Fall 12-20-2017

Conflict, constraint, and the evolution of the multivariate performance phenotype

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Recommended Citation

Cespedes, Ann M. PhD, "Conflict, constraint, and the evolution of the multivariate performance phenotype" (2017). *University of New Orleans Theses and Dissertations*. 2401.
https://scholarworks.uno.edu/td/2401

Conflict, constraint, and the evolution of the multivariate performance phenotype

A Dissertation

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy
in
Conservation Biology

by

Ann M. Cespedes

B.S. Biology University of New Orleans, 2008

December, 2017

Dedicated to to my mother, Liz Reeser, for supporting me, teaching me, and always being right, and to all the friends and family who were with me these past seven years.

In loving memory of Ernesto Raul Cespedes Sr., Earl Maddox, Lynn Reeves, Dorothy Wood, and Alex DeMuth

Acknowledgements

I would like to thank all of those who have helped make this dissertation possible. First, I would like to acknowledge my advisor, Dr. Simon Lailvaux, for contributing so much to the development of this project and its execution. His mentorship, guidance, good advice, and belief in me helped me through so many difficult times in my graduate career. I will forever be grateful for giving me this opportunity and for supporting both my creativity and my development as a good biologist. Secondly, I must thank the members of my committee, Dr. Charles Bell, Dr. Nicola Anthony, Dr. Jerome Howard, and Dr. Jerry Husak, who have each given me invaluable advice and support during my career. Finally, my friends Dr. Jessica Edwards, Dr. Laura Alexander, Dr. Alex Figueroa for being so helpful along the way.

I must of course thank my parents and step-parents, Liz and Charles Reeser and Ernie and Laura Cespedes, for their love and support. Also, my sisters, Andree and Amy, and their wonderful, and amazing families for being wonderful and amazing, and for motivating me at crucial times over the years. I would also like to thank Nick Pope, who has been there for me through so much, for being so supportive, caring, and loving.

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Abstract

Performance is key to survival. From day-to-day foraging events, to reproductive activities, to life-or-death crises, how well an organism performs these tasks can determine success or failure. Selection, therefore, both natural and sexual, act upon performance, and performance demands on individuals shape a population's morphological and physiological trait distributions. While studies of morphological adaptations to ecological pressures implicitly center on the idea that responses to selection improve performance via changes in morphology, the relationships between morphology, performance, and fitness are not always well understood. In this dissertation, I investigate these relationships explicitly, as well as determine the effects that different ecological and genetic contexts have on selection and how populations respond to performance pressures.

Using a model of lizard locomotor performance, I address three issues that may impact selection on performance that are often overlooked in performance studies. First, performance is not a static trait. Rather, individuals possess a range of performance abilities or intensities that can be expressed as needed. Using a novel, individual-based, quantitative genetic simulation model, I demonstrate the effects of variable performance expression and genetic constraints on how a population experiences and responds to selection on sprint and endurance performance. Second, sex differences in performance are expected in sexually dimorphic species, but empirical evidence for this is lacking. To this end, I measured and analyzed multivariate morphology and performance in *Anolis carolinensis* to identify sex-specific patterns in functional morphology and functional trade-offs within a broad suite of performance traits. Third, intralocus sexual conflict should constrain the evolution of the multivariate performance phenotype in both sexes. By extending the simulation model to include correlated trait inheritance between sexes and sex-specific selection on certain performance traits, I demonstrate the extent to which this sexual conflict constrains performance evolution. In combining studies of natural populations with simulation studies of selection, this dissertation embraces the complexity of performance to address the multiple contributing factors and constraints on performance evolution, and demonstrates the importance of accounting for such complexity when studying animal performance.

Keywords: Whole-organism performance; simulation study; functional morphology; sexual conflict; performance evolution; Anolis carolinensis

Introduction

Whole organism performance, defined as how well an organism performs a dynamic, ecologically relevant task (Bennet and Huey, 1990; Lailvaux & Irschick, 2006), is a primary target of selection and therefore fundamental to our understanding of adaptation (Arnold, 1983; Garland & Losos, 1994; Irschick & Garland, 2001). Performance traits represent the integrated output of a complex, multivariate functional system, and evolve only when there is heritable variation on the underlying morphological traits (Arnold, 1983; Garland, Bennett & Daniels, et al., 1990; Garland & Losos, 1994; Garland & Carter, 1994, Geffeney et al., 2002). Given the complex pathways connecting ecological and life history variables to whole organism performance, understanding and reconstructing the evolution of performance requires an explicitly integrative approach (for example, Brodie & Ridenhour, 2003). Locomotor performance, in particular, is thought to be under generally strong selection given its importance in the day to day life of so many organisms.

With over forty years of investigations into reptile locomotor performance traits and their role in ecomorphology and specialization from functional, ecological and morphological perspectives (Garland & Losos, 1994), reptiles and, in particular, lizards are model organisms for investigating how and when selection on performance traits drives phenotypic evolution and adaptation. The relationship between locomotor performance and habitat use is well established for many lizard groups, making them a model organism for studies of ecomorphology and adaptive radiation (Garland & Losos, 1994; Aerts et al., 2000; Irschick & Garland, 2001). Locomotor performance is important for a host of fitness-related activities, including predator escape, prey capture, and resource and mate acquisition (e.g., Vanhooydonck & Van Damme, 2003; Husak, 2006a), and is a function of both physiological and biomechanical properties (morphology – performance) and the environment (thermal properties, substrate, fluid surroundings). Lizard body plans are therefore adapted to particular environments, and this adaptation has given rise to the variety of functional forms seen today. Understanding the evolutionary ecology of locomotor performance traits in lizards and the role these traits and their constitutive morphological components play in day-to-day life is crucial to investigations of adaptive evolution.

Constraints and trade-offs characterize functional design in both biology and engineering. Functional constraints stem from optimization problems in design. In locomotion, for example, a design that optimizes speed may be at a disadvantage in terms of manoeuvrability due to the conflicting demands on the same functional apparatus. Due to such trade-offs, specialization of locomotion to a particular environment may often be correlated with decreased performance in other environments and would come at an evolutionary cost in the long run if the environment changes. Yet organisms depend on many performance traits for survival, and existing phenotypes thus represent compromises between many competing trade-offs (Alexander, 2003). However, it is the underlying genetic architecture of the organism that determines whether such compromises are possible. Indeed, genetic constraints on phenotypic evolution can be absolute in that the underlying properties of the genetic architecture may make it impossible for a given phenotype to exist, or they can impose biases on the course of evolution (Arnold, 1992). The information regarding correlations between traits (due to pleiotropy, for example) is summarized in the G-matrix, and from this information one can predict the response of a suite of traits in response to selection on one trait (Lande, 1979; Lande & Arnold, 1983; Arnold, Pfrender & Jones, 2001). This dissertation aims to arrive at a better understanding of how selection acts on suites of performance traits, leading to phenotypic shifts in populations in the context of these functional and genetic constraints. In particular, I aim to investigate performance evolution with regard to constraints imposed by two specific scenarios –intralocus sexual conflict and preferred versus maximal performance.

