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Complex reproductive traits and whole-organism performance

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ABSTRACT

Arnold's (1983) path-analytic paradigm, considering "morphology, performance, and fitness," has been elaborated in several ways. For example, current versions (e.g., Fig. 1 in Storz et al. 2015, Am. J. Physiol. 309:R197-R214) recognize the level of "behavior" (including aspects of motivation) as a filter between performance abilities (only measurable if motivation is maximal) and fitness components. Performance abilities constrain behavior, but behavioral choices may shield performance from selection. Conceptual and empirical issues remain, such as the extent to which individual variation in lower-level subordinate traits (e.g., circulating hormone concentrations) might directly affect behavior, growth rates, sexual maturation, etc., rather than having effects only through paths involving some aspect of performance. Moreover, empirical studies have yet to encompass more than a few possible paths in a given system, in part because life-history researchers rarely communicate with those focused on performance. Most life-history studies ponder trade-offs associated with reproductive effort, but studies of locomotor performance (e.g., maximal sprint speed) have rarely considered trade-offs with reproduction. This lack of connection is surprising because both life history (e.g., clutch size) and locomotor performance (e.g., locomotor stamina) traits require allocation of energy and other resources, so trade-offs between these trait types may be expected. These perspectives and cultures could be bridged by a focus on the ability of organisms to perform components of reproductive biology (e.g., lactation performance could be studied in animals maximally "motivated" by manipulation of litter size or endocrine function). Alternatively, one could study impacts of reproduction on performance, as when bats and live-bearing fishes lose maneuverability during gestation. We also consider sperm performance in the context of the paradigm and illustrate that the paradigm can easily be utilized as a frame-work within which to consider key aspects of sperm biology.

Introduction

The concept of whole-organism performance (e.g., Bennett 1980; Huey and Stevenson 1979) and what has come to be known as “the ecomorphological paradigm” (Arnold 1983; Garland and Losos 1994; Lailvaux and Husak 2014) has provided biologists a framework within which to consider the integrated effects of multiple levels of biological organization on how an animals interact with their environment in various ways that influence Darwinian fitness. Taking the example presented in Arnold’s (1983) seminal paper, one might study how individual variation in the sizes of snake jaw bones affect maximal swallowing ability, which could be measured through a series of trials in the laboratory, and then quantified by path analysis. If the individual snakes were then marked and released in the field, then one could determine components of fitness, such as survival and reproductive success, and then further apply path analysis to achieve an integrated picture of morphology, performance, and fitness (Arnold 1983).

Over time, this framework has been refined, modified, and expanded. For example, Arnold’s (1983) original model did not include behavior as an explicit or distinct level of organization, whereas one of us has viewed behavior as a potentially crucial "filter" intervening between selection and performance (Garland et al. 1990; Garland 1994a; 1994b; Garland and Carter 1994; Garland and Kelly 2006: Garland and Losos 1994). (Behavior can also be considered as a factor affecting performance via brain motivation and reward pathways, but the paradigm seems most applicable when one can presume that animals are maximally motivated to perform, such that motivation is a constant [100%] and hence falls out of the path diagram). Other important expansions have involved the addition of energetics (Arnold 1988; Careau and Garland 2012), use of the paradigm to elucidate trade-offs (e.g., Ghalambor et al. 2003; Oufiero and Garland 2007), and the placement of life history traits, such as survivorship, age at first reproduction, and fecundity (e.g., Oufiero and Garland 2007; Lailvaux and Husak 2014). A recent and relatively complete version of the paradigm in shown in Fig. 1 (Storz et al. 2015), and we use this as our taking-off point for what follows.

Despite the value of this paradigm demonstrated by various conceptual (see previous paragraph) and empirical (e.g., Aerts et al. 2000; Careau and Garland 2012; Enriquez-Ur et al. 2015; Garland and Losos 1994; Gomes et al. 2016; Goodman 2007; Irschick et al. 2005; Oufiero and Garland 2007; Santana and Miller 2016; Scales et al. 2009; Sinervo and Calsbeek 2003; Wainwright 1994; Walker 2007) studies, and its continued development, it has been rarely used to evaluate reproductive traits, such as litter size, gestation length or lactation performance. Here, we discuss reproductive performance traits, with a focus on how they could be measured as well as how they might be placed into the context of current versions of the ecomorphological paradigm. We highlight the enormous value in measuring this modality (reproduction) of animal performance for evolutionary biologists. For example, sperm performance has serious implications for male fitness and lactation performance largely dictates offspring growth rates during early ages in mammals. We also make strides to include sexual selection into the paradigm.

As with other performance traits, ensuring that measurement achieves “maximal” performance in fully “motivated” individuals are issues facing attempts to evaluate reproductive performance traits. Nevertheless, some such traits are clearly tractable but remain understudied in the context of the ecomorphological paradigm. Lactation performance is one such case. Although this term has been used in agriculture and is of enormous value for the dairy industry (Bell et al. 2000; Kung et al. 2000; DeFran et al. 2004), it remains largely ignored in the world of ecological and evolutionary physiology, except for studies in mice by two research groups (e.g., Hammond et al. 1996; Hammond and Diamond 1992; 1994; Hammond and Kristan 2000; Król and Speakman, J.R., 2003; Speakman et al. 2001; Speakman and Król 2005).

