; Zajitschek et al. 2012) in other taxa may be similarly explained when the complete selective scenario is considered and not just performance alone. The existence of sex differences in performance (e.g., Cullum 1998; Krasnov et al. 2003; Lailvaux et al. 2003; Berwaerts et al. 2006; Lailvaux 2007; Lailvaux and Irschick 2007a), or the lack of them when expected, may therefore have important implications for the evolutionary trajectory of performance traits themselves, as well as related key life-history traits, and should be incorporated into a revised ecomorphological paradigm.

## AGING

Aging has long been a key component of life-history theory (Gadgil and Bossert 1970; Charlesworth 1980), and both longevity and aging have clear, if occasionally counterintuitive, effects on overall fitness (Hunt et al. 2004a,b) and on the relevance of whole-organism performance to individual Darwinian fitness over the course of a lifetime. However, like many other aspects of how performance is linked to life history, our understanding of the way performance ages in nonhuman animals is almost nil. Moreover, even in humans where aging is of significant interest and age-related trends in various traits are relatively well documented, the proximate factors promoting and preventing aging are the subject of continuing controversy. Perhaps one of the most important results to emerge from the evolutionary study of aging is the realization that aging of a given trait is itself a life-history trait, and therefore may be plastic and subject to a variety of allocation tradeoffs and influences, some of which are not readily apparent (reviewed in Bonduriansky et al. 2008). Our knowledge of aging as a life-history trait is, in many cases, directly tied in with what we know of the plastic effects of diet on aging, and indeed diet and aging are frequently linked in the scientific literature (Chen and Maklakov 2012); caloric restriction in particular has been shown to extend longevity in a wide variety of animal taxa (Sohal and Weindruch 1996). In some cases, this poor state of knowledge reflects a general problem with studying aging, especially in taxa where such study presents significant logistical challenges, such as species that enjoy life spans extending across years or decades or those where it may be difficult to determine an individual's age.

If performance is also a life-history trait, and thus subject to resource allocation tradeoffs, then the aging of such performance traits is likely to reflect dynamic allocation that occurs over individual lifetimes. Consequently, expression of a given performance trait may not be constant, and could be altered by any selective context or environment that influences resource allocation decisions. Indeed, given the noted links between performance and both survival and reproduction, as well as the age-dependent, senescent nature of residual reproductive value (i.e., the opportunity for future reproduction; Williams 1966; Fischer et al. 2008), tradeoffs between current and future survival and/or fecundity could conceivably impact the age trajectory of performance and related traits. Although few studies have tested for effects of age on performance in short-lived animals, there is nonetheless compelling evidence that performance aging is indeed subject to life-history tradeoffs. For example, Reznick et al. (2004) showed that experimentally increasing predation in populations of guppies (*Poecilia reticulata*) resulted in earlier senescence in fast-start performance, but did not affect mortality or reproduction, suggesting that aging in performance might be distinct from that exhibited by other key life-history traits. Indeed, different performance traits can themselves show different patterns of aging, as demonstrated by Lailvaux et al. (2011), who found that aging trajectories of bite and jump performance in adult *Teleogryllus commodus* crickets are affected differently by different causal factors, including sex and mating frequency (see also Huey et al. 1990, who showed that sprint speed potentially declines whereas stamina increases with increasing age in *Sceloporus merriami* lizards). Surprisingly, diet, which has previously been shown to have striking effects on aging of reproductive investment in *T. commodus* (Maklakov et al. 2008, 2009), had no significant effect on the aging of whole-organism performance in this same species. The decoupling of reproduction, performance and, potentially, survival over individual lifetimes and environmental conditions has important implications for how we study performance because we cannot necessarily assume general links between performance and components of fitness based on examination of just one or a few age/sex classes. In *Crotaphytus collaris* lizards, for example, sprint speed predicts survival in hatchlings, but not adults (Husak 2006b), yet does predict adult male reproductive success (Husak et al. 2006, 2008). This concern is difficult to evaluate in a comparative context given that all other studies of performance aging and diet have focused exclusively on ontogeny, or aging from juvenile to adult stages (e.g., Royle et al. 2005), and have generally ignored aging effects on the remainder of animal lifetimes (but see Siwak et al. 2002 for a further example of environment-specific performance aging). Furthermore, those few studies that have considered performance aging have tended to do so outside the conceptual framework of reproductive investment, reproductive value, and residual reproductive value—that is, independent of the currency that is required to understand the costs and benefits of life-history evolution (Kokko et al. 2003). Manipulating reproductive investment in particular is a valuable technique for inducing allocation tradeoffs in life-history traits (e.g., Cox et al. 2014), and that approach should apply to the study of performance. Given the complex ways that residual reproductive value and aging may impact resource allocation, a proper life-history perspective on performance will include aging as an essential factor driving tradeoffs among performance and other traits.