Sexual conflict and performance

Sexual conflict adds to the complexity of selection on performance because males and females frequently experience divergent selective pressures on, and occupy different selective optima for, a given trait or traits, yet also share a genome. Thus, the evolution of any resolution to such conflict requires mechanisms that arise from and act on this shared genome. Intralocus sexual conflict (IASC) refers to the displacement of sexes from their respective phenotypic optimum due to selection on specific traits in one sex that are negatively correlated with performance traits on which the other sex relies. This is distinct from interlocus sexual conflict (IRSC), which is the antagonistic coevolution between loci in which one sex's reproductive success is enhanced at the other's expense (Bonduriansky & Chenoweth, 2009). A number of mechanisms are seen in nature as partial or complete resolutions to sexual conflict, and this project focuses particularly on the evolution of sexual size and shape dimorphism wherein the sexes can evolve along separate trajectories and achieve separate optima (Lande, 1980). Similarly of interest is the emergence of behavioural and physiological dimorphisms, which can act as compensatory mechanisms, mitigating some of effects arising from sexual conflict (e.g. Husak et al., 2011).

Although sexual dimorphism in reptiles is easily observed and has been well documented (e.g. Berry and Shine, 1980; Butler and Losos, 2002; Shine, 2003; Cox et al., 2007; Husak and Fox, 2008), demonstrating sexual differences in performance is less common and has only recently gained attention (reviewed in Lailvaux 2007; but see Lailvaux et al., 2003; Kaliontzopoulou, Bandeira & Carretero, 2013). Investigating sexual dimorphism in locomotor performance is important for a clear understanding of adaptive evolution, as ignoring the interactions between separate selective pressures on each sex necessarily produces misleading or incorrect inference of evolutionary processes (Husak and Lailvaux 2014). By better understanding the proximate and ultimate causes of sexual dimorphism, and the consequences of SD on multivariate performance response surfaces, we can better understand adaptive evolution in general.

Preferred and maximal performance

The connection between locomotor performance and fitness is paramount to understanding the evolution of morphological variation and adaptation within and among species, but how useful are maximal laboratory measures of performance for understanding the realized effects of morphology and performance trade-offs in nature? Furthermore, how do we interpret lab performance measures in an ecological and evolutionary context? It is well understood that animals do not necessarily always operate at maximal performance in nature, creating a mismatch between nature and laboratory measures (Irschick, 2003; Irschick et al., 2005). Energy efficiency probably plays a large role in limiting individual effort in everyday tasks in conjunction with innumerable costs incurred during daily life, and thus performance is subject to compromises beyond those at the morphological level. For example, survival in adult Collared Lizards showed a significant positive relationship with the speed used while escaping a predator, but not maximum sprint speed (Husak, 2006b). Aside from individual variation in performance traits, the environment itself affects expressed performance traits. Temperature determines much of an ectotherm's ability to function and perform tasks (e.g. Huey, 1974, 1982; Huey & Stevenson, 1979; Bennett, 1980; Marsh & Bennett, 1986; Lailvaux, 2007; Lailvaux & Irschick, 2007) and properties of the substrate, such as slope, perch diameter, friction, and compressibility or compliance all have measurable effects on lizard performance (Huey & Hertz, 1982; reviewed in Garland &Losos, 1994; Losos & Irschick, 1996; Losos & Sinervo, 1989; Sinervo & Losos,1991; Losos et al., 1993). Thus operating at suboptimal temperatures or on suboptimal substrates incurs costs, either in the form of performance costs or other costs of mitigating the effects behaviourally.

Because this framework of costs and energy efficiency probably drives the choice of optimal speeds that animals select in nature (Wilson et al. 2015), any useful model of preferred/optimal speed should incorporate those costs when attempting to explain why animals perform at the levels that they do. Furthermore, ecological processes involve many highly complex causal paths between a great many variables, and this complexity may have unpredictable consequences for how we determine and interpret phenotypic responses to selection on whole organism performance. One approach to dealing with these challenges is the use of simulation models, which allow us to incorporate complexity, examine responses over a wide range of conditions and ultimately check some of our assumptions (Judson 1994; Peck 2004). By manipulating selection pressures and measuring the response to that selection under specific evolutionary scenarios, we are able to generate artificial evolutionary lineages that we can follow over the course of multiple generations, and that we can use to directly test the effect of specific factors (such as the extent of maximum performance capacities used during routine ecological tasks) on evolutionary trajectories under known conditions (e.g., heritability parameters, sex ratios, starting morphological trait distributions and environmental parameters).

Aims and hypotheses

With many various and interrelated pathways and variable selective contexts, our understanding of deterministic processes regarding the effects of selection on performance starts to break down. What are our null hypotheses regarding adaptation and evolution when so many parameters are identified and interrelated? Are our attempts to simplify these processes realistic? We know that behaviour, performance trade-offs, compensatory mechanisms, sex-specific selection, and a host of life history factors complicate the relationships between morphology, performance and fitness (Lailvaux & Husak, 2014; Husak & Lailvaux 2014). We also know there is a stochastic component to differential fitness in that the ecological and environmental context ultimately affects whether or not a given phenotype survives to reproduce (and that its offspring survive to reproduce, and so on). Therefore, it is imperative that we incorporate this complexity into our understanding and interpretation of ecological data and ecomorphological questions. In complex systems, emergent properties arise that cannot be predicted from only data on the individual parts. Thus, this dissertation aims to build on the prevailing reductionist paradigm in functional morphology and describe such emergent properties, detangle their effects on our perception of adaptive evolution of locomotor performance and determine when and how the whole may be greater than the sum of all parts.

With this in mind, this dissertation tests three specific hypotheses:

1) Organisms that operate at some submaximal, preferred level of performance in nature enjoy a fitness advantage over those that employ the full extent of their maximum performance capacities in nature at all times. Testing this hypothesis involves building a quantitative genetic simulation model harboring individual agents that survive and reproduce under pre-defined selective regimes and subject to constraints regarding the use of their maximum performance capacities.
2) Males and females may be sexually dimorphic for both morphology and performance, and that dimorphism could drive sex-specific patterns of trade-offs among whole-organism performance traits. Trade-offs among suites of performance traits are seldom measured in non-human animals, and the sex-specific nature of those trade-offs have been almost

entirely ignored. Empirical data pertaining to such trade-offs are required to understand how morphology-performance relationships might differ between males and females.

3) The evolution of sex differences in the multivariate performance phenotype is constrained by both the genetic architecture among component performance traits, and the functional trade-offs among types of performance that rely on conflicting functional mechanisms for optimal expression. By extending the above quantitative genetic model to a multivariate scenario and imposing sex-specific selection on one aspect of the multivariate phenotype, we can test the extent to which intralocus sexual conflict impedes the evolution of sex differences in performance traits that are not necessarily always maximally expressed.