For studies examining “classic” performance traits - such as maximal sprint speed - reproduction is still worth considering beyond being a “nuisance” variable. Specifically, although a gravid female will most likely be slower in terms of maximal sprint speed (barring changes in plastic traits that could compensate for the negative effects of pregnancy: cf. Oufiero and Garland 2007), the details of how her performance changes across gestation is itself an interesting and important (particularly in regards to natural selection) question (Garland 1985; Garland and Else 1987; Kuo and Irschick *in-prep*). One might examine the impact of reproduction itself on performance. For example, gravid lizards run and jump poorly as compared with non-gravid individuals, and female bats and live-bearing fishes lose maneuverability during gestation (Table 1). We simply do not know how such performance traits change across the course of gestation (but see; Scales and Butler 2007). Thus, despite being well-documented, changes in mass, gait, endocrine function, and metabolism associated with gestation remain poorly understood in the context of their effects on whole-organism performance. Such changes are sure to have important consequences for Darwinian fitness (lifetime reproductive success), and can be viewed in the general contexts of constraints and trade-offs and constraints (Garland 2014). However, trade-offs and selective pressures may differ between the sexes.

Including reproductive traits in studies of performance may help efforts to reveal some of the many potential sex-specific types of selection on performance traits. Presuming that traits in the two sexes positively genetically correlated, then sex-specific selection (including aspects of sexual selection) may "pull" the phenotype of the opposite sex along and as a result may limit (or enhance) the capacity and thereby performance of both sexes (see Kaliontzopoulou et al. 2015). For example, if females require greater endurance to compensate for the burdens of carrying eggs or developing embryos, then selection may have shaped certain aspects of their biology (for example, morphology or physiology) to compensate (Veasey et al. 2001), either with respect to their baseline performance abilities or plastic changes during pregnancy, including possible behavioral changes (e.g., Bauwens and Thoen 1981; Brodie 1989; Downes and Bauwens 2002). Interestingly, female reproduction may improve performance (McCoy et al. 1994). Similarly, because changes in body size are part of their usual biology, females may also recover faster in response to mass changes relative to males (e.g., via tail-loss), as seen in skinks (Chapple and Swain 2002).

Males and females also share genes for many traits although selection on traits may differ between the sexes. Shared genes for some subordinate traits including those that affect performance may lead to selection in one sex pulling along the performance of another sex. For example; females may experience selection for greater endurance to escape predators while pregnant which, could lead to selection on an inheritable trait (ex- oxygen binding affinity of hemoglobin or a complex trait like lung capacity) and the offspring of successful females, both daughters and sons, might inherit these genes leading to high endurance in not just daughters but also sons. The potential nuances of how sex-specific selection (via natural or sexual selection), interact to result in unique solutions that may enable or limit performance remains an area of enormous theoretical and empirical interest. The implications for how reproduction might impact performance, both across evolutionary time and via phenotypic plasticity, are highly deserving of additional study within the context of the ecomorphological paradigm.

Our goal here is to more fully integrate reproductive biology and sexual selection theory with the ecomorphological paradigm. After reviewing the paradigm, we discuss how this integration of paradigm, reproductive biology, and sexual selection might be done, where reproductive traits fit into the paradigm, and how they can be treated as aspects of performance. We also support the view that the field of sexual selection might benefit from placing many traits into the ecomophology paradigm (see; Husak and Fox 2008; Lailvaux et al. 2010; Lailvaux and Husak 2014; Lailvaux and Irschick 2006; Oufiero and Garland 2007).

We review cases in which the ecomorphological paradigm might intersect reproductive biology and address three main questions:

(1) How might reproduction itself impact performance and hence fit into the ecomorphological paradigm?

(2) What reproductive traits might be considered as performance traits and what is the utility in dong so?

(3) What kinds of experiments might be done from the perspective of an expanded paradigm?

Review

What the paradigm is (at present)

Consistently updated subsequent to its initial presentation as a path-model, the ecomorphological paradigm (Arnold 1983; Lailvaux and Husak 2014; Storz et al. 2015) has proven extremely useful for the investigation of traits in a framework that facilitates their consideration relative to other levels of selection (Fig. 1 reproduced from Storz et al. 2015).

Most versions of the paradigm start with **"subordinate traits."** In Fig. 1, subordinate traits are on the left and are those, at lower levels of biological organization, that act together with other such traits to affect or determine characteristics at higher levels of organization. For example, as above (Fig. 1) the oxygen affinity of hemoglobin might interact with maximal heart rate and various aspects of muscle function to dictate stamina.

Arnold (1983) defined **performance** as a "score in some ecologically relevant activity" that must be "phylogenetically interesting." Performance is also "the ability of an individual to conduct a task when maximally motivated" (Careau and Garland 2012). A good deal has been written on what might be considered a performance trait, and two key issues are prevalent in the literature, the aforementioned issue of achieving maximal motivation during measurements and ecological relevance (i.e. "ecological performance": Irschick 2003; Irschick and Garland 2001).