### EXERCISE

Exercise and training can have significant influence on individual morphology and whole-organism performance, and have been particularly well studied in humans. Type and frequency of exercise has clear effects on body composition, including percentages of body fat and lean muscle, which in turn are likely to affect the amount of stored energy available for resource allocation and overall individual energy balance, respectively. Training may also alter the way in which humans store and use energetic resources; for example, studies have shown that endurance training roughly doubles muscle capacity to store glycogen (Greiwe et al. 1999), and that trained and untrained subjects may differ in their response to diet type (Helge et al. 1996). Individual susceptibility to training is also variable in humans, with studies reporting up to tenfold interindividual trainability in human endurance capacity and anaerobic performance (reviewed in Van Damme and Wilson 2002), and a recent study demonstrated a genetic basis to human endurance trainability as well (Timmons et al. 2010). However, in contrast to the large literature on exercise in humans, studies examining exercise effects on nonhuman performance are much rarer (He et al. 2013; Palstra and Planas 2013). Researchers have, for example, documented training effects on locomotor performance and protein turnover in rainbow trout (Houlihan and Laurent 1987), and endurance and sprint performance respond significantly differently to a rigorous exercise regimes in different lizard species (Garland et al. 1987; Husak unpublished data), although experimental methodology has complicated the interpretation of results (Gleeson 1979; Garland et al. 1987; O'Connor et al. 2011). The costs of recovery from vigorous exercise have also been investigated in some reptiles and amphibians (e.g., Gleeson 1991, 1996; Scholnick and Gleeson 2000), yet placing exercise and training within a rigorous life-history framework is again problematic given the overall paucity of studies on this area.

One potential explanation for the lack of attention paid to training effects in nonhuman animals is the long-held belief that animals routinely perform at near-maximum levels in nature, but this belief is poorly supported by empirical studies (e.g., Irschick 2003; Irschick et al. 2005; Husak and Fox 2006). From a life-history perspective, exercise is likely to be enormously important given that any resources that are allocated toward increasing muscle mass or elevating cardiovascular function are unavailable for allocation to other potentially important fitness-enhancing tasks. However, the effects of aerobic exercise may be much more complex, as some have argued that increased aerobic activity was associated with increased brain size (an energetically expensive investment) during human evolution (Raichlen and Polk 2013). Thus, exercise effects (perhaps on some traits more than others) may be involved in any number of ecologically relevant tradeoffs that will remain obscured so long as it is assumed, either implicitly or explicitly, that exercise has negligible effects on whole-organism performance of nonhuman animals in natural populations. For example, performance traits that are short bursts of activity, such as sprinting, may be relatively unaffected by infrequent use, whereas activities of sustained duration may enhance endurance capacity, which might not require frequent use of maximal capacity. In the former case, one would not predict altered resource allocation due to effects of sprint use, whereas in the latter case one would predict diversion of resources from other aspects of the phenotype to enhance endurance capacity. Thus, one could choose to study exercise in terms of individual variation in the use of performance, or activity rate, which does show substantial variation (Irschick et al. 2005; Husak and Fox 2006). Indeed, activity rates are evolutionarily correlated across species with laboratory measures of endurance capacity (Garland 1999). If we were to apply this broad approach to the phenotypic effects of exercise, similar to approaches used to study other forms of phenotypic plasticity (West-Eberhard 2003), then we might begin to better understand why organisms do not seem to use maximal capacities in nature, why there is substantial interindividual variation in performance despite there often being strong directional selection for superior performers or stabilizing selection on optimal performance (Irschick et al. 2008), and what such variation in use of performance means for variation in resource acquisition and allocation.