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Chapter 1

An individual-based simulation approach to the evolution of locomotor performance

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Integrative and Comparative Biology. (2015)

Received: June 5, 2015 Initial acceptance: June 26, 2015 Final acceptance: July 1, 2015

Abstract

Maximal whole-organism performance traits measured in the laboratory and the levels of performance expressed in the field often exhibit a mismatch, complicating our understanding of the selection pressures influencing the evolution of performance traits. To better understand the evolution of locomotor performance, we built an individual-based simulation to test hypotheses about selection on locomotor performance. Starting with a population of individuals with two correlated but variable performance traits, we simulated these individuals surviving and reproducing in a complex environment, presenting each individual with successive ecological challenges requiring specific performance capabilities over their lifespan. While most challenges require sub-maximal speeds, intermittent bouts requiring increased performance, such as escape from predators, introduce strong, but infrequent, selection for maximal performance. By comparing the results of simulations run with individuals that only perform at their maximum levels versus those that adjust this effort, we show that intra-individual variation in speed confers a selective advantage, regardless of the extent of that variation. We also show that the direction and strength of the correlation between the two performance traits affects the evolutionary trajectory of phenotypic change. Ultimately, this model allows us to simulate the evolution of movement speeds over a range of selective contexts, offering insight into the factors affecting the evolutionary relationship between optimal and maxim performance.

Introduction

Whole-organism performance capacities (defined as quantitative measures of the ability of an individual to perform dynamic, ecologically relevant tasks such as jumping, running, or biting) (Bennett & Huey 1990; Irschick & Garland 2001; Lailvaux and Irschick 2006) provide a direct and intuitive link between the individual and fitness across several different selective contexts (Husak and Fox 2008; Irschick et al. 2008). In turn, locomotor performance represents the outcome of a variety of interacting selection pressures, all of which have operated over evolutionary time to shape the diversity of performance traits that we see today (Lailvaux & Husak 2014). However, the selective benefits maintaining a trait can differ from those driving its origin (Chandler et al. 2013). Understanding the evolution of locomotor performance therefore requires not only quantifying contemporary selection pressures in nature, but also testing hypotheses regarding how selection may have acted on performance in the past.

Measuring selection on performance in nature presents a number of challenges. These range from incomplete or inaccurate characterization of the long-term, dynamic selective environment (Kingsolver and Pfennig 2007; Irschick et al. 2007; Bell 2010) to limitations in our understanding of the relationships both among performance traits (Vanhooydonck et al. 2001; Van Damme et al. 2002; Wilson et al. 2014) and between performance and other key traits that are important to fitness (Ghalambor et al. 2003; Lailvaux and Husak 2014). An additional challenge is comprehending the relationships between the maximal performance capacities commonly measured in the laboratory and the extent to which animals use those capacities in the field (Irschick 2003). It is well understood that animals do not necessarily always perform at maximal capacity in nature, creating a mismatch between field and laboratory measures (Irschick et al. 2005). For example, *Crotaphytus collaris* lizards do not rely consistently on their maximal sprint capacities in nature, and will alter their sprint speed depending on whether they are foraging, escaping from a predator, or defending a territory (Husak and Fox 2006). Consequently, measures of selection on maximal performance capacity may be misleading if organisms perform at their maximum only rarely or infrequently (Irschick 2003). Alternatively, it may be that high maximal capacities are meaningful in nature, and are maintained due to their extreme importance in relatively rare situations, with disproportionate effects on survival or fitness.

Predicting the evolution of preferred movement speed depends not only on our understanding of the integrated selective context, but also of the factors enabling the response to selection within that context. Prime among these factors are 1) the additive genetic variance of the trait in question, and 2) the covariation between that trait and other traits that might be under either concordant or conflicting selective pressures (Lande and Arnold 1983; Blows 2007). Performance exists within an integrated, multivariate phenotype (Ghalambor et al. 2003), and as such the evolution of single performance traits cannot be considered in isolation from the rest of that phenotype (Ghalambor et al. 2004; Lailvaux and Husak 2014). Any estimate of preferred performance evolution should therefore consider the relationships among the performance trait of interest and other, related traits in addition to accounting for the behavioral modulation of the performance trait itself (Garland and Losos 1994). Conducting this type of integrated and comprehensive evolutionary study is by no means trivial, and empirical attempts to characterize selection on preferred performance have thus far met with limited success. In particular, our current poor understanding of the additive genetic (co)variances underlying both performance and correlated traits that are also key targets of selection (Lailvaux and Husak 2014) precludes this predicted evolutionary approach in all but a few species (e.g. Le Galliard et al. 2004; Lailvaux et al. 2010).

Individual-based simulations have proven to be useful in situations in which conducting complex, large-scale selection studies is difficult or unfeasible (e.g. Jones et al. 2003, 2004; Melo and Merroig 2015). These simulations therefore constitute a promising alternative approach to investigating the evolution of preferred performance. Here we present such an approach to modelling selection on two correlated whole-organism performance traits. We apply our approach to an idealized population of lizards occupying a small portion of a reasonably large habitat. By starting with this “virgin population” and changing the selective context via the introduction of predators that put pressure on low-sprint speed phenotypes, we consider the effects of the heritability and distribution of traits, and of inter- and intra-individual variability in performance on the evolutionary trajectories of each trait. We therefore aim to understand not only those factors currently maintaining preferred performance, but also to simulate the basic selective conditions that might have led to contemporary performance capacities. Specifically, we test the following hypotheses: 1) Varying between non-maximal (i.e. preferred) and maximal performance used acts to buffer the effect of selection on performance; 2) Maximal and optimal trait values depend on both the selective environment, and the nature of the genetic correlation underlying the two performance traits.

Materials and Methods

The model

We used NetLogo (Wilensky 1999), a Java-based, programmable modelling environment tailored to agent-based simulations to build and execute our model. NetLogo is a simple and customizable interface for running and interacting with simulations. With this platform, we built a quantitative genetic simulation model (Supplementary File S1) of performance evolution consisting of a population of lizards living, eating, reproducing, and dying in an environment according to simple, explicit rules (Figure 1). Individuals in our model have two performance traits, sprint and endurance, which are subject to selection based on user-defined “rules”. The expression of each trait is linked to the individual’s available energy budget via trait-specific cost-of-transport functions. The utility of each trait in our model is context-specific: sprint speed is used by individuals to mediate successful or unsuccessful encounters with predators, while endurance capacity dictates the size of the area an individual can search for food, and, consequently, the probability that an individual will acquire energy. We define the energetic costs of performance as a function of the expressed performance. Survival and reproduction depend on both performance capacity and energy efficiency, depending on the environmental parameter values. An overview of the simulation is presented in Figure 1.