Taken together, multiple performance traits (abilities) constrain behavior. In other words "performance abilities set an "envelope" (or "performance space"; Bennett 1989) within which behavior is confined" (Careau and Garland 2012). **Behavior** can be defined as "the… actions and mannerisms made by individuals, organisms, systems, or artificial entities in conjunction with themselves or their environment…Conscious or subconscious, overt or covert, and voluntary or involuntary." (Wikipedia). Simply put, behavior is anything an animal does (or fails to do!).

Behaviors occur during all daily activities (e.g, foraging) and also allow an organism to respond immediately to its environment. Some behaviors can lead directly to fitness, such as mating or parental care or evasive strategies that allow escape from a predator (Fig. 1).

Primary Fitness Components are demographic parameters of Darwinian fitness. Such traits are what most people measure as a surrogate for Darwinian fitness, but unless all of them are measured fitness cannot be accurately quantified. Moreover, additional interesting reproductive traits can be measured as components of the three primary fitness components, such as number of offspring sired, survival of young to weaning, and attractiveness of male offspring to females. We have added several such subcomponents of primary fitness (Fig. 1). Thus, the paradigm ranges from the level of the gene (not shown in Fig. 1) to the cell (as part of the depicted Subordinate Traits) and eventually to Darwinian fitness.

Unlike the enormous body of literature subsequent to Arnold's (1983) paper that has found utility in the ecomorphological paradigm (in particular, research in the areas of ecological and evolutionary physiology), the field of sexual selection has functioned largely in isolation of this paradigm (but see; Husak and Fox 2008; Irschick and Garland 2001; Lailvaux and Irschick 2006; Lailvaux and Husak 2014; Lailvaux et al. 2010; Oufiero and Garland 2007), likely due to lack of research overlap. However, we argue that the ecomorphological paradigm may provide a beneficial frame-work for the field of sexual selection, and that several traits currently the focus of sexual selection research may be of interest to those in ecological and evolutionary physiology (Bennett and Huey 1990; Feder et al. 1987; 2000; Garland and Carter 1994).

Sexual selection theory

Since its inception by Darwin (1859; 1871), sexual selection has focused on the role of diverse traits, both physical and behavioral, for increasing mating opportunities and thereby contributing to fitness. Competition was a key factor Darwin considered when formulating his ideas of sexual selection. Darwin's ideas regarding mating competition and sexual selection are summarized well by Andersson (1994). "Competition is here used in a similar sense as in ecology: competition occurs whenever the use of a resource (in this case, mates) by one individual makes the resource harder to come by for others. This is so whether or not the rivals meet in actual contests; the only requirement is that a user makes the resource less available to others. Mate choice by one sex therefore usually implies (indirect) competition over mates in the other sex, even if rivals never meet each other." (Andersson 1994 p 9).

In scientific research, sexual selection is usually discussed in the context of either 1) male-male competition (intra-sexual selection on combat traits, ritualized behaviors, and weapons) and/or 2) through female choice (inter-sexual selection on showy traits of possible mates, such as elaborate tails of some birds [note that males may also choose mates by these same processes, although females are usually the "choosier" sex (*sensu* Fisher 1930)]. Both processes involve selection related to differences in number of mates (Andersson 1994; Darwin 1859, 1871; Kvarnemo & Simmons 2013) and impact primary fitness components such as fecundity that underlie Darwinian fitness (Fig. 1). Sexual selection is known to shape both primary (sex-specific traits used for reproduction, such as genitalia (Arnqvist 1998; Hosken and Stockley 2004) and secondary (sex-specific traits not used for actual reproduction, such as coloration) (Andersson 1994; Zuk et al. 1992) sexual characteristics.

Some researchers have successfully examined secondary sexual characteristics within the ecomorphological paradigm to show the putative costs (or lack thereof) of such sexual traits for performance (Mowles and Jepson 2015; Oufiero & Garland 2007; Sewall 2015 and others). Some such studies have found a negative impact of sexually selected traits on performance (ex. fiddler crabs; Allen and Leinton 2007; side-blotched lizards; Brandt 2003; and cockroaches Mowles and Jepson 2015), while others have not found performance costs associated with such traits (e.g., Anolis lizards; Vanhooydnk et al. 2005 a, b). Despite the growing number of studies of sex-specific traits in the context of performance and the ecomorphological paradigm this remains an uncommon area of study and, many additional aspects of sexual selection remain entirely unconsidered (Table 2) in the ecomorphological paradigm (but see discussions in; Irschick et al. 2007; Oufiero and Garland 2007).

Since the 1970s, sexual selection theory has grown to encompass not just pre-copulatory mate choice but also post-copulatory processes. Post-copulatory sexual selection broadly includes the many processes after mating that can result in differential fertilization success. As with pre-copulatory sexual selection, post-copulatory sexual selection operates on both sexes. The primary mode of male-centered post-copulatory sexual selection is “sperm competition”; which occurs when females mate with multiple males whose ejaculates and associated sperm aim to out number, out swim or in some other way “beat” each other to fertilize an ovum (Parker 1970; 1979). Female-centered post-copulatory sexual selection on the other hand centers on processes under the broad term “cryptic female choice“ that females use to control fertilization for example by selectively using sperm e.g., by directing sperm from certain males to the ovum while dumping sperm from other males (Eberhard 1996; Thornhill 1983). Because conception involves traits of both sexes, post-copulatory sexual selection often results in co-evolution (antagonistic or otherwise) between male traits like the piercing syringe-like gentialia of male bed-bugs and female traits like the correspondingly thicker body tissues of female bed-bugs (Andersson 1994; Arnqvist & Rowe 1996; Eberhard 1996; Siva-Jothy 2006).