## Proximate Mechanisms Governing Allocation Tradeoffs

Life-history tradeoffs and the mechanisms underlying differential resource allocation have long remained opaque to researchers. Among the most important of the proposed mechanisms affecting tradeoffs are hormones, which play a central role in coordinating behavior and physiology, responding to environmental variability, and regulating transitions among life-cycle stages (Adkins-Regan 2005; Wada 2008; McCormick 2009; Moore and Hopkins 2009; Careau and Garland 2012). Hormones can travel through the body to potentially impact any tissue that is reached by the circulatory system, so long as there are appropriate receptors for that hormone in the cells of the tissue. These potentially widespread effects make some types of hormones important intermediaries in the resource allocation process (Ketterson and Nolan 1992; McGlothlin and Ketterson 2008), and as such the significance of various hormones, especially testosterone and glucocorticoids in vertebrates, cannot be overstated. Whereas testosterone tends to enhance traits important to mating and reproductive success (Hau 2007; Hau et al. 2010), it is also associated with suppressed immune function (see above) and reduced survival (Dufty 1989; Reed et al. 2006; Hau et al. 2010). Glucocorticoids, at baseline levels, are important for energy intake, storage, and mobilization (Sapolsky et al. 2000; Hau et al. 2010), but acute, stress-induced levels increase locomotor performance and immune function, while suppressing reproduction (Sapolsky et al. 2000; Hau et al. 2010). We note, however, that chronic stress may have different effects, and this phenomenon has been reviewed elsewhere (Sapolsky et al. 2000; Landys et al. 2006; Romero et al. 2009). Steroid hormones have therefore figured prominently in the literature as proximate mediators of life-history traits and tradeoffs (Reed et al. 2006; Miles et al. 2007; Hau et al. 2010). Despite the numerous studies and reviews linking hormones to life histories, our understanding of the links among performance, hormones, and life history nonetheless remains incomplete (Miles et al. 2007).

Numerous recent reviews elucidate the known and predicted effects of T on life histories (Ketterson et al. 1992; Ketterson and Nolan 1994; Hau 2007; Hau et al. 2010; Hau and Wingfield 2011). Because of its effects on skeletal muscle growth, T is also a potentially important modulator of various types of whole-organism performance traits. The performance consequences of exogenous, supplemental steroid use in humans are well studied (Bhasin et al. 2001; George 2003; Hartgens and Kuipers 2004), but less is known about effects relative to endogenous physiological levels (Husak and Irschick 2009; West et al. 2010). Despite some uncertainties regarding the mechanisms, it appears that T enhances at least some performance traits, and this appears be the case in humans, as well as other vertebrates (reviewed in Husak and Irschick 2009; Higham and Irschick 2013). Perhaps more intriguing than a simple "more-T-equals-better-performance" relationship are findings that T may differentially affect muscle fiber types, muscles in various parts of the body, and thus different performance traits (Husak and Irschick 2009). These specific effects are likely caused by variation in expression of androgen receptors (and perhaps other pathways, including growth hormone and growth factors), but whether this variation is adaptive and involved in life-history decisions remains essentially unknown.

Testosterone is typically thought to organize major transitions during ontogeny, such as sexual maturation, but life-history effects may be more subtle. For example, the size class (and most likely, age) of sexually mature male green anole lizards (*Anolis carolinensis*) determines the magnitude of their relative dewlap size (i.e., their colorful, secondary sexual throat fan) and head shape, with smaller "lightweight" males having relatively smaller dewlaps and heads than larger "heavyweight" males (Lailvaux et al. 2004; Vanhooydonck et al. 2005). These differences within adult males represent a major ontogenetic transition after sexual maturity, with heavyweights having disproportionately wider and deeper heads and higher bite-force capacities. This phenomenon is associated with higher T levels in heavyweights, but evidently only through the effects of body size: lightweights have lower T on average than heavyweights, and T significantly scales to body size in lightweights, but not heavyweights (Husak et al. 2007). Experimental stimulation of the hypothalamus-pituitary-gonad axis with gonadotropin-releasing hormone revealed that neither sexually mature lightweights nor heavyweights are capable of producing higher T levels than circulating baseline levels during the breeding season (Husak et al. 2009a). The positive correlation between body size and T in lightweights (but not heavyweights) suggests that male green anoles suppress T levels until they approach a body size where they are competitive for a territory. Thus, T seems to be associated with a very important life-history transition for male green anoles, influencing morphology, performance, behavior, and perhaps through those traits, fitness. Since there is a high amount of variation in T levels among lightweight males, exploration of how that variation is linked to variation in morphology and behavior will be useful for examining potential tradeoffs during this crucial life-history transition. Given the multitude of other potential effects of T on the phenotype (i.e., immune function, growth behavior; Wingfield et al. 2001; Hau 2007; Rosvall 2013), there is much to learn from considering endocrine regulation of life-history transitions, growth, and performance after sexual maturation (see also McCormick 2009).

