

## SYMPOSIUM

# Complex Reproductive Traits and Whole-Organism Performance

T. J. Orr<sup>\*,1</sup> and Theodore Garland, Jr.<sup>†</sup>

<sup>\*</sup>Department of Biology, University of Utah, Salt Lake City, UT 84112, USA; <sup>†</sup>Department of Biology, University of California, Riverside, CA 92521, USA

From the symposium “Integrative Life-History of Whole-Organism Performance (SICB wide)” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2017 at New Orleans, Louisiana.

<sup>1</sup>E-mail: [teri.orr@utah.edu](mailto:teri.orr@utah.edu)

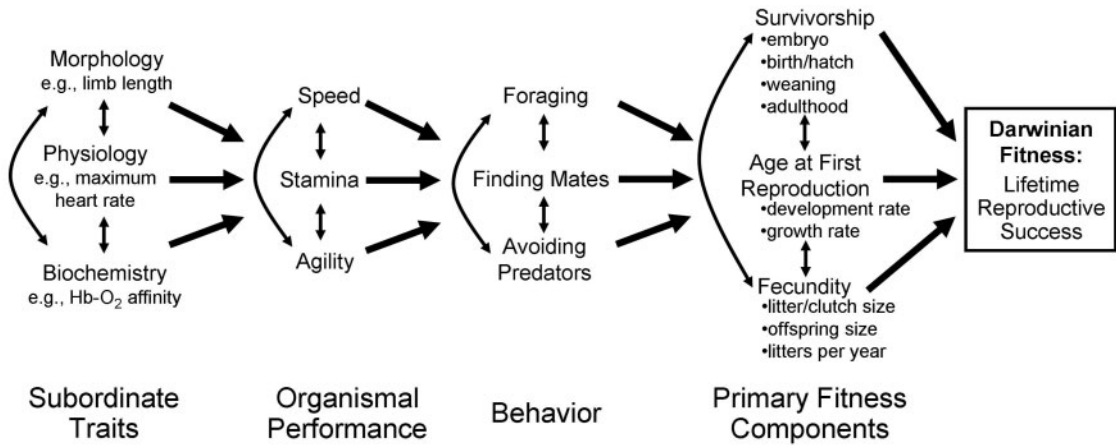
**Synopsis** Arnold’s 1983 path-analytic paradigm, considering “morphology, performance, and fitness,” has been elaborated in several ways. For example, current versions recognize the level of “behavior” (including aspects of motivation) as a filter between performance abilities (only measurable if motivation 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

An emphasis on the importance of whole-organism performance (e.g., Huey and Stevenson 1979; Bennett 1980) 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 and Losos 1994; Garland 1994a; 1994b; Garland and Carter 1994; Garland and Kelly 2006). (Behavior can also be considered as a factor affecting performance via brain



**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.

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 1983](#); [Careau and Garland 2012](#)), use of the paradigm to elucidate trade-offs (e.g., [Ghalambor et al. 2004](#); [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 is 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., [Garland and Losos 1994](#); [Wainwright 1994](#); [Aerts et al. 2000](#); [Sinervo and Calsbeek 2003](#); [Irschick et al. 2005](#); [Oufiero and Garland 2007](#); [Goodman 2007](#); [Scales et al. 2009](#); [Careau and Garland 2012](#); [Enriquez-Urzelai et al. 2015](#); [Gomes et al. 2016](#); [Santana and Miller 2016](#)) 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 (e.g., see [Bennett and Huey 1990](#); [Careau and Garland 2012](#)), 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](#); [DeFrain 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 and Diamond 1992](#); [1994](#); [Hammond et al. 1996](#); [Hammond and Kristan 2000](#); [Speakman et al. 2001](#); [Król and Speakman 2003](#); [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 C. Y. Kuo and D. J. Irschick](#), manuscript in preparation). 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 Husak and Lailvaux 2014; 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). However, motivation and behavior may ameliorate performance costs for example; female collared lizards do not maximally perform when gravid in response to a human predator but instead change their behavior to compensate for reproduction (Husak 2006). (Whether this observation would hold if the lizards were observed when approached by natural predators is unknown and an important area for future study). 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 might experience selection for greater endurance to escape predators while pregnant, which could lead to the evolution of such traits as oxygen binding affinity of hemoglobin or lung capacity. Unless the loci that responded to selection were on the sex chromosomes, both daughters and sons would inherit the “high-endurance” genes, thus leading to the evolution of higher endurance capacity in both sexes. The potential nuances of how sex-specific selection via natural or sexual selection (for example see Husak and Lailvaux 2014 for an in-depth discussion of inter and intralocus conflict and compensation), interact to result in unique solutions that may enable or limit performance remains an area of enormous theoretical and empirical interest (e.g., see Garland et al. 2011).

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 ecomorphology paradigm (see; Lailvaux and Irschick 2006; Oufiero and Garland 2007; Husak and Fox 2008; Lailvaux et al. 2010; Lailvaux and Husak 2014).

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

- (1) How might reproduction itself impact performance (dynamic and/or regulatory ecologically relevant activities, such as maximal running speed or thermoregulatory tolerances (see discussion below) and hence fit into the ecomorphological paradigm?
- (2) What reproductive traits might be considered as performance traits and what is the utility in doing so?
- (3) What kinds of experiments might expand the current ecomorphological paradigm by illuminating novel causal links among diverse traits from the perspective of a broadened paradigm?