The increasing consideration of post-copulatory sexual selection has not yet included ties to the ecomorphological paradigm. In particular, primary sexual traits (e.g., genitalia, gonads, gametes) remain characteristics that have not been examined in the context of the paradigm. Sexual selection can also lead to different types of mating systems which in turn impact allocation and life history strategy differences between the sexes (see below). Thus, the expansion of the paradigm to include life history traits (Lailvaux and Husak 2014; Storz et al. 2005; this issue) presents an opportunity to place these traits within the paradigm.

For example, sexual selection theory has also included attempts to understand which sex should invest in parental care and to what extent. In turn, it has been shown that parental care can lead to diverse mating systems and vice-versa (Orians 1969). Such interactions between which sex is “tied” to a reproductive event (with gestation being a shackle between a female and her current reproductive investment that many male vertebrates entirely avoid) form the basis of the theory of parental care (e.g., who undergoes gestation, can lactate etc.). These same traits lead to differential offspring survival (Fig. 1, “survivorship”) (paternal care, maternal care), and thus are clearly important for Darwinian fitness. We now consider how researchers might integrate the ecomorphological paradigm with reproductive biology in general.

How we might update the ecomorphological paradigm and/or reconsider what traits should be emphasized

How might reproduction impact current models?

Although it is not common practice, reproductive traits can be added to current versions of the ecomorphological paradigm. In many cases these reproductive traits would be depicted as arrows going back from fecundity to performance (whereby such traits are usually assumed to negatively impact performance) (Fig. 2). However, reproduction can also result in increased performance such as in the case of male *Sceloporus* that have greater endurance while “reproductive” (seeking and courting mates, defending territories) (John-Alder et al. 2009). This increase in performance is underpinned by increased testosterone and corticosterone levels in these same males during this time-frame (John-Alder et al. 2009).

Performance changes associated with gestation are caused by various aspects of a female’s physiology or morphology (i.e., subordinate traits in Fig. 1) being impacted by gestation. A few examples of these changes include: an increase in body mass, greater drag, altered posture, and decreases in available energy. The impacts of these changes have been documented by a series of studies in a variety of taxa (Table 1). These studies demonstrate that gestation commonly negatively impacts maximal sprint speed, endurance, acceleration as well as a few other performance traits.

However, this non-exhaustive summary of studies on the influence of gravidity on performance indicates a taxonomic bias, with a focus on squamates. The paucity of data on mammals is especially noteworthy. From a theoretical stand-point, mammals are particularly interesting in regards to reproduction given the extensive time over which embryos are maintained *in-utero*. Meanwhile, females continue about (most of) their usual behaviors that require various performances (e.g., running, jumping, biting). Table 1 indicates that in mammals and many other taxa the nuances of how gestation impacts performance remains an understudied area of comparative, ecological, and evolutionary physiology.

Predictions: gestation and performance

A series of predictions can be made for the direction, magnitude, and type of change in performance as a result of gestation. First, we might predict to see gradual and relatively linear changes. Such changes may cause a decrease in performance, but this may not always be the case and instead an increase in performance might occur. For example, female Finnish endurance runners had increased performance early in pregnancy, perhaps related to haemodynamic changes (Penttinen and Erkkola 1997). In a group of German runners no change in running performance was seen until after 36 weeks of pregnancy (Bung et al. 1988). Energetic cost of locomotion of obese women across pregnancy, both during resting and walking, did not change with pregnancy (Byrne et al. 2011). Second, the impact of reproduction on performance may not be linear but instead step-wise as a pregnancy passes through key events, such as implantation and various fetal developmental milestones). Third, performance costs of gestation may be more severe in taxa with particular types of locomotion (flight vs. swimming, etc.). Fourth, as with many other traits, we might expect to see phylogenetic differences. For example, the "matrotrophy index" (defined by Reznick as "the ratio of the estimated dry mass of offspring at birth divided by the estimated dry mass of eggs at fertilization" (Reznick et al. 2007)) varies among closely related taxa but also at a clade-level (Reznick et al. 2002;

Pires et al. 2011; Pollux et al. 2014). The matrotrophy index may in turn correlate to degree of performance loss due to gestation.

However, reproductive traits themselves can be considered as performance traits. They are clearly “phylogenetically interesting” (Arnold 1983) and “ecologically relevant” (Irschick 2003; Irschick and Garland 2001), and behaviors such as finding mates, fighting with rivals or defending your from predators may often involve maximal motivation (Careau and Garland 2012). Thus, we might start to place these traits themselves into the paradigm. Below we attempt this with two reproductive traits: lactation (Fig. 3) and sperm production (Fig. 4).

What reproductive traits might be considered performance traits?