In addition to T, several other hormones have been implicated in regulating resource allocation tradeoffs among fitness components. We have some understanding of how immunity and reproduction trade off via leptin (French et al. 2011), melatonin (Bentley et al. 1998; Moore and Siopes 2000; Hotchkiss and Nelson 2002), or combinations of these hormones with steroid hormones (Demas et al. 2012). Within insects specifically, juvenile hormone (JH) serves similar broad functions to T in trait integration, development, and life history (Flatt et al. 2005; Harshman and Zera 2007) and is also linked to immunity (Rolff and Siva-Jothy 2002) and secondary sexual trait expression (Rantala et al. 2003; Contreras-Garduño et al. 2009, 2011) in a manner comparable to that of T. Indeed, the effect of JH on immune function is also sex-dependent (Villanueva et al. 2013), as is the case with T. The adipokinetic hormones of insects also appear to regulate many traits involved with life-history tradeoffs, such as energy metabolism, neuromodulatory control of locomotion, larval development, and egg production, among others (Kodrík 2008; Lorenz and Gäde 2009), serving roles similar to vertebrate glucagon (Goldsworthy 1994), catecholamines (Gäde 2004), or glucocorticoids. Each of these better-known molecules may interact with other signaling pathways, leading to complex connections (and possibly tradeoffs) among metabolism, reproduction, immunity, aging, and other traits. For example, the "hunger hormone" ghrelin is important to energy balance in vertebrates, and is a strong promoter of feeding (Kaiya et al. 2013), but ghrelin is also known to interact with leptin and stimulate the release of growth hormone and glucocorticoids (Kaiya et al. 2013), as well as directly affect reproductive function via interaction with multiple components of the hypothalamus-pituitary-gonad axis (Barreiro and Tena-Sempere 2004; Muccioli et al. 2011). The connections among ghrelin, growth hormone, and feeding behavior are suggestive of a link to whole-organism performance, and recent studies on humans confirm this possibility. Both aerobic and resistance exercise decrease the acylated (biologically active) form of ghrelin in adult humans (Broom et al. 2007, 2009), but in children exercise increases acylated ghrelin, with the proportional increase correlating with exercise duration and maximal performance (Sauseng et al. 2011). The age effect of exercise on ghrelin levels in rats, however, does not appear to be the same (Hsu et al. 2011). Clearly, future studies are needed to clarify these relationships and discern variation among species. Comparative studies of such pathways and trait correlations that go beyond model laboratory organisms have resulted in major advances in our understanding of how resources might be differentially allocated to growth, somatic maintenance, aging, reproduction, and immunity.

Such allocation mechanisms can be explicitly tied into pathways that mediate whole-organism performance to give a clearer picture of how resources are allocated and what chemical signals are used to make those "decisions" during an organism's lifetime. Although these connections have not been made broadly, several individual studies have done so. For example, a number of recent studies have begun to pry open the black box of resource allocation and reveal the specific biochemical pathways affecting key life-history characteristics. These pathways hold much promise for understanding life-history tradeoffs, but a proper synthesis with life-history traits affecting fitness is only now underway. Of special interest in this regard is recent research implicating key cellular signaling pathways in the allocation of acquired resources to different phenotypic traits. Emlen et al. (2012) showed experimentally that disabling the insulin/insulin-like growth factor (IGF) pathway in developing dung beetle (*Trypoxylus dichotomus*) larvae inhibited horn growth by approximately 16% and significantly reduced wing size, but had no effect on the size of genitalia. These results suggest that differential condition-dependence of various phenotypic traits may be underpinned by variation in IGF sensitivity, and provides a testable mechanism for understanding condition-dependence and susceptibility to life-history tradeoffs, including those involving performance. It is also of interest to note that reduction in IGF signaling via dietary restriction has been implicated in life-span extension in a variety of species, including insects and some mammals (Mair and Dillin 2008; Suh et al. 2008). Given the links between whole-organism performance and secondary sexual traits in a variety of animal species (reviewed in Lailvaux and Irschick 2006), IGF constitutes a likely lynchpin life-history pathway integrating performance, diet, secondary sexual traits, and longevity/aging. However, we are not aware of any studies that have established or investigated potential links between performance and IGF at either single or multiple points in individual lifetimes. What makes the IGF pathway so appealing as a general mechanism linking phenotypic traits is the near-ubiquity of the IGF/IGF-like system in such a diversity of animal taxa (Hwa et al. 1999; Nakae et al. 2001; Dantzer and Swanson 2012; Emlen et al. 2012). Further, the IGF pathway interacts with testosterone (Gibney et al. 2007; Serra et al. 2011), potentially linking multiple disparate fields with a single mechanistic pathway. Future research that includes IGF effects on the performance phenotype in combination with the underlying nutritional structure, in addition to other hormones, may give novel insights on resource allocation.