The environment is a grid of cells that can contain either a predator or a resource, or both, or none. Predators exist in the same location for the entire simulation, and have a sprint speed assigned at the start of the simulation (i.e. in the P1 generation), drawn at random from a normal distribution with a mean of one standard deviation below the mean sprint speed for the population (Table 1). Food is redistributed before the beginning of every step of the simulation. Resources are depleted during each step of the simulation as agents consume them. The probability that a resource will be depleted after being consumed by a single agent is hardcoded as 0.5, thus introducing density effects on the agents’ abilities to acquire resources. The more lizards that are foraging, the greater the chances are that a resource becomes locally depleted. There are no constraints on movement within the environment except for the distance an agent can travel given its endurance capacity.

Trait assignment and inheritance

During the initial setup, a starting population of 500 individuals is created and assigned maximal sprint capacities drawn at random from a normal distribution with mean and standard deviation set by global simulation parameters (Table 1). Maximal endurance capacity is then determined by a regression line with a slope equal to the covariance between sprint and endurance (Table 1). For our two-trait model, we use a parent-offspring regression approach to characterize sprint speed transmission (inheritance) (Lynch and Walsh 1998). We thus assigned sprint speed a heritability (h^2) equal to the slope of the mid-parent regression line between the parental and F1 generations as well as a separate parameter governing the correlation between sprint and endurance (Table 1) (Lynch and Walsh 1998). Thus, a mating pair’s average sprint capacity determines the expected mean value of that pair’s clutch, and each individual offspring within the clutch is assigned a value drawn at random from a specified normal distribution defined by this value and a standard deviation equal to that for sprint speed. The offspring's endurance and sex are set using the same procedures as in the initial setup. Thus, sprint speed and endurance are genetically correlated in our model such that heritable changes in sprint speed effect changes in endurance determined by the value of the shared genetic covariance.

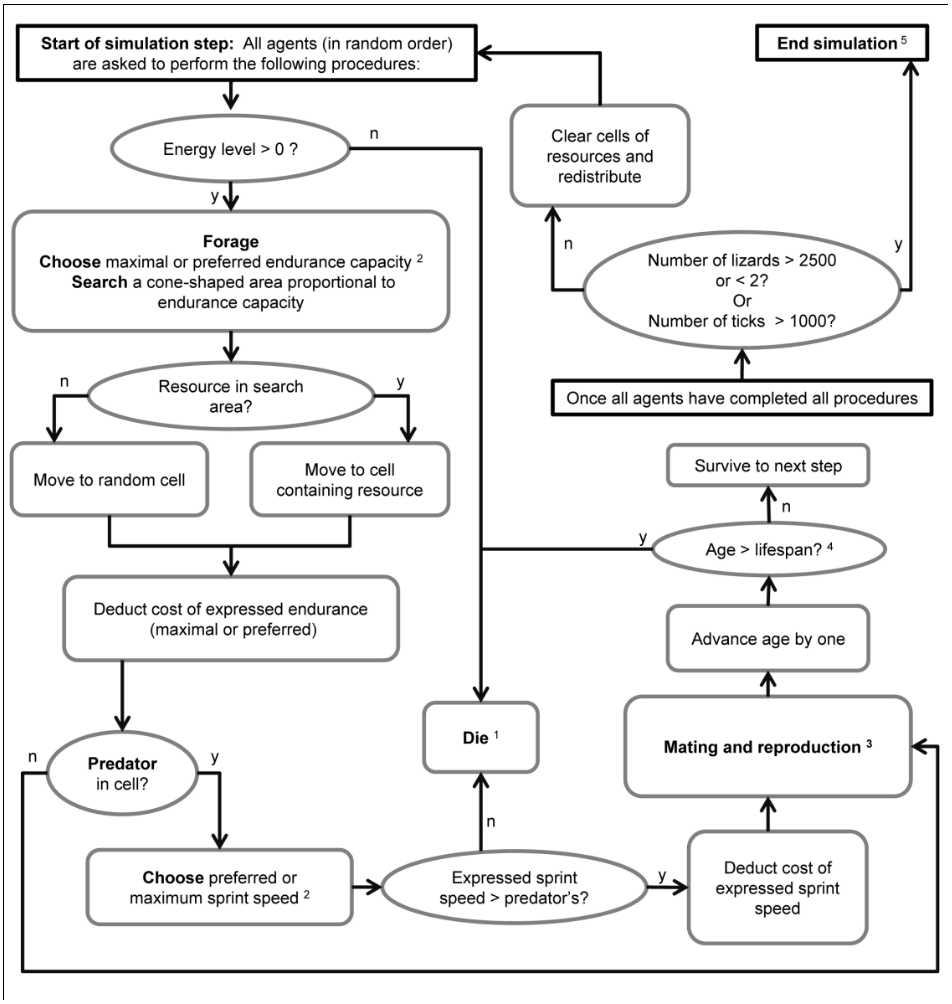

Figure 1: Simulation processes and scheduling.

[1] At death, agents record age, number of offspring, and cause of death (predator, depletion of energy, or old age).

[2] Decision determined by probability of choosing maximum capacity (Table 1).

[3] Mating occurs only every 40 steps. If the agent is female and has energy greater than an assigned threshold, she is randomly paired with a male that also has sufficient energy. The female's surplus energy determines the clutch size, and both male and female incur energy costs proportional to the clutch size (Table 1). Mates' identities are recorded as well as that of each parent-child pair, allowing for the analysis of pedigrees and determination of the number of offspring that survive to reproduce.

[4] Occurs only every 50 steps.

[5] At the end of a simulation, any remaining lizards update their records and record their cause of death as "alive," and all output is written to file.