## Review

### What the paradigm is (at present)

Consistently updated subsequent to its initial presentation, the ecomorphological paradigm (Arnold 1983; Lailvaux and Husak 2014; Storz et al. 2015) has proven extremely useful for the investigation of

**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
<b>Invertebrates</b>	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
<b>Fishes</b>	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 $\Delta$ 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
<b>Amphibian</b>	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
<b>Squamates</b>	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 ( <i>Draco</i> )	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, No $\Delta$ in sprint swimming speed	Decrease in swimming speed was associated with litter mass.	Aubret et al. 2005
	Seim-aquatic snake ( <i>Seminatrix pygaea</i> )	↓ crawling speed, ↓ swimming speed	↓ related to reproductive investment in some habitats.	Winne and Hopkins 2006
	Water snakes	↓ growth, survival		Brown and Weatherhead 1997

<b>Birds</b>	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
<b>Mammals</b>	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 $\Delta$ in metabolic cost of locomotion (walking)	Study done on obese women, may not extend to other body conditions.	Byrne et al. 2011

**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
<b>Invertebrates</b>			
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
Guppies	↓ Fast-start swimming	males	Ghalambor et al. 2004
Dwarf seahorses	↑ specific metabolic rate when gravid (10-52%)		Masonjones 2001
Mosquitofish	↓ $U_{crit}$ (likely due to aerobic changes), No $\Delta$ 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
<b>Amphibian</b>			
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
<b>Squamates</b>			
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		Webb 2004
Skinks (various)	↓ speed		Shine 1980
Broadhead skink	↓ speed, 25% slower ↓ endurance, 50% slower		Cooper et al. 1990
Flying lizards ( <i>Draco</i> )	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 associated with litter mass.	Aubret et al. 2005
Seim-aquatic snake ( <i>Seminatrix pygaea</i> )	No $\Delta$ in sprint swimming speed ↓ crawling speed, ↓ swimming speed	↓ related to reproductive investment in some habitats.	Winne and Hopkins 2006
Water snakes	↓ growth, survival		Brown and Weatherhead 1997



<b>Birds</b>	Starlings	↓ speed and angle of ascent	Lee et al. 1996
	Blue tits	↓ speed, 20%	Kullberg et al. 2002
<b>Mammals</b>	Zebra finches	↓ take off speed	Yeasey et al. 2001
	Bottlenosed dolphins	↓ maximum swim speed, 62-44% decrease	Noren et al. 2011
	Humans	↑ running "performance"	Penttinen and Erkkola 1997
	Humans	No $\Delta$ in metabolic cost of locomotion (walking)	Byrne et al. 2011

Independent of body mass.

May not be maximally motivated. Swimming after a reward/toy.

Exact "performance" unclear, highly trained athletes may not extend to females in other conditions

Study done on obese women, may not extend to other body conditions.

traits in a framework that facilitates their consideration relative to other levels of biological organization (Fig. 1 reproduced from Storz et al. 2015). Most versions of the paradigm start with "subordinate traits" those traits on the left of Fig. 1 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, (Fig. 1) the oxygen affinity of hemoglobin might interact with maximal heart rate and various aspects of muscle function to dictate stamina.

The initial considerations of "performance," in the sense used here, emphasized traits at the whole-organism level (Huey and Stevenson 1979; Bennett 1980). Subsequently, performance was defined as a "score in some ecologically relevant activity" that must be "phylogenetically interesting" (Arnold 1983). Performance is also "the ability of an individual to conduct a task when maximally motivated" (Careau and Garland 2012). Furthermore, performance can be placed into one of two categories: dynamic (movement of the whole body, e.g., sprint speed, bite force) or regulatory (e.g., thermoregulatory tolerance, growth, gamete production) (Husak et al. 2009). However categorized, performance traits are expected to be under relatively direct selection, as compared with lower-level traits (e.g., limb length or hormone levels) (Bennett and Huey 1990; Lailvaux and Irschick 2006). Indeed, a good deal has been written on what might be considered a performance trait, and three key issues are prevalent in the literature: measurement at the whole-organism level, achieving maximal motivation during measurements, and ecological relevance (i.e., "ecological performance": Irschick and Garland 2001; Irschick 2003). Other important considerations are repeatability of measurements (i.e., some consistency of individual differences across time) and heritability (Bennett and Huey 1990). We accept all of those elements as essential and do not attempt to re-define performance. Rather, we suggest it may be valuable to consider additional, currently neglected traits that might fit with these pre-existing definitions.

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 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, the field of sexual selection has functioned largely in isolation of this paradigm (but see; Irschick and Garland 2001; Lailvaux and Irschick 2006; Oufiero and Garland 2007; Husak and Fox 2008; Byers et al. 2010; Lailvaux et al. 2010; Husak and Lailvaux 2014; Lailvaux and Husak 2014), likely due to lack of research overlap. However, we argue that the ecomorphological paradigm may provide a beneficial framework 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 (Feder 1987, 2000; Bennett and Huey 1990; 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).

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 "chooser" sex (*sensu* Fisher 1930)]. Both processes involve selection related to differences in number of mates, which typically results in increased number of offspring (Darwin 1859, 1871; Bateman 1948; Andersson 1994; Kvarnemo and 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) (Zuk et al. 1992; Andersson 1994) 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 (Oufiero and Garland 2007; Husak and Swallow 2011; Mowles and Jepson 2015; Sewall 2015 and others). Some such studies have found a negative impact of sexually selected traits on performance (ex. fiddler crabs; Allen and Levinton 2007; side-blotched lizards; Brandt 2003; and cockroaches; Mowles and Jepson 2015). 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



**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

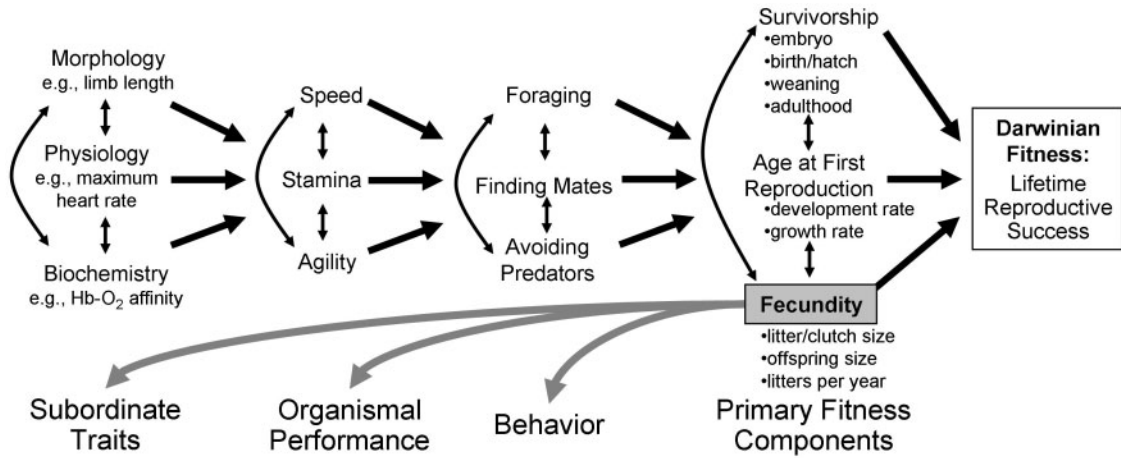
Ecomorphology paradigm Category	1' sexually selected characteristics	2' sexually selected characteristics	Other fundamental aspects of reproduction
Subordinate traits			
Physiology	Endocrinology, Spermatogenesis, Oogenesis		Gamete osmoregulation
Biochemical	Composition of the ejaculate (proteins, pH), 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		

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 (Thornhill 1983; Eberhard 1996). 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 genitalia of male bed-bugs and female traits like the correspondingly thicker body tissues of female bed-bugs (Andersson 1994; Arnqvist and Rowe 2013; Eberhard 1996; Siva-Jothy 2006; Husak and Lailvaux 2014).