A separate pathway that *has* clearly been linked with both whole-organism performance and life history is the hypoxia-inducible factor pathway (HIF). This evolutionarily conserved pathway controls the morphogenesis of branching networks of tubes involved in oxygen delivery in most macroscopic organisms. Marden et al. (2013) showed that polymorphism in an HIF pathway gene is associated with both variation in oxygen delivery, flight metabolic performance, and mitochondrial aging in the butterfly *Melitaea cinxia* (again, hinting at a relationship between this pathway and aging/longevity, as with IGF), and pointed out the implications of such variation for the evolution of life histories and for dynamic tradeoffs among key physiological traits relevant to Darwinian fitness. For aerobic performance traits, this pathway is potentially of paramount importance, and perturbation or modification of HIF is apt to strongly influence oxygen-dependent whole-organism performance. Indeed, human athletes often train at high altitude, thereby deliberately activating the HIF pathway and gleaning the performance benefits of enhanced oxygen delivery via the physiological response that this triggers (Hoppeler and Vogt 2001). Equivalent pathways that affect anaerobic performance are likely to act via different biochemical intermediaries, and might thus be expected to affect other life-history traits in different ways. As such, the life-history tradeoffs involved with endurance versus sprinting, for instance, might be expected be quite different, particularly given the potential for different training effects on various performance traits (see above).

## EVOLUTIONARY CONSTRAINTS AND THE MULTIVARIATE PERFORMANCE PHENOTYPE

The Y-model of resource acquisition and allocation (Figure 2A) has some important implications for understanding both the existence and evolution of life-history tradeoffs. In particular, it describes situations where tradeoffs are rendered either undetectable or dynamic. In addition to variation in acquisition masking allocation decisions, as mentioned above, allocation decisions could be made at a hierarchy of levels, with binary splits at several nodes instead of just one (Roff and Fairbairn 2007b; Figure 2B). In this sequential or hierarchical model, correlations at the end of the hierarchy depend heavily on patterns of allocation at the beginning; thus, measuring simple bivariate tradeoffs may not be sufficient to understand factors driving them. The hierarchical Y-model also constitutes an explanation for how allocation decisions and tradeoffs can change with age. Consequently, a multivariate approach is preferable to examining bivariate tradeoffs, and identifying relationships among suites of traits is essential (Figure 3).

Allocation decisions among multiple fitness-related traits, and activation of the pathways that regulate them, are ultimately controlled by the genetic architecture underlying such traits (de Jong and van Noordwijk 1992), the heritable components of which are summarized in the genetic variance-covariance matrix (*G*; Houle 1991; Steppan et al. 2002). This *G* matrix is critical to understanding the evolution of phenotypic traits because it identifies multivariate "directions" of genetic variation (i.e., combinations of traits and their genetic covariances) along which evolutionary change is possible, as well as those where change is constrained (Blows and Hoffmann 2005). To clarify, we note that we are considering "absolute" constraints (Mezey and Houle 2005; Roff and Fairbairn 2007b), i.e., evolutionary trajectories that are unavailable to selection (Kirkpatrick and Lofsvold 1992), as opposed to constraint in the sense of a bias, which impedes but does not prevent evolution in a particular direction. As such, the *G* matrix, along with life-history theory, provides the necessary framework for interpreting the evolutionary significance of a given trait or trait combination. Unfortunately, like many other traits with important fitness ramifications, the genetic basis of whole-organism performance remains largely unknown. Simple heritabilities for individual performance traits have been determined in a handful of species: for example, locomotor capacities in lizards (Tsuji et al. 1989; Sorci et al. 1995; Warner and Andrews 2002; Le Galliard et al. 2004), *Thamnophis* garter snakes (Garland 1988), and humans (reviewed in Van Damme and Wilson 2002) and take-off performance in the butterfly *Pararge aegeria* (Berwaerts et al. 2008). Garland and collaborators in particular have maintained a valuable long-term selection study on locomotor performance in mice (e.g., Garland and Freeman 2005), which has offered significant insight into the integrated evolutionary relationship between morphology and performance. Recent studies have also begun to consider the