Lactation performance

Lactation and milk composition are important aspects of mammalian life history through their relations with reproductive investment (Hinde et al. 2015; Millar 1975). They have been shown to vary among species in relation to both phylogeny (Hayssen 1993; Oftedahl 1984) and ecology (Boness and Bowen 1996; Skibiel et al. 2013). We argue that lactation is also a performance trait that can be conceptualized in the context of the ecomorphological paradigm (Fig. 3).

We are not the first to suggest that lactation is a performance trait. In the dairy sciences, lactation performance is already a commonly discussed concept defined as “peak yield and persistence” (Husvéth 2011). Furthermore, much is known about the genetics and subordinate traits underlying lactation performance, including the influences of such hormones as oxytocin and cortisol. Lactation performance is demonstrably dependant upon nutrition, hormones, and mammary gland morphology (Fig. 3). All these traits interact with such life history traits as parity, age, and even the sex of current and previous offspring (Hayes et al. 2010; Hinde et al. 2009; 2015; Lucy et al. 1993).

To measure “maximal lactation performance,” as for other aspects of whole-organism performance in the ecomorphological paradigm, it would be necessary to maximally motivate females.

In principle, this could be done in several ways, including adding pups (Hammond and Diamond 1992), changing the duration of lactation/weaning (Hammond and Diamond 1994), and shaving lactating females to increase heat loss and hence avoid possible overheating (Król et al. 2007). Furthermore, hormones associated with lactation (e.g., oxytocin) provide an easy and well-understood way to manipulate milk let down.

Another way forward in studies of lactation performance would be to utilize pre-existing "model" systems. For lactation, this would certainly include dairy cattle, which have been selectively bred for lactation performance for centuries (ex- 6000-5000 BC in Asia; Evershed et al. 2008). Specifically, the Holstein breed holds the current records for highest lactation performance (Hasheider 2011).

The data-rich papers on dairy cattle reveal much about the relationships between lactation performance and other levels of the ecomorphological paradigm. Lactation performance is predicted by parity, age, temperature, diet, sex of offspring, and a mother's condition (health) (Hayes et al. 2010; Hinde et al. 2009; 2015; Lucy et al. 1993). Further relationships that can be added to the paradigm include epigenetics (e.g., DNA methylation that affects gene expression) and complex clusters of functional genes associated with metabolism (e.g., signal transduction, peroxisome proliferator-activated receptors, immune and inflammatory processes and cell death) (Loor 2010).

Gamete production and performance

Gametes can be viewed as haploid organisms (Reinhard 2015). Gametes much like viruses may not meet the usual criteria of a "whole organism" as commonly considered in the context of "whole organism performance." However, if one is to take classic definitions of performance more broadly they would be left with a demonstrably useful theoretical framework within which to investigate an important biological trait: gamete performance. Gametes are essential for sexual reproduction and thereby major effectors of Darwinian fitness, but to our knowledge they remain unconsidered in the context of the ecomorphological paradigm. We suggest that gamete production is logically viewed as a whole-organism performance trait influenced by subordinate traits. Like lactation, it is also “ecologically relevant” and “phylogenetically interesting” (Arnold 1983). Gamete performance could be quantified as total number of gametes over a distinct period of time (e.g., month, season or life-span) as well as gamete quality.

Sperm performance

We are not alone in questioning traditional consideration of gametes as “whole-organism” as evidenced by the recent exciting paper discussion “sperm ecology” (Reinhard 2015). Examination of gamete specific metrics in this context would allow researchers to measure aspects of these cells that may approximate quality. The ecomorphological paradigm can provide a theoretical framework currently lacking in the field of sexual selection that would allow for the consideration of sperm traits across levels of organization and relative to traits leading to Darwinan fitness (see; Fitzpatrick and Lüpold 2014). Furthermore, when considered as such (a performance trait) gamete performance is easily conceptualized within the paradigm (Fig. 4).

What metrics are we talking about when we say sperm or gamete performance? Many spermatozoa and ejaculate traits have been quantified (especially in the fields of reproductive medicine and animal science) and found to be key for fertilization. Such traits are sperm velocity, linearity of swimming path, fertilization capability (often related to amount or type of acrosomal enzymes), aging rate (e.g., longevity; Firman et al. 2015), as well as many other traits (Fitzpatrick and Lüpold 2014).

Furthermore, trade-offs are known to occur between these sperm traits (which can also be placed in the model) (see; Garland 2014 for discussions of trade-offs Lailvaux and Husak 2014 and other papers in this issue for further discussion of the placement of trade-offs in the paradigm). Returning to sperm, one well-known trade-off occurs between sperm speed and longevity (Fitzpatrick and Lüpold 2014), and this trade-off may have very important implications for sperm competition, particularly in the context of female sperm storage (Orr and Brennan 2015). Finally, although we have focused on spermatozoa in the context of the paradigm it is evident that female gametes (eggs) could similarly be considered in this frame-work.

What experiments might be done using an updated model?

An interesting aspect of considering reproductive performance traits within the context of the ecomorphological paradigm is that few studies on classic performance traits have examined natural changes in performance across time (as discussed in the context of seasons by Irschick et al. 2006). The nature of reproduction is highly transitive in most organisms, and thus would require measuring seasonal variation in performance or considering repeatability of performance. Although it is clear that gestation can impact classic performance traits, disentangling the specifics of exactly how gestation impacts performance would require longitudinal data.