Post-copulatory sexual selection in particular, primary sexual traits (e.g., genitalia, gonads, gametes) remain characteristics that have not been examined in the context of the paradigm (but see Husak and Lailvaux 2014 for a discussion of these traits in the context of sexual conflict and compensation). 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 (Storz et al. 2015; Lailvaux and Husak 2014) 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. 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.



**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 offspring 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. Gravity 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).

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

### How might reproduction impact current models?

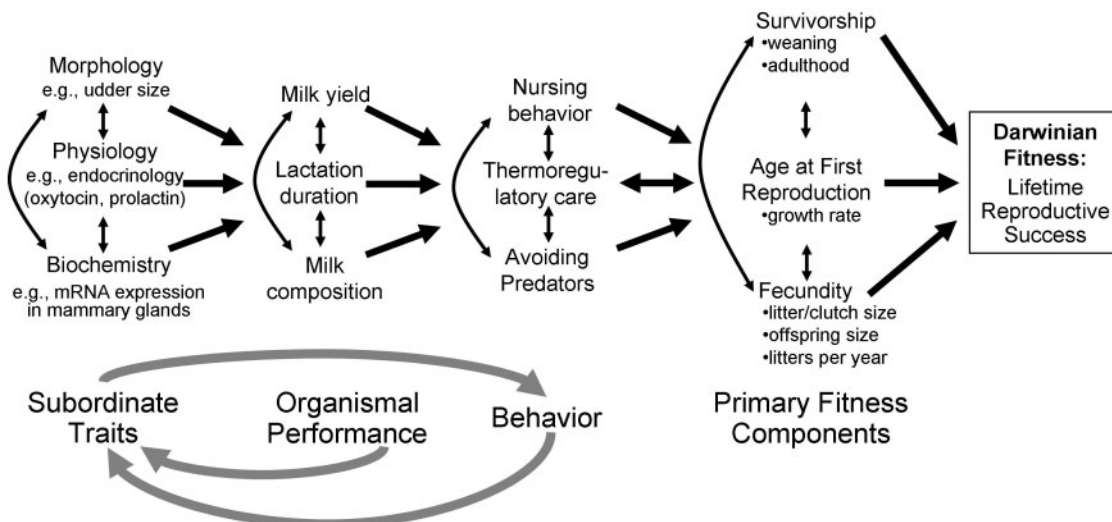
Although it is not common practice, reproductive traits can be added to current versions of the ecomorphological paradigm. In many cases these reproductive traits would be depicted as arrows going back from fecundity to performance (whereby such traits are usually assumed to negatively impact performance) (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 hemodynamic 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 costs of locomotion of obese women across pregnancy, both during resting and walking, did not change with pregnancy (Byrne et al. 2011). Hormones secreted by the placenta have profound direct and indirect



**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 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 Figs. 1 and 2, arrows indicate relationships as either: causal (single-headed) or correlative (double-headed). We illustrate the complex and dynamic causal relationship of subordinate traits (hormones such as prolactin and oxytocin) on behavior ([Husak et al. 2009](#)). 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 offspring and their own subsequent lactation performance ([Hinde et al. 2015](#); [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](#)).

effects on maternal physiology, including but not limited to, increased blood pressure, insulin resistance and glucose intolerance ([Petry et al. 2007](#)). Such hormones are notably serving a role of regulating reproduction and maintaining homeostasis of the developing embryo (regulatory performance), but may also impact the mother (dynamic performance) ([Husak et al. 2009](#)). 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.

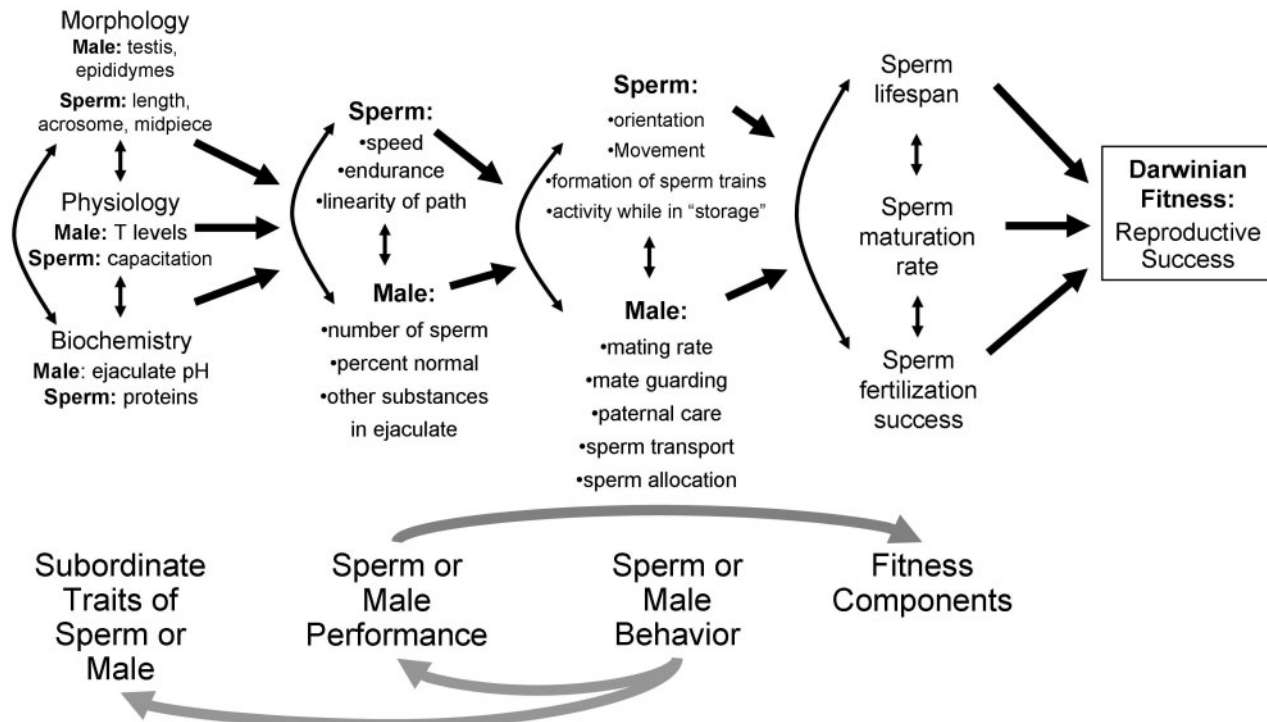
However, reproductive traits themselves can be considered as performance traits. They are clearly “phylogenetically interesting” ([Arnold 1983](#)) and