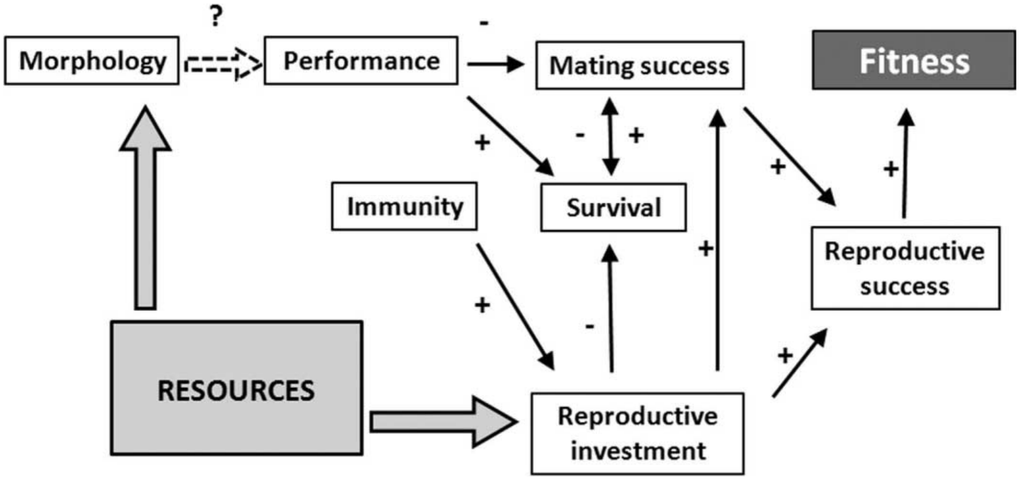

FIGURE 4. LIKELY QUALITATIVE RELATIONSHIPS AMONG LIFE-HISTORY VARIABLES IN *TELEOGRYLLUS COMMODUS* CRICKETS

Likely qualitative relationships among key measured life-history variables, including jumping performance, following the allocation strategy described by the major axis of genetic variation ($g_{max}$) in adult male *Teleogryllus commodus* crickets, and based on Hunt et al. 2004a; Lailvaux et al. 2010, 2011; Drayton et al. 2012; Zajitschek et al. 2012. Note that the morphology→jump performance relationship has not yet been rigorously quantified in this species. Several of these relationships are also subject to aging effects in this species (Zajitschek et al. 2009, 2012; Lailvaux et al. 2011).

genetic variances underlying complex functional systems (Parnell et al. 2012), the evolutionary dynamics of which might be expected to differ from those of simpler morphology→performance relationships (Alfaro et al. 2004). However, while we can be reasonably confident that genetic variation in morphology and related performance traits probably exists, in most cases the information that can be gleaned from metrics such as univariate heritability alone is minimal.

Far more useful, albeit more challenging, are studies that have estimated not only the additive genetic variance underlying whole-organism performance traits, but also the genetic relationships between performance and important components of life history. For example, tethered flight duration has been shown to be either positively genetically correlated (Gu and Barker 1995) or uncorrelated (Dingle 1991), with life-history traits such as development time and fecundity in several insect species. Studies examining the quantitative genetics underlying the "migratory syndrome" (i.e., the morphology and physiology associated with migration) in winged insects have been instructive in this regard, although we note that actual flight performance is typically not measured (Roff and Fairbairn 2007a). In the most comprehensive multivariate, life-history performance study to date, Lailvaux et al. (2010) showed that jumping ability is negatively genetically correlated with both longevity and sexual attractiveness in male *T. commodus* crickets, and moreover that jumping is aligned along the same multidimensional axes of genetic variation as development. The directions of these alignments along the major axis of genetic variation ($g_{max}$) suggest that males who develop quickly and are good jumpers are unattractive males who do not live very long (Figure 4); however, Lailvaux et al. (2010) also found evidence for two additional minor axes that nonetheless account for significant proportions of the overall genetic variation, and which exhibit qualitatively and quantitatively different sets of tradeoffs among these same traits. These genetic patterns are consistent with differences in resource allocation to different functions, rather than differences in overall resource allocation (Houle 1991), and are indicative of diverse allocation strategies used by individuals of different genotypes to maximize their own fitness. The results of Lailvaux et al. (2010) strongly imply that species may exhibit multiple patterns of resource allocation, each with their own unique set of tradeoffs, and that selection along any of these minor axes, although likely to elicit a lesser response than selection along $g_{max}$, would result in different correlated responses in each case. Studies such as this underscore the value of the combined quantitative genetic life-history approach for uncovering the complex relationships among performance and other key fitness-related traits, and emphasize that changes in performance are unable to be viewed as independent of the rest of the organismal phenotype.