Global Parameter	Value(s)	Description
Preferred sprint	0, 60 , 70, 80, 90, 100	Percent of maximal sprint capacity an individual can use in a simulation
Covariance (sprint, endurance)	-1, 0, 1	Slope of the line determining endurance capacity from the inherited sprint capacity
Preferred endurance	70	Percent of maximal endurance capacity an individual can use in a simulation
h^2	0.7	Heritability of sprint speed, slope of the midparent-offspring regression
Trait means	100	Population means for maximal sprint and endurance capacities
Trait variances	3.5	Population variance for sprint and endurance capacities
Size of environment	101 x 101 cells	
Maximum Lifespan	400 (steps)	
Initial lizard population density	4.91	Starting population for all simulations is composed of 500 individuals
Predator density	~ 5	
Mean predator sprint speed	98.13	Mean predator speeds are set to the prey population mean minus one standard deviation
Resource density	~ 19	
Resource quality	50	Units of energy added to an individual's energy budget when a resource is consumed
Cost of Reproduction	2	Amount of energy deducted per offspring
Threshold for 'surplus energy'	80	Minimum amount of energy an individual can have in order to reproduce during a reproductive event
Energy budget	100	Maximum energy an individual can have at one time
Initial energy	80	Amount of energy assigned to an individual at birth defined as a constant or function of parental investment
Sex ratio	0.5	Determined by probability of being assigned female
Probability of using preferred trait	0.5	Governs agent's decision to use preferred versus maximal capacity
Search Radius	$⍰⍰⍰⍰⍰h\ ⍰⍰⍰⍰⍰⍰_{⍰⍰⍰} = 20$ $⍰⍰⍰⍰⍰h\ ⍰⍰⍰⍰⍰⍰_{⍰⍰⍰} = 1$	Translates expressed endurance capacity into a distance that defines the radius of the cone-shaped foraging area. For agent *i*: $⍰⍰⍰⍰⍰h\ ⍰⍰⍰⍰⍰⍰_{⍰} = \frac{⍰⍰⍰⍰⍰⍰⍰⍰⍰_{⍰} - ⍰⍰⍰⍰⍰⍰⍰⍰⍰_{⍰⍰⍰}}{⍰⍰⍰⍰⍰⍰⍰⍰⍰_{⍰⍰⍰} - ⍰⍰⍰⍰⍰⍰⍰⍰⍰_{⍰⍰⍰}}(⍰⍰⍰⍰⍰h\ ⍰⍰⍰⍰⍰⍰_{⍰⍰⍰} - ⍰⍰⍰⍰⍰h\ ⍰⍰⍰⍰⍰⍰_{⍰⍰⍰}) + ⍰⍰⍰⍰⍰h\ ⍰⍰⍰⍰⍰⍰_{⍰⍰⍰}$
Cost of endurance	$a = 2$, $b = 0.5$, $c = 0$	$C_{endurance} = a^{(b * \text{search radius} - c)}$
Cost of sprint	Mean = 100 SD = 20	$C_{sprint} = P(X < sprint_{\text{agent}}) * \text{energy budget}$ Where X is a random variable drawn from a normal distribution with mean and SD parameters

Table 1: Parameters and settings for simulations investigating intra-individual variation in sprint speed. All combinations of preferred sprint speed and Covariance (sprint, endurance) were run multiple times (SI 2). All parameters may also be defined by functions rather than constants. Heritability determines how closely offspring resemble their parents with 1 being a perfect correlation between parent and offspring trait values, and zero denoting that each offspring's sprint capacity will always be drawn from the same distribution as the initial population. $Endurance_{min}$ and $endurance_{max}$ are the population's minimal and maximal endurance capacities and are defined as three standard deviations below and above the mean value of the trait, respectively.

Costs of Performance

We calculated the costs of sprint speed using a cumulative distribution function for a normal distribution, the shape of which corresponds to a nearly linear relationship between energetic cost and speed near the mean sprint capacity for the population, but with decreasing slope as one moves towards extremely low or high speeds, ultimately reaching a plateau (Biewener 2003). The parameters describing the shape of the distribution are scaled such that individuals employing sprint speeds near the population mean incur intermediate costs. Low sprint performers incur little to no energetic costs, but failing to outsprint a predator means certain death. As we did not wish for endurance to overly affect relative fitness, we modeled costs of endurance as an exponential function. We parameterized this curve so that costs gently increase in a roughly linear fashion (assuming a constant metabolic rate) (Taylor et al. 1982) over the range of values of endurance for the initial population. Thus, most individuals incur low to intermediate costs. However, costs for endurance capacities far beyond the range of the starting population become prohibitive, as endurance capacity is limited by physiology and aerobic capacity (Biewener 2003; Bennett 1982), which are assumed to be unchanging in our model. The functions and parameter settings for sprint and endurance are presented in Table 1.

Intra-individual variation in sprint speed: preferred versus maximal

To determine the consequences of varying sprint speed for the intensity and direction of selection on maximal sprint speed, we ran replicate simulations with all environmental variables and selection pressure parameters held constant, with only the nature of the correlation between sprint and endurance (positive, negative and no correlation) and the magnitude of the difference between preferred and maximal sprint speeds allowed to vary between runs. Resource density was set such that the average distances between cells containing resources were approximately less than or equal to the average search radius of the population. Resource quality was set sufficiently high such that individuals of intermediate phenotypes would remain in positive energy balance for an entire step of a simulation when considering the costs of locomotion. Predator density was calibrated so that all individuals would have a high probability of encountering a predator within their lifetimes, resulting in detectable selection on sprint speed. We determined these settings (Table 1) during parameter sweeps during development and debugging of the model, as well as by a parameter sweep of the current model, summarized in Supplementary file S2.

Preferred performance is measured as the percent of maximal capacity that an individual can use, and in all simulations individuals had a 0.5 probability of using a submaximal or “preferred” trait value instead of their maximum. We ran at least 15 simulations for all combinations of correlation type (i.e. -, 0, or +) and each of the following preferred speeds: 0; 60; 70; 80; 90; and 100% of maximal sprint capacity. When preferred speed is equal to 100%, individuals do not vary sprint speed and always use their maximal capacity. Endurance, for all simulations, was set to vary between maximal and 70% of maximum, again with a 0.5 probability of using either preferred or maximum, allowing for variation in foraging distance and softening the constraints on the system imposed by the costs of endurance. As resource densities were sufficiently high, lower foraging distances do not greatly affect survival. Simulations were allowed to run for 15 generations. Simulations ended prematurely if the population became extinct or exceeded 5000 individuals, as larger populations would typically cause the simulation to crash.

While Netlogo comes with broad mathematical functionality, we used the R-extension (Thiele and Grimm 2010) for performing many of the calculations during simulations and also to prepare and export the simulation output. Data recorded during a simulation is outlined in Fig. 1, and we used customized R scripts to process this data and calculate selection parameters (Supplementary file S1). For each generation of a simulated population, we were able to calculate the changes in trait means and variances over time, as well as the intensity of selection on sprint speed, i_{sprint}, which is the change in mean sprint speed after selection and before reproduction (i.e. the univariate selection differential) standardized by the trait’s variance (Lande and Arnold 1983). We also estimated the linear selection coefficient for sprint speed (β_{sprint}) for each generation within each simulation from the regression of relative fitness on sprint speed. To describe nonlinear selection affecting the variance of sprint speed phenotypes, we derived a metric similar to the intensity of selection by calculating the difference in variance during each interval between reproductive events. Finally, we have also included a method for computing the multivariate selection coefficients for the linear, nonlinear, and correlated selection coefficients for both traits, the details of which are presented in the Supplementary file S1.

We used generalized linear mixed models for continuous data with an identity link function (GLMM; lme function, R package: nlme) (Pinheiro et al. 2015) to model how the form and intensity of selection change over time during a simulation, as well as how these metrics are affected by both variation in sprint speed and by the correlation between the two locomotor traits. For each dependent variable (i_{sprint}, β_{sprint}, and the magnitude of the change in variance), we constructed models with random intercepts for individual simulation runs, and fixed effects for 1) generation, 2) the covariance between sprint and endurance (slope of the regression determining an individual's endurance capacity given their sprint capacity), and 3) preferred sprint speed. We first fit the saturated model with all predictors and all interactions using maximum likelihood and found the minimum adequate model via log-likelihood ratio deletion tests (stepAIC; R package: MASS) (Venables and Ripley 2002), and refit this model using REML.