“ecologically relevant” ([Irschick and Garland 2001](#); [Irschick 2003](#)), and behaviors such as finding mates, fighting with rivals or defending offspring from predators may often involve maximal motivation ([Careau and Garland 2012](#)). Finally, these traits are likely to be direct targets of selection. 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](#)) and ecology ([Boness and Bowen 1996](#)) and are clearly targets of natural selection ([Ofstedahl 1984](#); [Skibieli 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](#)).



**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).

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" ([Husv eth 2011](#)). Furthermore, much is known about the genetics and subordinate traits underlying lactation performance, including the influences of key hormones such as oxytocin, cortisol and prolactin. Hormones are well-studied aspects of reproduction but they have largely been treated as a "black-box" with complex causal relationships to performance ([Husak et al. 2009](#)). By considering reproductive performance per se, some strides may be made towards disentangling these relationships by asking if these dynamic traits are linked and if there is antagonism between different types of performance traits. 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 ([Lucy et al. 1993; Hinde et al. 2009, 2015; Hayes et al. 2010](#)).

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 ([Kr ol 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](#)). Within this system, it has been well-documented how subordinate traits determine lactation performance ([Akers 2000](#)). Indeed, despite being the product of human intervention, data on dairy cattle provide an excellent illustration of the ecomorphological paradigm, even if the literature has not been couched in those terms.



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) (Lucy et al. 1993; Hinde et al. 2009, 2015; Hayes et al. 2010). 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 (Reinhardt 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. Sexual selection theory provides a plethora of examples where sperm performance is the target of selection (Gage and Morrow 2003; Fitzpatrick and Lüpold 2014).

### Sperm performance

We are not alone in questioning traditional consideration of gametes as “whole-organism” as evidenced by the recent exciting paper that considers aspects of “sperm ecology” (Reinhardt 2015). Specifically, by considering sperm as whole-organisms the “environments” that sperm have evolved to inhabit, including the epididymis and female reproductive tract, can be considered using ecological measurements. 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 Darwinian 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). Variability of sperm morphology and performance has been found to be both heritable (Simmons and Kotiaho 2002; Birkhead et al. 2005) and under selection (Morrow and Gage 2001; Gage and Morrow 2003) in a variety of taxa. Testis size (a subordinate trait) as well as associated number of sperm produced (a performance trait as suggested above) is heritable in Herford bulls (Neely et al. 1982).

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 framework. Regardless of what type of gamete is investigated in future studies, it is especially important to understand heritable variation that underpins performance of gametes. Thereby, future work might investigate traits subject to sexual conflict and compensation (see Husak and Lailvaux 2014) using the framework of the ecomorphological paradigm as presented here (ex. Fig. 4) to carefully conceptualize these functional traits.

### What studies might follow the 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). Ideally, future work would be expanded to observe animals during real predation events, which is difficult to do but has been accomplished in some cases, such as with cheetah (Wilson et al. 2013) and rattlesnakes (Higham et al. 2017). Whether in the lab or wild, the nature of reproduction is highly transitive in most organisms, and thus would require measuring seasonal variation and repeatability of performance. Although it is clear that gestation can impact classic performance traits, disentangling the specifics of exactly how this occurs would require longitudinal data. This could be revealed by simultaneously documenting performance of females as they gestate and those that are non-reproductive.

## 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 and 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. We hope future work will consider new and previously neglected performance traits from the perspective of 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.

## Acknowledgments

We thank Simon Lailvaux and Jerry Husak for inspiration and organizing the symposium. We also thank Jerry Husak and an anonymous reviewer for insightful comments. Chi-Yun Kuo, Denise Dearing, Tom Eiting, and Casey Gilman offered insightful conversations.

## Funding

The symposium was supported by both NSF [grant # IOS-1637160] and Company of Biologists [grant EA1233, to Simon Lailvaux and Jerry Husak], and by SICB divisions DAB, DCB, DEC, DEDE, DEE, DNB, and DVM.

## Supplementary data

Supplementary data available at *ICB* online.

## References

- Aerts P, Van Damme R, Vanhooydonck B, Zaaf A, Herrel A. 2000. Lizard locomotion: how morphology meets ecology. *Netherlands J Zool* 50:261–77.
- Akers RM. 2000. Selection for milk production from a lactation biology viewpoint. *J Dairy Sci* 83:1151–8.
- Allen BJ, Levinton JS. 2007. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Func Ecol* 21:154–61.
- Andersson MB. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Arnold SJ. 1983. Morphology, performance and fitness. *Am Zool* 23:347–61.
- Arnqvist G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393:784–6.
- Arnqvist G, Rowe L. 2013. *Sexual conflict*. Princeton (NJ): Princeton University Press.
- Aubret F, Bonnet X, Maumelat S. 2005. Tail loss, body condition and swimming performances in tiger snakes, *Notechis ater occidentalis*. *J Exp Zool Part A: Ecol Genetics Phys* 303:894–903.



- Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–68.
- Bauwens D, Thoen C. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J Anim Ecol* 50:733–43.
- Bell AW, Burhans WS, Overton TR. 2000. Protein nutrition in late pregnancy, maternal protein reserves and lactation performance in dairy cows. *Proc Nutr Soc* 59:119–26.
- Belk MC, Tuckfield RC. 2010. Changing costs of reproduction: age-based differences in reproductive allocation and escape performance in a livebearing fish. *Oikos* 119:163–69.
- Bennett AF. 1980. The thermal dependence of lizard behaviour. *Animal Behav* 28:752–62.
- Bennett AF. 1989. Integrated studies of locomotor performance. In: Wake DB, Roth G, editors. *Complex organismal functions: integration and evolution in vertebrates*. New York (NY): John Wiley & Sons, Ltd. p. 191–202.
- Bennett AF, Huey RB. 1990. Studying the evolution of physiological performance. In: Futuyama DJ, Antonovics J, editors. *Oxford surveys in evolutionary biology*. Oxford: Oxford University Press. p. 251–84.
- Bennett AF, Huey RB. 1990. Studying the evolution of physiological performance. *Oxford Surv Evol Biol* 7:251–84.
- Birkhead TR, Pellatt EJ, Brekke P, Yeates R, Castillo-Juarez H. 2005. Genetic effects on sperm design in the zebra finch. *Nature* 434:383–7.
- Blair HT, Jenkinson CMC, Peterson SW, Kenyon PR, Van der Linden DS, Davenport LC, Mackenzie DDS, Morris ST, Firth EC. 2010. Dam and granddam feeding during pregnancy in sheep affects milk supply in offspring and reproductive performance in grand-offspring. *J Anim Sci* 88:E40–50.
- Boness DJ, Bowen WD. 1996. The evolution of maternal care in pinnipeds. *Biosci* 46:645–54.
- Brandt Y. 2003. Lizard threat display handicaps endurance. *Proc R Soc Lond B Biol Sci* 270:1061–8.
- Brodie III ED. 1989. Behavioral modification as a means of reducing the cost of reproduction. *Am Nat* 134:225–38.
- Brown, G. P. and Weatherhead P. J. 1997. Effects of reproduction on survival and growth of female northern water snakes, *Nerodia sipedon*. *Can. J. Zool* 75:424–32.
- Bung P, Spätling L, Huch R, Huch A. 1988. Performance training in pregnancy. Report of respiratory and cardiovascular physiologic changes in a pregnant high-performance athlete in comparison with a sample of normal pregnant patients. *Geburtshilfe und Frauenheilkunde* 48:500–11.
- Byers JA, Hebets EA, Podos J. 2010. Female mate choice based upon male motor performance. *Animal Behav* 79:771–8.
- Byrne NM, Groves AM, McIntyre HD, Callaway LK. BAMBINO group. 2011. Changes in resting and walking energy expenditure and walking speed during pregnancy in obese women. *Am J Clin Nutr* 94:819–30.
- Careau V, Garland T Jr. 2012. Performance, personality, and energetics: correlation, causation, and mechanism. *Phys Bioch Zool* 85:543–71.
- Chapple DG, Swain R. 2002. Effect of caudal autotomy on locomotor performance in a viviparous skink, *Niveoscincus metallicus*. *Func Ecol* 16:817–25.
- Cooper WE, Vitt LJ, Hedges R, Huey RB. 1990. Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behav Ecol Sociobiol* 27:153–57.
- Darwin C. 1859. *On the origin of the species by natural selection*. 3rd ed. London: W. Clowes and Sons.
- Darwin C. 1871. *The descent of man*. New York: Appleton and Company.
- DeFraain JM, Hippen AR, Kalscheur KF, Jardon PW. 2004. Feeding glycerol to transition dairy cows: effects on blood metabolites and lactation performance. *J Dairy Sci* 87:4195–206.
- Downes S, Bauwens D. 2002. Does reproductive state affect a lizard's behavior toward predator chemical cues? *Behav Ecol Sociobiol* 52:444–50.
- Eberhard WG. 1996. *Female control: sexual selection by cryptic female choice*. Princeton (NJ): Princeton University Press.
- Enriquez-Urzelai U, Montori A, Llorente GA, Kaliontzopoulou A. 2015. Locomotor mode and the evolution of the hindlimb in western Mediterranean anurans. *Evol Biol* 42:199–209.
- Evershed RP, Payne S, Sherratt AG, Copley MS, Coolidge J, Urem-Kotsu D, Kotsakis K, Özdoğan M, Özdoğan AE, Nieuwenhuys O, et al. 2008. Earliest date for milk use in the Near East and southeastern Europe linked to cattle herding. *Nature* 455:528–31.
- Feder ME. 1987. New directions in ecological physiology: conclusion. In: Feder ME, Bennett AF, Burggren W, Huey RB, editors. *New directions in ecological physiology*. Cambridge, UK: Cambridge University Press. p. 347–51.
- Feder ME, Bennett AF, Huey RB. 2000. Evolutionary physiology. *Ann Rev Ecol Syst* 31:315–41.
- Finkler MS, Sugalski MT, Claussen DL. 2003. Sex-related differences in metabolic rate and locomotor performance in breeding spotted salamanders (*Ambystoma maculatum*). *Copeia* 2003: pp. 887–93.
- Firman RC, Young FJ, Rowe DC, Duong HT, Gasparini C. 2015. Sexual rest and post-meiotic sperm ageing in house mice. *J Evol Biol* 28:1373–82.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford: Oxford University Press.
- Fitzpatrick JL, Lüpold S. 2014. Sexual selection and the evolution of sperm quality. *Mol Human Repro* 20:1180–9.
- Gage MJ, Morrow EH. 2003. Experimental evidence for the evolution of numerous, tiny sperm via sperm competition. *Current Biol* 13:754–7.
- Garland T Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J Zool* 207:425–39.
- Garland T Jr. 2014. Trade-offs. *Curr Biol* 24:R60–1.
- Garland T Jr, Else PL. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Am J Phys-Reg, Int Comp Phy* 252:R439–49.
- Garland T Jr, Losos JB. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright PC, Reilly SM, editors. *Ecological morphology: integrative organismal biology*. Chicago: University of Chicago Press. p. 240–302.
- Garland T Jr, Bennett AF, Daniels CB. 1990. Heritability of locomotor performance and its correlates in a natural population. *Experientia* 46:530–3.
- Garland T Jr. 1994a. Quantitative genetics of locomotor behavior and physiology in a garter snake. In: Boake