In addition to tradeoffs that might be involved in antagonistic genetic correlations or are otherwise genetically constrained, the evolution of locomotion in particular is especially prone to functional tradeoffs that prevent the simultaneous optimization of conflicting performance tasks (Van Damme and Wilson 2002). Animals often rely on the same structural elements to perform an assortment of functionally disparate actions, such as jumping, running, climbing, swimming, or flying. Biomechanics and physiology predict different phenotypic solutions to each of these functional challenges, and while tradeoffs among different performance traits requiring specialized physiology and/or morphology have proven surprisingly difficult to demonstrate (Van Damme and Wilson 2002), a handful of studies using vertebrates suggest that excellence in a particular performance task comes at the expense of average or poor performance in mechanically conflicting abilities (Vanhooydonck et al. 2001; Van Damme et al. 2002; Pasi and Carrier 2003; Herrel and Bonneaud 2012; but see Sorci et al. 1995), particularly after controlling for individual "quality" (Wilson et al. 2014). The relevance of such functional constraints to life-history is that certain life-history syndromes will be unavailable to species that are morphologically or physiologically adapted to a particular functional or environmental regime. For example, greyhounds that have been artificially bred for racing exhibit smaller percentages of appendicular muscle in their distal limbs, and exhibit a twofold higher potential for the storage and recovery of elastic work in the extensor muscle-tendon system of the ankle joints than do pit bull terriers, which were originally bred for fighting and exhibit the exact opposite pattern (Pasi and Carrier 2003). If endurance and power indeed cannot be simultaneously maximized, as evidence suggests, then any distinct life-history costs and benefits associated with each performance syndrome likely overlap little within an individual. Indeed, such intraspecific functional conflicts may even contribute to the displacement of males and/or females from their fitness optima, and constitute an important functional component of intralocus sexual conflict (Cameron et al. 2013).

## Synthesis and Future Prospects

Although the study of life-history traits and whole-animal performance has historically been conducted by separate research groups and with different approaches, there is much that can be learned by combining the two. By considering both types of traits simultaneously in a research program that recognizes performance as a life-history trait, we can begin to address several lingering unanswered questions raised by studying each in isolation. First, why are classic morphology-performance relationships not always found? Second, why are bivariate performance tradeoffs often not detected within and among species? Third, how does diet quality influence performance and life-history tradeoffs? Fourth, what is "exercise" in free-living animals, and how does it fit into the evolution of performance capacities and life-history traits? Fifth, what mechanisms link various performance and life-history traits? Sixth, what life-history traits trade off with performance, and how are such tradeoffs affected by aging and by changes in residual reproductive value? Finally, are there intraspecific differences in resource acquisition or allocation, and how do these shape the evolutionary trajectories of performance traits, as well the classic survival-fecundity relationships? We argue here that these and other related questions can be addressed only by adopting a comprehensive, multivariate approach to understanding how whole-organism performance relates to other key fitness-related traits, and by interpreting such relationships within a rigorous life-history/quantitative genetic framework over individual lifetimes. In particular, we suggest that continued emphasis on simple univariate traits or bivariate trait relationships are of limited value, and that future progress in understanding the evolution and ecology of performance can only come through a fundamental shift in how we view performance and its relationship to the overall phenotype.

Much of our review centers on understanding how performance and life-history traits might be linked phenotypically to each other, noting a general lack of data on how performance trades off and interacts with other life-history traits. Understanding the complex relationships among performance and such traits is crucial for comprehending performance expression and, in particular, the myriad selective factors affecting performance. For instance, selection could have both direct effects, whereby a performance trait is specifically selected for in a particular direction, and/or indirect effects, whereby selection on a trait that is genetically, phenotypically, or functionally linked to performance affects the level of performance expression. The strength of that indirect selection will be affected by the nature of the covariance relationship between performance and the target trait and, consequently, the effects of selection on a related trait could be alleviated, amplified, or inverted relative to the target trait depending on the way in which they are linked. The potential complexity of such relationships is illustrated in Figure 3, which shows how several key life-history tradeoffs might be generally related both to performance and to Darwinian fitness in a hypothetical species. Here, increased investment in a costly trait such as immunity (see above) could come at the expense of allocation to performance, compromising survival in one respect while at the same time enhancing it in another. In this scenario, the link between performance and fitness might even be negated entirely, forcing any gains in fitness to be achieved through allocation to reproductive investment instead, with the relationship between immunity and reproductive investment possibly mediated by an intermediate hormone such as leptin (French et al. 2011). Alternatively, a variety of other routes to fitness might exist depending on the amount and type of resources available and the direction and magnitude of the subsequent allocation decisions. However, we emphasize in this review that many of the relationships posited and depicted in Figure 3 are only poorly understood, if not entirely unknown, and they certainly have not received appropriate statistical scrutiny with path analyses as proposed originally by Arnold (1983). Consequently, we are currently unable to make rigorous general predictions about how selection on traits that covary with performance might affect the relationship between performance and fitness. The potential complexity of these relationships is illustrated empirically by a study of phenotypic tradeoffs in the lizard *Zootoca vivipara*, which showed that the links between endurance capacity, survival, and parasitism are such that endurance might be connected to fitness through multiple pathways in the integrated phenotype (Clobert et al. 2000). Similarly, a qualitative summary of the currently known relationships among measured life-history traits in adult male *T. commodus* crickets suggests that the nature of the link between jumping performance and Darwinian fitness hinges on the relationship between survival (assessed here as longevity) and mating success, which is itself a function of reproductive investment and thus, ultimately, diet macronutrient composition in this species (Maklakov et al. 2008, 2009; Figure 4).