Results

Varying individual sprint speed has clear effects on the form and intensity of selection. In the scenarios wherein individuals always use 100% of their maximum capacity, i_{sprint}, β_{sprint}a and the magnitude of the decrease in variance due to selection are initially very high relative to scenarios in which individuals vary sprint speed (Figs. 2 and 3), and within two to three generations, predator-imposed selection becomes negligible while the population expands exponentially, rapidly exceeding 5000 individuals. When individuals are allowed to employ lower-cost, preferred speeds, however, selection on sprint speed is less intense and fluctuates asymptotically over time (Fig. 2). The best-fit model explaining i_{sprint} for all simulations in this experiment (Table 2A) and for the subset of all simulations, excluding populations that never vary in sprint performance (Table 2B), included terms for generation (time), correlation structure between sprint and endurance, preferred speed, and interactions between generation and covariation and generation and preferred speed (Table 2). The coefficient for the preferred-speed term and the interaction of generation and preferred speed changes signs between the two datasets, indicating that within the non-variable groups, the effect of this interaction is reversed.

The slope of the linear relationship between maximimal sprint speed and relative fitness, β_{sprint}, behaved similarly to i_{sprint} over the course of our simulations. The best-fit GLMM for β_{sprint} included terms for generation (time), covariation between traits, preferred speed, and interactions between time and covariation, time and preferred speed, and covariation and preferred speed (Table 3A). When we excluded simulations in which individuals used only their maximum, the best model was the saturated model, with all terms and interactions (Table 3B). To compare with the previous model (Table 3A), we also fit the model without the three-way interaction, and there was a sign change for all terms involving preferred speed (Table 3C).

Differences in selection on the variance of sprint speed were also evident in our simulations (Fig. 3). As with our previous selection metrics, the non-varying populations experienced a more dramatic effect than those that varied sprint speed. The covariance between sprint and endurance did not however significantly alter the trends observed between the variable and non-variable groups, and this term was not retained in the best-fit GLMM. Only time and preferred speed had significant effects on the changes in sprint variance over time (Table 4A). However, a GLMM performed with only the variable sprint speed populations did retain terms for time and covariance, although the coefficient estimated for covariance was not large relative to its standard error. Furthermore, differences in preferred speed did not affect selection on the variance of sprint speed over time within this subset (Table 4B). As nonlinear selection acts on the variance of a trait, this metric is descriptive of how populations experience nonlinear selection in our simulation model.

Varying sprint speed not only affects the relationship between sprint capacity and relative fitness, but also has indirect effects on endurance, especially when sprint and endurance share positive genetic covariation. We found evidence of significant, negative nonlinear selection on endurance characterized 249 out of 267 simulations (Supplementary file S3), with the remaining simulations characterized by negative linear selection on endurance, reflecting the high energetic costs of endurance. When individuals operated solely at their maximum, selection on sprint capacity was either positive linear (higher sprint speeds had higher relative fitness) or negative nonlinear in conjunction with a negative coefficient for the interaction term between sprint and endurance (selection for a negative correlation between traits). However, when individuals vary sprint speed, the form of selection was highly variable, even when all other parameters were equal (Supplementary file S3).

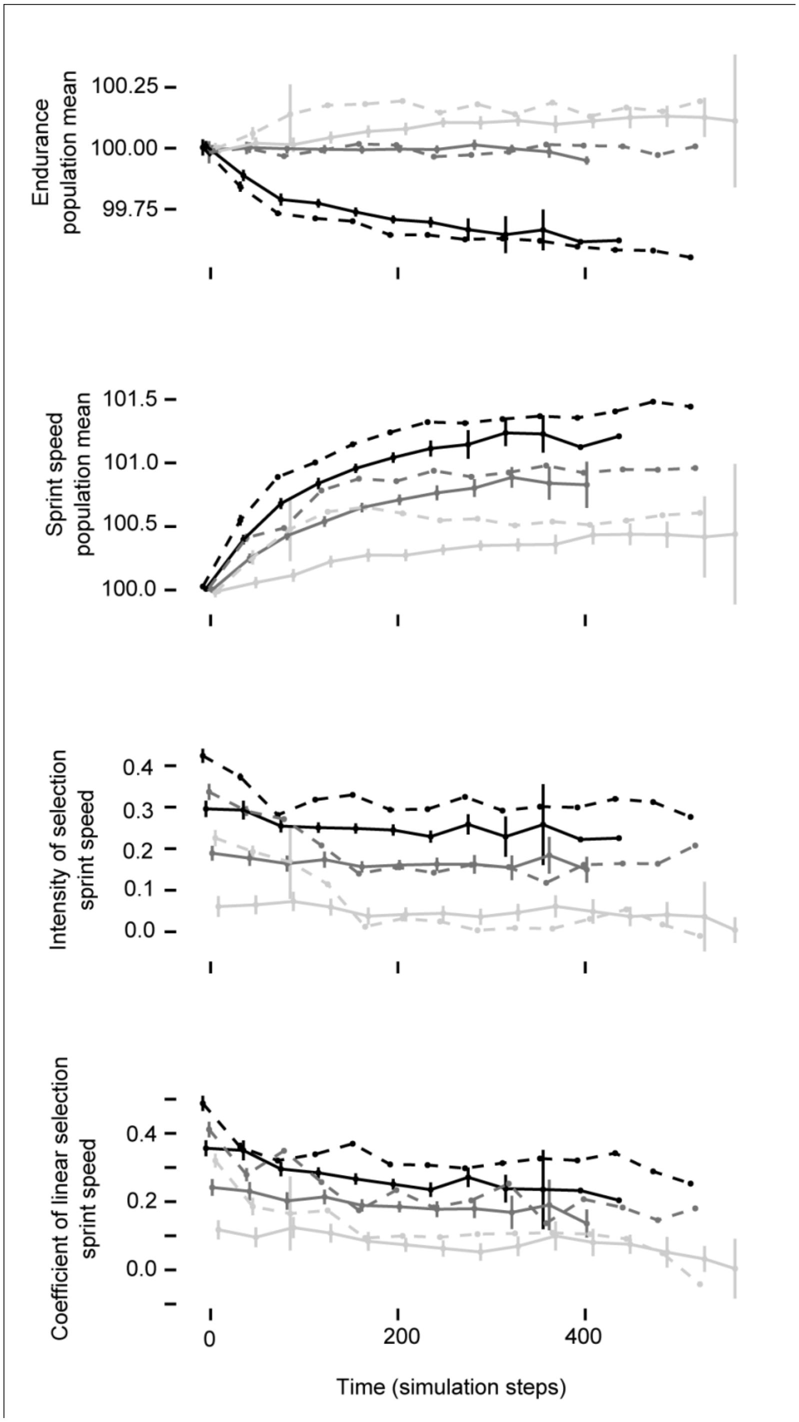

Figure 2: Correlation between traits affects the trajectory of phenotypic change in simulated populations. For each type of correlation between sprint and endurance (negative – black; none – dark gray; positive – light gray) and performance strategy (individuals only use maximum sprint – dashed line; sprint speed variable – solid line), the mean maximum sprint speed increases over time, but the rate depends on the nature of the correlation between traits. Intensity of selection (i_{sprint}) and the coefficient of linear selection (β_{sprint}) decrease over time and differ depending on the nature of the trait's correlation and strategy. Error bars represent 95% confidence intervals.