Concluding Remarks

Most life-history studies focus on trade-offs associated with reproductive effort, but studies of locomotor performance (e.g., maximal sprint speed) have rarely considered trade-offs with reproduction. Here we have shown the value of integrating these areas, in particular reproductive traits with the ecomorphological paradigm. Given limited space, we have focused on just a few of the many possible areas within which the paradigm might be applied to the consideration of reproductive characteristics, as well as to traits evolving via sexual selection. We have provided two examples (Figs. 3, 4) as to how these other traits may integrate with the paradigm; lactation performance and gamete (sperm) performance. In both cases, subordinate traits as well as fitness components relating to reproductive performance (lactation performance or gamete performance) are evident from the path diagram outlined by the ecomorphological paradigm.

Reproductive traits, such as gestation, can also impact "classic" performance traits, such as sprint speed (Table 1). The implications of this type of effect are of substantial theoretical interest, as they may present a playing field for male- versus female- focused selection to operate and may set metabolic ceilings. Thus, investigations into this nexus of performance and reproductive state can advance our understanding of the physiological limits to performance. To this end, we have outlined one such study that could be done to evaluate changes in performance due to gestation (i.e., the effects of a progressing pregnancy on maximal sprint speed). We suggest that longitudinal studies are needed to tease apart the "whole-organism" impact of pregnancy on performance.

We believe the utility of the ecomorphological paradigm far exceeds the traits it has been used to consider thus far. In particular, the field of sexual selection may benefit from the use of this trusted and useful paradigm (Table 2), whereas those who measure "classic" performance traits may gain much by evaluating crucial additional aspects of biology, namely reproduction.

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Figure Captions

Fig. 1. Path diagram modified (with permission) from Storz et al. (2015), illustrating proposed relationships across several levels of biological organization and leading ultimately to Darwinian fitness. Here we have added several subcomponents of primary fitness components (bulleted), which are primarily life history traits. Following the convention of path diagrams, arrows indicate relationships as either: putatively causal (single-headed) or correlative (double-headed). See text for further explanation.

Fig. 2. Modified from Storz et al. 2015 (used with permission) to illustrate the impact of fecundity (in this case having developing embryos inside the body or as in some males carrying developing embryos on the dorsum). Fecundity includes such subcomponents as pup size, litter size, and number of litters per year. The state of being gravid can affect physiology beyond the direct changes due to mass loading. Gravidity is known to influence many aspects of physiology, for example through altering the hormonal milieu, which in turn impacts behaviors and motivation for locomotor performance (see text). As in Fig. 1, arrows indicate relationships as either: causal (single-headed) or correlative (double-headed).

Fig 3. A modified version of Storz et al. 2015 (used with permission), illustrating some of the known relationships between female mammalian reproduction, in particular lactation performance and a variety of other traits. The goals here here are to illustrate how lactation might be placed into the ecomorphological paradigm and to show a few known relationships across levels of organization. As in both Fig. 1 and 2, arrows indicate relationships as either: causal (single-headed) or correlative (double-headed). Not illustrated are the effects of parity on future performance (ex. second time moms do not need the same hormonal priming to initiate maternal behaviors associated with nursing (Pawluski et al. 2006) and have larger mammary glands (Hassiotou and Geddes 2013). Also not depicted is the effect of corticosterone or leptin in milk that can change the development of pups and their own subsequent lactation performance (Hinde et al. 2014; Ilcol et al. 2006; Sullivan et al. 2011). Epigenetic relationships, including via DNA methylation, are also known to influence the milk production of daughters (Blair et al. 2010; Singh et al. 2010; 2012).

Fig 4. A modified version of Storz et al. 2015 Fig. 1 (used with permission), illustrating how sperm biology and associated male traits can be conceptualized within the context of the ecomorphological paradigm. Epigenetic transmission has been noted for sperm in mice (Puri et al. 2010), but is not depicted here. Sperm "behavior" here includes movement by spermatozoa (e.g., via microtubules or pseudopod extension), remaining "still" while in storage (Orr and Brennan 2015), the formation of "sperm trains" where multiple sperm interact to move within the female's reproductive tract (Immler et al. 2007), and directed motion to certain areas through chemotaxis. As in figures above, arrows indicate relationships as either causal (single-headed) or correlative (double-headed).

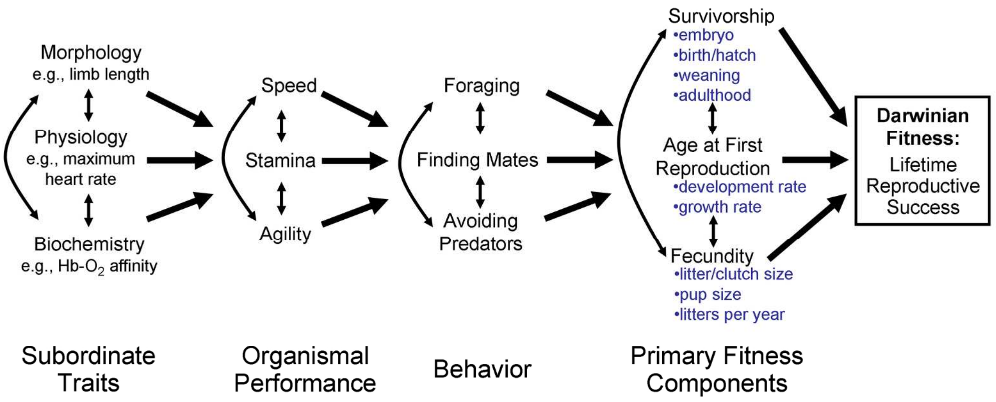
Table 1. Studies that have been done to understand the impact of being gravid on whole-organism performance (citations in Appendix 1).