- CRB, editor. Quantitative genetic studies of behavioral evolution. Chicago (IL): University of Chicago Press. p. 251–77.
- Garland T Jr. 1994b. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Vitt LJ, Pianka ER, editors. Lizard ecology: historical and experimental perspectives. Princeton (NJ): Princeton University Press. p. 237–59.
- Garland T Jr, Carter PA. 1994. Evolutionary physiology. *Ann Rev Physiol* 56:579–621.
- Garland T Jr, Kelly SA. 2006. Phenotypic plasticity and experimental evolution. *J Exp Biol* 209:2344–61.
- Garland T Jr, Kelly SA, Malisch JL, Kolb EM, Hannon RM, Keeney BK, Van Cleave SL, Middleton KM. 2011. How to run far: multiple solutions and sex-specific responses to selective breeding for high voluntary activity levels. *Proc Royal Soc B Biol Sci* 278:574–81.
- Ghalambor CK, Reznick DN, Walker JA. 2004. Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *Am Nat* 164:38–50.
- Gomes V, Carretero MA, Kaliontzopoulou A. 2016. The relevance of morphology for habitat use and locomotion in two species of wall lizards. *Acta Oecologica* 70:87–95.
- Goodman BA. 2006. Costs of reproduction in a tropical invariant-clutch producing lizard (*Carlia rubrigularis*). *J Zool* 270:236–43.
- Goodman BA. 2007. Divergent morphologies, performance, and escape behaviour in two tropical rock-using lizards (*Reptilia: Scincidae*). *Biol J Linn Soc* 91:85–98.
- Hammond KA, Diamond J. 1992. An experimental test for a ceiling on sustained metabolic rate in lactating mice. *Physiol Zool* 65:952–77.
- Hammond KA, Diamond J. 1994. Limits to dietary nutrient intake and intestinal nutrient uptake in lactating mice. *Physiol Zool* 67:282–303.
- Hammond KA, Lloyd KC, Diamond J. 1996. Is mammary output capacity limiting to lactational performance in mice? *J Exp Biol* 199:337–49.
- Hammond KA, Kristan DM. 2000. Responses to lactation and cold exposure by deer mice (*Peromyscus maniculatus*). *Physiol Biochem Zool* 73:547–56.
- Hasheider P. 2011. The family cow handbook: a guide to keeping a milk cow. Minneapolis (MN): Voyageur Press Inc.
- Hassiotou F, Geddes D. 2013. Anatomy of the human mammary gland: current status of knowledge. *Clin Anat* 26:29–48.
- Hayes BJ, Pryce J, Chamberlain AJ, Bowman PJ, Goddard ME. 2010. Genetic architecture of complex traits and accuracy of genomic prediction: coat colour, milk-fat percentage, and type in Holstein cattle as contrasting model traits. *PLoS Genet* 6:e1001139.
- Hayssen V. 1993. Empirical and theoretical constraints on the evolution of lactation. *J Dairy Sci* 76:3213–33.
- Higham TE, Clark RW, Collins CE, Whitford MD, Freymiller GA. 2017. Rattlesnakes are extremely fast and variable when striking at kangaroo rats in nature: three-dimensional high-speed kinematics at night. *Sci Reports* 7:40412.
- Hinde K, Power ML, Oftedal OT. 2009. Rhesus macaque milk: magnitude, sources, and consequences of individual variation over lactation. *Am J Phys Anthro* 138:148–57.
- Hinde K, Skibiell AL, Foster AB, Del Rosso L, Mendoza SP, Capitano JP. 2015. Cortisol in mother's milk across lactation reflects maternal life history and predicts infant temperament. *Behav Ecol* 26:269–81.
- Hosken DJ, Stockley P. 2004. Sexual selection and genital evolution. *Trends Ecol Evol* 19:87–93.
- Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* 357–66.
- Husak JF. 2006. Do female collared lizards change field use of maximal sprint speed capacity when gravid? *Oecologia* 150:339–43.
- Husak JF, Fox SF. 2008. Sexual selection on locomotor performance. *Evol Ecol Res* 10:213–28.
- Husak JF, Lailvaux SP. 2014. An evolutionary perspective on conflict and compensation in physiological and functional traits. *Curr Zool* 60:755–67.
- Husak JF, Swallow JG. 2011. Compensatory traits and the evolution of male ornaments. *Behaviour* 148:1–29.
- Husveth F. 2011. Physiological and reproductional aspects of animal production. Veszprém, Hungary, Master's Thesis: Debrecen University, University of West Hungary, Pannon University.
- Ilcó YO, Hizli ZB, Ozkan T. 2006. Leptin concentration in breast milk and its relationship to duration of lactation and hormonal status. *Int Breastfeed J* 1:21.
- Immler S, Moore HD, Breed WG, Birkhead TR. 2007. By hook or by crook? Morphometry, competition and cooperation in rodent sperm. *PLoS One* 2:e170.
- Irschick DJ. 2003. Measuring performance in nature: implications for studies of fitness within populations. *Integr Comp Biol* 43:396–407.
- Irschick DJ, Garland T Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Ann Rev Ecol Syst* 32:367–96.
- Irschick DJ, Herrel A, Vanhooydonck B, Damme RV. 2007. A functional approach to sexual selection. *Funct Ecol* 21:621–6.
- Irschick DJ, VanHooydonck B, Herrel A, Meyers JAY. 2005. Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol J Linn Soc* 85:211–21.
- Irschick DJ, Ramos M, Buckley C, Elstrott J, Carlisle E, Lailvaux SP, Bloch N, Herrel A, Vanhooydonck B. 2006. Are morphology–performance relationships invariant across different seasons? A test with the green anole lizard (*Anolis carolinensis*). *Oikos* 114:49–59.
- John-Alder HB, Cox RM, Haenel GJ, Smith LC. 2009. Hormones, performance and fitness: natural history and endocrine experiments on a lizard (*Sceloporus undulatus*). *Integr Comp Biol* 49:393–407.
- Kaliontzopoulou A, Carretero MA, Adams DC. 2015. Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. *J Evol Biol* 28:80–94.
- Kight Sprague SL, Kruse J, Johnson KC, L. 1995. Are egg-bearing male water bugs, *Belostoma flumineum* Say (Hemiptera: Belostomatidae), impaired swimmers? *J Kansas Entomol Soc*: 68:468–70.
- Król E, Murphy M, Speakman JR. 2007. Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice. *J Exp Biol* 210:4233–43.