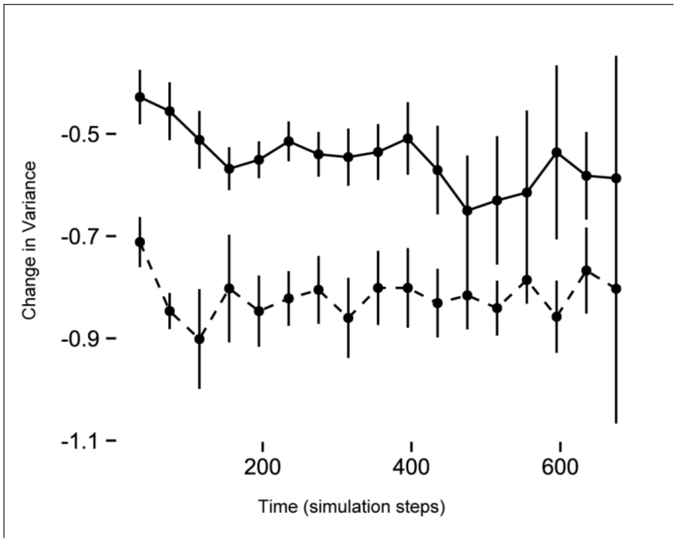

Figure 3: The difference in the change in variance between reproductive events (individuals only use maximum sprint – dashed line; sprint speed variable – solid line). Initially the variance decreases, as directional selection on the first generation truncates the distribution of phenotypes in a population, and this decrease is greater (more negative) in the non-variable group. As populations in either scenario respond to selection, and the mean for sprint speed increases (Fig. 2), selection on high endurance and sprint speed costs further reduces variance. Covariation structure did not significantly alter the trends within variable and non-variable simulations.

Discussion

Explaining the maintenance of higher maximal performance capacities than are typically used in nature is a persistent problem in evolutionary physiology. We used an individual-based simulation approach to model the evolution of two correlated performance traits, sprint and endurance, under conditions of varying and non-varying sprint performance. Our results show that varying sprint capabilities in a population has clear implications both for the form and intensity of selection and for the efficiency of the response to selection. Both intensity of selection (i_{sprint}) and the linear coefficient of selection on sprint speed (β_{sprint}) over time follow a similar pattern across the three different trait correlation conditions, but both metrics overall decrease as the correlation between sprint and endurance goes from negative to positive. Furthermore, when these traits are positively correlated, endurance capacity for the population tracks sprint capacity. Because the costs for endurance are much higher than for sprint speed in our model, this suggests that endurance capacity imposes indirect costs on high-speed phenotypes, manifesting as stabilizing selection on sprint speed. A positive relationship between sprint speed and endurance therefore causes the relationship between individual sprint speed and fitness to eventually become negative at higher speeds (Fig. 2). Also, as the population's mean sprint speed responds to selection and increases over time, the variance is continually reduced by selection, stemming from indirect costs of high endurance when there is a positive correlation between sprint and endurance, or from the increasing energetic costs of extremely high sprint speeds when the correlation with endurance is negative or zero.

The change in sign for term coefficients involving preferred speed from our entire dataset (Table 2A) to just those simulations in which individuals had variable sprint speeds (Table 2B) indicates that populations that never vary performance experience the same selective pressures in fundamentally different ways from those that do vary their performance. Surprisingly, selection is not greatly affected as preferred speed decreases relative to maximal capacity; populations that used preferred speeds always experienced less intense selection than those that used maximal speeds, but selection intensities were less influenced by the "level" of preferred performance. Thus, the magnitude of the difference between maximum and preferred speed does not seem to alter the population's phenotypic trajectory. What we may conclude from this is that perhaps specific preferred speeds are not optimal speeds, and what *is* optimal is the fact that there is variation in speed at all. Thus, populations in our simulations could ameliorate the influence of selection on sprint speed simply by not moving at maximal speeds all the time. The form of selection, as estimated by our best-fit selection models, met our expectations for simulation runs in which individuals only operated at their maximal sprint speeds, in that the selection we imposed via predators favored higher sprint capacities, and high costs for high endurance (exponential cost function) favored intermediate endurance capacities.

	Model term	Coefficient	SE		Model term	Coefficient	SE
A	Intercept	0.15	0.009	B	Intercept	0.18	0.007
	Gen	-1.1×10^{-4}	4.8×10^{-5}		Gen	-1.9×10^{-4}	4.3×10^{-5}
	Cov	-0.12	0.004		Cov	-0.11	0.004
	Preferred	9.0×10^{-4}	1.1×10^{-4}		Preferred	-1.0×10^{-4}	1.0×10^{-4}
	Gen x Cov	8.3×10^{-5}	2.1×10^{-5}		Gen x Cov	6.2×10^{-5}	2.0×10^{-5}
	Gen x Preferred	-1.7×10^{-6}	6.1×10^{-7}		Gen x Preferred	9.8×10^{-7}	5.7×10^{-7}

Table 2. Best-fit model for intensity of selection on sprint speed (i_{sprint}) including terms for generation (Gen), covariation between sprint and endurance (Cov) and preferred speed (Preferred). A. Simulations with variable and nonvariable sprint speed included together, and B. variable sprint speed only. Notice the sign of the coefficients for terms and interactions involving preferred speed changes between models.

The behavior of our simulation when individuals vary sprint speed may stem from multiple sources. While varying performance introduces stochasticity to predator interactions, it may also serve to artificially increase the cut-off for predator selection away from the mean phenotype, which would lead to erroneous quadratic estimates (Schluter 1988). Thus, estimating selection without accounting for intra-individual variation in performance is likely to be misleading. Furthermore, the indirect constraints on the phenotypic response to selection imposed by the costs of endurance clearly demonstrate the necessity of multivariate selection analyses. The observed variation in results for selection metrics involving sprint speed alone (Tables 2, 3; Fig. 2) was explained by differences in correlation with endurance and with the performance strategy. Therefore, such estimates of the effects of selection on mean phenotypes of one trait are hardly informative out of context, when other relevant fitness predictors are not measured (Mitchell-Olds and Shaw 1987).