	Organism	Traits impacted by gravidity/pregnancy	Notes*	Reference
Invertebrates	Funnel-web spiders	↓ speed in mated females*	Cost due to sperm storage not pregnancy per say	Pruitt and Troupe 2010
	Common striped scorpion	↓ speed (84%) Refusal to run in 65% of females*	Behavior and performance both ↓	Shaffer and Formanowicz 1996.
	Giant water-bugs	↓ speed while carrying eggs (on back)*	males	Kight et al. 1995
Fishes	Guppies	↓Fast-start swimming		Ghalambor et al. 2004
	Dwarf seahorses	↑ specific metabolic rate when gravid (10-52%) *	males	Masonjones 2001
	Mosquitofish	↓ U_{crit} (likely due to aerobic changes), No Δ in swimming kinematics, ↓ escape speed*	Escape speed is only impacted in older females not younger females (Belk and Tuckfield 2010)	Plaut 2002, Belk and Tuckfield 2010
Amphibian	Spotted salamanders	↓ burst swimming speed	No differences in voluntary crawling between the sexes, all females (gravid or not) had higher oxygen consumption than males.	Finkler et al. 2003
Squamates	Garden skinks	↓ speed	↓ speed is comparable to eating full meal.	Shine 2003
	Northern red-throated skinks	↓ speed, 23-33%	Independent of relative clutch size.	Goodman 2006
	Common/viviparous lizard	↓ sprint speed		Van Damme et al. 1989
	Northern Death Adder	↓ speed, 30% slower	Independent of clutch size.	Webb 2004
	Skinks (various)	↓ speed		Shine 1980
	Broadhead skink	↓ speed, 25% slower ↓ endurance, 50% slower		Cooper et al. 1990
	Flying lizards (*Draco*)	UNK but compensatory sexual size dimorphism		Shine et al. 1998
	Side-blotched lizards	↓endurance		Miles et al. 2000; Zani et al. 2008
	Green iguanas	Likely force-limited in direction of motion, compensation noted (200% ↑ in vertical power)	Musculoskeletal changes noted in females may lead to evolution of sexual size dimorphism.	Scales and Butler 2007
	Western fence lizards	↓ sprint speed 20-45%	Population differences in performance ↓.	Sinervo et al. 1991
	Garter snakes	↓speed ↓ endurance		Seigel et al. 1987
	Tiger water snakes	↓swim speed,* ↓time swimming,	Decrease in swimming speed was	Aubret et al. 2005

		No Δ in sprint swimming speed	associated with litter mass.	
	Seim-aquatic snake *(Seminatrix pygaea)*	↓ crawling speed, ↓ swimming speed	↓ related to reproductive investment in some habitats.	Winne and Hopkins 2006
	Water snakes	↓ growth, survival		Brown and Weatherhead 1997
	Birds (Starlings)	↓ speed and angle of ascent		Lee et al. 1996
	Blue tits	↓ speed, 20%		Kullberg et al. 2002
	Zebra finches	↓ take off speed	Independent of body mass.	Veasey et al. 2001
Mammals	Bottlenosed dolphins	↓ maximum swim speed, 62-44% decrease*	May not be maximally motivated. Swimming after a reward/toy.	Noren et al. 2011
	Humans	↑ running “performance”	Exact “performance” unclear, highly trained athletes may not extend to females in other conditions	Penttinen and Erkkola 1997
	Humans	No Δ in metabolic cost of locomotion (walking)*	Study done on obese women, may not extend to other body conditions.	Byrne et al. 2011

Table 2. Suggested relationships between established parameters of the ecomorphological paradigm and areas of reproductive biology and sexual selection that could be placed into the paradigm.

Ecomorphology Paradigm Category	**1' sexually selected characteristics**	**2' sexually selected characteristics**	**Other fundamental aspects of reproduction**
Subordinate traits			
Physiology	Endocrinology, Spermatogensis, Oogensis		Gamete osmoregulation
Biochemical	Composition of the ejaculate (proteins, pH), Ovarian fluids (proteins, pH)	Pheromones	Other aspects of reproductive endocrinology
Morphology	Spermatozoa, Ova, Genital morphology	Dimorphic feathers, fins, pigments, structures for producing courtship sounds	Uterus, placenta, mammary glands (Fig. 3)
Performance	Gamete "performance" including sperm swimming, gamete production (Fig. 4), percent normal, ovum viability, selective implantation, Sperm capacitation production (Fig. 4), Egg production, ovulation	Sperm competition, Cryptic female choice	Lactation (Fig. 3), implantation or any other aspect of pregnancy
Behavior	Mating Sperm (Fig. 4) and egg "behaviors" for example sperm "cooperation" through formation of trains (Immler et al. 2007)	Male-male competition Courting and mate choice, Obtaining copulations	
Primary Fitness			
Survivorship	Sperm storage		Parental care including nursing and other behaviors (Fig. 3)
Fecundity	Sperm (Fig. 4) and egg interactions		