- Król E, Speakman JR. 2003. Limits to sustained energy intake VI. Energetics of lactation in laboratory mice at thermoneutrality. *J Exp Biol* 206:4255–66.
- Kullberg C, Houston DC, Metcalfe NB. 2002. Impaired flight ability—a cost of reproduction in female blue tits. *Behav Ecol* 13:575–79.
- Kung L, Treacher RJ, Nauman GA, Smagala AM, Endres KM, Cohen MA. 2000. The effect of treating forages with fibrolytic enzymes on its nutritive value and lactation performance of dairy cows. *J Dairy Sci* 83:115–22.
- Kvarnemo C, Simmons LW. 2013. Polyandry as a mediator of sexual selection before and after mating. *Philos Trans R Soc B* 368:p.20120042.
- Lailvaux SP, Husak JF. 2014. The life history of whole-organism performance. *Q Rev Biol* 89:285–318.
- Lailvaux SP, Irschick DJ. 2006. A functional perspective on sexual selection: insights and future prospects. *Anim Behav* 72:263–73.
- Lailvaux SP, Hall MD, Brooks RC. 2010. Performance is no proxy for genetic quality: trade-offs between locomotion, attractiveness, and life history in crickets. *Ecology* 91:1530–7.
- Lee SJ, Witter MS, Cuthill IC, Goldsmith AR. 1996. Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris*. *Proc R Soc Lond B: Biol Sci* 263:619–623.
- Loor JJ. 2010. Genomics of metabolic adaptations in the peripartal cow. *Animal* 4:1110–39.
- Lucy MC, Hauser SD, Eppard PJ, Krivi GG, Clark JH, Bauman D, Collier RJ. 1993. Variants of somatotropin in cattle: gene frequencies in major dairy breeds and associated milk production. *Dom Anim Endocrinol* 10:325–33.
- Masonjones HD. 2001. The effect of social context and reproductive status on the metabolic rates of dwarf seahorses (*Hippocampus zosterae*). *Comp Biochem Phys Part A: Mol Int Phys* 129:541–55.
- McCoy JK, Fox SF, Baird TA. 1994. Geographic variation in sexual dimorphism in the collared lizard, *Crotaphytus collaris* (Sauria: Crotaphytidae). *Southwest Nat* 39:328–35.
- Millar JS. 1975. Tactics of energy partitioning in breeding *Peromyscus*. *Can J Zool* 53:967–76.
- Miles DB, Sinervo B, Frankino WA. 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. *Evolution* 54:1386–95.
- Morrow EH, Gage MJ. 2001. Artificial selection and heritability of sperm length in *Gryllus bimaculatus*. *Heredity* 87:356–62.
- Mowles SL, Jepson NM. 2015. Physiological costs of repetitive courtship displays in cockroaches handicap locomotor performance. *PLoS One* 10:p.e0143664 published online (doi: 10.1371/journal.pone.0143664).
- Neely JD, Johnson BH, Dillard EU, Robison OW. 1982. Genetic parameters for testes size and sperm number in Hereford bulls. *J Anim Sci* 55:1033–40.
- Noren SR, Redfern JV, Edwards EF. 2011. Pregnancy is a drag: hydrodynamics, kinematics and performance in pre- and post-parturition bottlenose dolphins (*Tursiops truncatus*). *J Exp Biol* 214:4151–59.
- Oftedahl OT. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. In: Peaker M, Vernon RG, Knight CH, editors. *Physiological strategies in lactation: the proceedings of a symposium held at the Zoological Society of London*. London: Academic Press.
- Orians GH. 1969. On the evolution of mating systems in birds and mammals. *Am Nat* 103:589–603.
- Orr TJ, Brennan PL. 2015. Sperm storage: distinguishing selective processes and evaluating criteria. *Trends Ecol Evol* 30:261–72.
- Oufiero CE, Garland JT. 2007. Evaluating performance costs of sexually selected traits. *Funct Ecol* 21:676–89.
- Parker GA. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol Rev* 45:525–67.
- Parker GA. 1979. Sexual selection and sexual conflict. In: Blum MS, Blum NA, editors. *Sexual selection and reproductive competition in insects*. New York (NY): Academic Press. p.123–66.
- Pawluski JL, Walker SK, Galea LA. 2006. Reproductive experience differentially affects spatial reference and working memory performance in the mother. *Horm Behav* 49:143–9.
- Penttinen J, Erkkola R. 1997. Pregnancy in endurance athletes. *Scand J Med Sci Sports* 7:226–8.
- Petry CJ, Ong KK, Dunger DB. 2007. Does the fetal genotype affect maternal physiology during pregnancy? *Trends Mol Med* 13:414–21.
- Pires MN, Bassar RD, McBride KE, Regus JU, Garland T Jr, Reznick DN. 2011. Why do placentas evolve? An evaluation of the life-history facilitation hypothesis in the fish genus *Poeciliopsis*. *Funct Ecol* 25:757–68.
- Plaut I. 2002. Does pregnancy affect swimming performance of female Mosquitofish, *Gambusia affinis*? *Func Ecol* 16:290–295.
- Pollux BJA, Meredith RW, Springer MS, Garland T Jr, Reznick DN. 2014. The evolution of the placenta drives a shift in sexual selection in livebearing fish. *Nature* 513:233–6.
- Pruitt JN, Troupe JE. 2010. The effect of reproductive status and situation on locomotor performance and anti-predator strategies in a funnel-web spider. *J Zool* 281:39–45.
- Puri D, Dhawan J, Mishra RK. 2010. The paternal hidden agenda: epigenetic inheritance through sperm chromatin. *Epigenetics* 5:386–91.
- Reinhardt K, Dobler R, Abbott J. 2015. An ecology of sperm: sperm diversification by natural selection. *Ann Rev Ecol Evol Syst* 46:435–59.
- Reznick DN, Mateos M, Springer MS. 2002. Independent origins and rapid evolution of the placenta in the fish genus *Poeciliopsis*. *Science* 298:1018–20.
- Reznick D, Meredith R, Collette BB. 2007. Independent evolution of complex life history adaptations in two families of fishes, live-bearing halfbeaks (*Zenarchopteridae*, *Beloniformes*) and *Poeciliidae* (*Cyprinodontiformes*). *Evolution* 61:2570–83.
- Santana SE, Miller KE. 2016. Extreme postnatal scaling in bat feeding performance: a view of ecomorphology from ontogenetic and macroevolutionary perspectives. *Integr Comp Biol* 56:459–68.
- Scales J, Butler M. 2007. Are powerful females powerful enough? Acceleration in gravid green iguanas (*Iguana iguana*). *Integr Comp Biol* 47:285–94.
- Scales JA, King AA, Butler MA. 2009. Running for your life or running for your dinner: what drives fiber-type evolution in lizard locomotor muscles? *Am Nat* 173:543–53.
- Seigel RA, Huggins MM, Ford NB. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia* 73:481–85.