In addition to these many likely indirect connections, understanding how different biotic and abiotic environmental factors interact to affect trait plasticity and tradeoffs remains even more challenging to students of life history. In a recent review, Kasumovic (2013) noted that complex environments comprise multiple selective factors, each of which might trigger resource allocation or different types of plasticity, either independently or in conjunction with one or more other factors. This perspective is especially important for performance traits, which experience context-specific selection (Irschick et al. 2008); for example, the developmental trajectory of a given performance trait such as burst locomotor performance could conceivably be subject not only to environmental resource availability as a juvenile (e.g., Brown et al. 2006; Lee et al. 2010), but also (and simultaneously) to the presence or absence of predators in the juvenile environment, which has been previously shown to drive shifts in performance expression and overall life history (Relyea 2002; Hoverman and Relyea 2012; Groner et al. 2013). By considering different selection pressures on performance, along with other "classic" life-history traits, future investigators may be better able to link abiotic and biotic factors that govern such plasticity and tradeoffs.

A common issue bedevilling many functional and whole-organism performance studies of life history is sample size. Several of the topics we have discussed in this review would require arguably larger sample sizes than are typically used in most performance studies to address the above questions rigorously, especially for the demonstration of tradeoffs in males and females and hypothesis testing involving multiple factors and traits. The issue of sample size is particularly germane to multivariate studies of genetic linkages and tradeoffs, which traditionally require the measurement and maintenance of many hundreds of individuals. Although long-term laboratory selection studies have proven useful for testing the genetic links between performance and other traits such as immunity and corticosterone (e.g., Dlugosz et al. 2013), the multitude of logistical issues pertaining to laboratory manipulations means that for many animal species the future of this line of research most likely lies in the field, by applying the quantitative genetic "animal model" to natural populations of known pedigree (Postma and Charmantier 2007; Wilson et al. 2010a). Thus far, no study has measured field estimates of heritabilities and genetic correlations involving whole-organism performance traits. Studies that attempt to do so on a long enough time scale also face significant challenges, but are poised to reveal enormous insight into the evolutionary potential of whole-organism performance and of the associated life-history traits, each of which has been posited for decades to have strong direct impacts on fitness.

A recurring theme of this review is not only how little is known about the factors that affect performance in most animals, but also in many cases how much is known about performance in humans. Data on human performance are highly relevant to the morphology→performance gradient in particular, yet despite previous calls for greater integration and collaboration between ecomorphology and sports science (e.g., Van Damme and Wilson 2002) and the clear value of human athletic data to the study of performance tradeoffs (Van Damme et al. 2002; Wilson et al. 2014) and aging (Baker and Tang 2010; Lailvaux et al. 2014) among other topics, human performance is still only seldom considered within the explicit context of ecomorphology (see Carrier et al. 2011; Morgan and Carrier 2013 for some recent examples). In addition to circumventing issues with sample sizes in many cases, studies of human performance are often conducted over a variety of organizational levels, incorporating aspects of morphology, biochemistry, and physiology that are relevant to performance (Garland and Losos 1994) to an arguably greater extent than in any other animal species, and the literature examining the effects of training and exercise on human locomotor performance in particular is unrivaled (reviewed in Noakes 2003). This vast body of literature constitutes an important foundation and reference point for studying training effects in other animals. Recent studies have also begun to test for relationships between human performance and attractiveness (Postma 2014), thereby taking tentative steps toward completing the human ecomorphological gradient. As such, studies of human performance have much to add to the conversation regarding locomotor performance expression and evolution, and should ideally be considered within the same life-history framework as other animal taxa.

## CONCLUSION

In this paper, we have highlighted several avenues for future research that we believe will advance both the fields of ecomorphology and life history in useful ways. We have stressed the links between whole-organism performance and other key fitness-related traits, and emphasized the potential complexities of the relationships, noting the need for appropriate multivariate experimental studies that tease apart those connections within a framework that considers resource acquisition, allocation, the proximate mechanisms involved, and the ultimate factors driving the evolution of an overall, integrated phenotype. We suggest that such an approach, using Arnold's (1983) seminal ecomorphological paradigm as a foundation, holds a great deal of promise for understanding the evolution and expression of the key determinants of Darwinian fitness.

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