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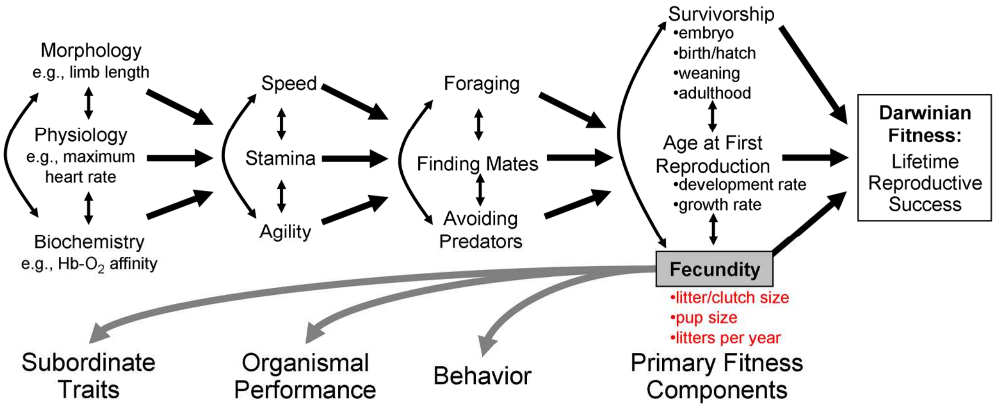

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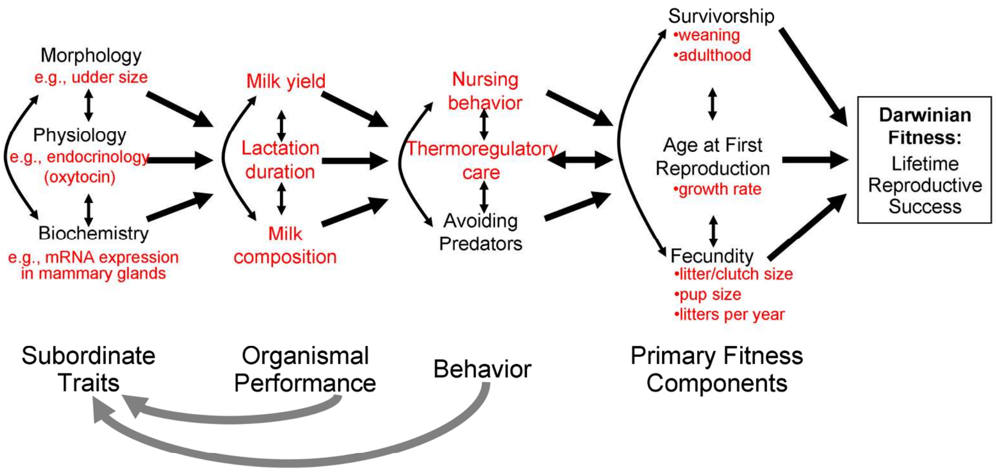

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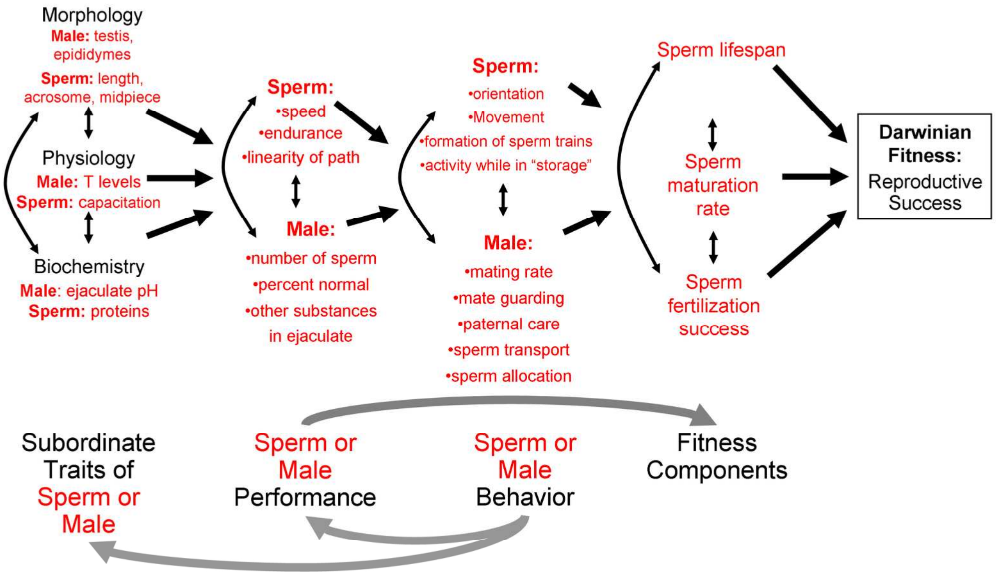

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Orr and Garland, Appendix 1

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