- Seewall KB. 2015. Androgen receptor expression could contribute to the honesty of a sexual signal and be the basis of species differences in courtship displays. *Func Ecol* 29:1111–3.
- Shaffer LR, Formanowicz DR Jr. 1996. A cost of viviparity and parental care in scorpions: reduced sprint speed and behavioural compensation. *Anim Behav* 51:1017–24.
- Shine R. 1980. “Costs” of reproduction in reptiles. *Oecologia* 26:92–100.
- Shine R, Keogh S, Doughty P, Giragosyan H. 1998. Costs of reproduction and the evolution of sexual dimorphism in a ‘flying lizard’ *Draco melanopogon* (Agamidae). *J Zool* 246:203–13.
- Shine R. 2003. Effects of pregnancy on locomotor performance: an experimental study on lizards. *Oecologia* 136:450–56.
- Simmons LW, Kotiaho JS. 2002. Evolution of ejaculates: patterns of phenotypic and genotypic variation and condition dependence in sperm competition traits. *Evolution* 56:1622–31.
- Sinervo B, Hedges R, Adolph SC. 1991. Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *J Exp Biol* 155:323–36.
- Sinervo B, Calsbeek R. 2003. Physiological epistasis, ontogenetic conflict and natural selection on physiology and life history. *Integr Comp Biol* 43:419–30.
- Singh K, Erdman RA, Swanson KM, Molenaar AJ, Maqbool NJ, Wheeler TT, Arias JA, Quinn-Walsh EC, Stelwagen K. 2010. Epigenetic regulation of milk production in dairy cows. *J Mamm Gland Biol Neoplas* 15:101–12.
- Singh K, Molenaar AJ, Swanson KM, Gudex B, Arias JA, Erdman RA, Stelwagen K. 2012. Epigenetics: a possible role in acute and transgenerational regulation of dairy cow milk production. *Animal: Int J Anim Biosci* 6:375.
- Siva-Jothy MT. 2006. Trauma, disease and collateral damage: conflict in cicimids. *Philos Trans R Soc Lond B Biol Sci* 361:269–75.
- Skibieli AL, Downing LM, Orr TJ, Hood WR. 2013. The evolution of the nutrient composition of mammalian milks. *J Anim Ecol* 82:1254–64.
- Speakman JR, Król E. 2005. Limits to sustained energy intake IX: a review of hypotheses. *J Comp Phys B* 175:375–94.
- Speakman JR, Gidney A, Bett J, Mitchell IP, Johnson MS. 2001. Limits to sustained energy intake. *J Exp Biol* 204:1957–65.
- Storz JF, Bridgham JT, Kelly SA, Garland T Jr. 2015. Genetic approaches in comparative and evolutionary physiology. *Am J Physiol-Regul Integr Comp Physiol* 309:R197–214.
- Sullivan EC, Hinde K, Mendoza SP, Capitanio JP. 2011. Cortisol concentrations in the milk of rhesus monkey mothers are associated with confident temperament in sons, but not daughters. *Dev Psychobiol* 53:96–104.
- Thornhill R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am Nat* 122:765–88.
- Van Damme R, Bauwens D, Verheyen RF. 1989. Effect of relative clutch mass on sprint speed in the lizard *Lacerta vivipara*. *J Herpetol* 23:459–61.
- Vanhooydonck B, Herrel AY, Van Damme R, Irschick DJ. 2005a. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Funct Ecol* 19:38–42.
- Vanhooydonck B, Herrel AY, Van Damme R, Meyers JJ, Irschick DJ. 2005b. The relationship between dewlap size and performance changes with age and sex in a green anole (*Anolis carolinensis*) lizard population. *Behav Ecol Sociobiol* 59:157–65.
- Veasey JS, Houston DC, Metcalfe NB. 2001. A hidden cost of reproduction: the trade-off between clutch size and escape take-off speed in female zebra finches. *J Anim Ecol* 70:20–4.
- Wainwright PC. 1994. Functional morphology as a tool in ecological research. In: Wainwright PC, Reilly SM, editors. *Ecological morphology: integrative organismal biology*. Chicago (IL): University of Chicago Press. p. 42–59.
- Walker JA. 2007. A general model of functional constraints on phenotypic evolution. *Am Nat* 170: 681–89.
- Webb JK. 2004. Pregnancy decreases swimming performance of female northern death adders (*Acanthophis praelongus*). *Copeia* 2004:357–63.
- Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW. 2013. Locomotion dynamics of hunting in wild cheetahs. *Nature* 498:185–9.
- Winne CT, Hopkins WA. 2006. Influence of sex and reproductive condition on terrestrial and aquatic locomotor performance in the semi-aquatic snake *Seminatrix pygaea*. *Func Ecol* 20:1054–61.
- Zani PA, Neuhaus RA, Jones TD, Milgrom JE. 2008. Effects of reproductive burden on endurance performance in side-blotched lizards (*Uta stansburiana*). *J Herpetol* 42:76–81.
- Zuk M, Ligon JD, Thornhill R. 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. *Anim Behav* 44:999–1006.