	Model term	Coefficient	SE
B	Intercept	0.25	0.01
	Gen	-4.5×10^{-4}	6.8×10^{-5}
	Cov	-0.13	0.012
	Preferred	-2.7×10^{-4}	1.4×10^{-4}
	Gen x Cov	2.9×10^{-4}	7.6×10^{-5}
	Gen x Preferred	2.5×10^{-6}	9.0×10^{-7}
	Cov x Preferred	2.3×10^{-4}	1.7×10^{-4}
	Gen x Cov x Preferred	-2.1×10^{-6}	1.0×10^{-6}

	Model term	Coefficient	SE
A	Intercept	0.21	0.010
	Gen	-2.3×10^{-4}	6.0×10^{-5}
	Cov	-0.12	0.009
	Preferred	6.7×10^{-4}	1.2×10^{-4}
	Gen x Cov	1.5×10^{-4}	2.6×10^{-5}
	Gen x Preferred	-2.2×10^{-6}	7.6×10^{-7}
	Cov x Preferred	1.5×10^{-4}	1.0×10^{-4}

	Model term	Coefficient	SE
C	Intercept	0.25	0.010
	Gen	-3.8×10^{-4}	5.9×10^{-5}
	Cov	-0.11	0.008
	Preferred	-2.0×10^{-4}	1.3×10^{-4}
	Gen x Cov	1.4×10^{-4}	2.6×10^{-5}
	Gen x Preferred	1.6×10^{-6}	7.7×10^{-7}
	Cov x Preferred	-3.4×10^{-5}	1.0×10^{-4}

Table 3. Best fit model β_{sprint} at each generation of each simulation. Best-fit models for (A.) simulations with variable and nonvariable sprint speed included together and (B.) variable sprint speed only, as well as (C.) the same model predictors as (A.) but using the dataset for (B.).

	Model term	Coefficient	SE		Model term	Coefficient	SE
A	Intercept	-0.44	0.03	B	Intercept	-0.47	0.01
	Gen	-1.4×10^{-4}	4.5×10^{-5}		Gen	-2.5×10^{-4}	5.0×10^{-5}
	Preferred	-1.5×10^{-3}	3.1×10^{-4}		Cov	-0.019	0.01

Table 4. Best fit model for the change in variance during each interval between reproductive events for for (A.) simulations with variable and nonvariable sprint speed included together and (B.) variable sprint speed only. When all simulations are considered, (A.) time (Gen) and the percent of maximal sprint capacity (Preferred) are significant, and the magnitude of the decrease in variance becomes greater over time. However, when non-variable simulations are excluded (B.), only terms for time and the covariance between sprint and endurance (Cov) are retained, although the coefficient estimate for the covariance term is not large compared to its standard error. Thus, within the variable sprint group there is little difference between simulations with differing preferred speeds.

As per our first hypothesis, intra-individual variation in movement speeds therefore does indeed appear to “buffer” a population from selection. If we consider the differences in responses between populations that always employed maximal sprint speed versus those that did not, the former experienced more intense selection, and an immediate positive shift in the phenotypic distribution for sprint capacity (Fig. 2), as well as a more dramatic decrease in the variance (Fig.3). While this efficiency in response to a novel threat is beneficial in the short term, such a response would rapidly erode the available genetic variation, constraining the potential for adaption in the long-term (Hoffman 2013). In our simulations the selective pressures were essentially static for the entirety of each run. However, selective pressures experienced by natural populations may fluctuate (Sinervo and DeNardo 1996; Siepielski et al. 2009), which could favor lineages employing a conservative bet-hedging strategy that maintains a low variance in fitness in the long term rather than a less conservative strategy in which fitness is maximized in the short term (Simons, 2002). Thus, maintaining phenotypic variation in the face of strong selection may be an optimal strategy ifselective pressures are ephemeral or fluctuate over time or if adaptive trends reverse (e.g., Losos et al. 2006).

Our second hypothesis states that the selective environment as well as the genetic underpinnings and correlations between performance traits determine and maintain maximal and optimal values of performance. Indeed, in our model the strength of selection and the resultant response to selection were modulated by the severity of environmental pressures in the form of predator and resource densities as well as the amount of energy a resource contains. We also found clear evidence that the genetic correlation between sprint and endurance had a measurable effect on the trajectory of populations in phenotypic space over time (Fig. 2). A negative correlation with endurance facilitated a rapid, positive shift in maximal sprint capacity, while a positive correlation with endurance constrained this response.

Although the effects seen here are specific to the context of our particular energetic paradigm, these findings nonetheless clearly demonstrate the utility of individual-based simulation approaches to performance evolution. In building our model, we made a number of simplifying assumptions, as do all modellers, and while our relatively simplistic model focused on only two correlated traits, we were nonetheless able to observe emergent variation in the form and intensity of selection given only one or two changes in parameters. Increasing the complexity of our model will add further biological realism and allow testing of more detailed hypotheses related to the evolution of whole-organism performance. For example, by allowing other organismal features such as the size of the energy budget to respond to selection (via assigning a mode of heritability as we have with performance traits), the model could be used to predict evolutionary responses in cases in which species adjust energy acquisition rather than "choose sides" in an energetic trade-off (Roff and Fairbairn 2012). Furthermore, for more realistic long-term data, the model can be adjusted to include dynamic predator-prey interactions (e.g. Brodie and Ridenhour 2003). We chose to measure only a maximum of 15 generations for each simulation as we would expect a real population to experience a change in environmental and genetic conditions over that span (Roff and Fairbairn 2012). To focus on variation in selection in the short-term response to only intra-individual variation in sprint speed and its genetic correlation with endurance, we chose to disregard co-evolution in our initial model, nor do we consider evolved changes in the genetic correlations between traits or in performance-use strategy. However, incorporating the evolution of these parameters is feasible and interpretable within the simulation framework presented here.

While collecting real-world performance data is still limited by logistic constraints, there has been a positive trend towards measuring multiple traits (see Lailvaux and Husak 2014). This inclusive approach is necessary to avoid the pitfalls of taking things out of the integrated organismal context, such as making inferences about selection on one trait while ignoring relevant, covarying traits also under selection (Mitchell-Olds and Shaw 1987; Ghalambor et al. 2004; Hall et al. 2010; Lailvaux and Husak 2014). Organismal data always constitute a snapshot of the present, yet are representative not only of current conditions, but of a complex selective and evolutionary past. Individual-based simulations allow us to preserve this complexity and create what are essentially a vast number of artificial selection lines for which we can acquire complete, longitudinal data on fitness and phenotype in the context of known environmental parameters. Beyond quantifying current trait distributions in study populations, we have shown that considering such data in the context of a complex, explicitly modelled system is both feasible and capable of alerting investigators to many varied explanations bridging ecological processes and the evolutionary dynamics of performance.

In conclusion, individual-based simulations represent a promising approach to understanding the origins and maintenance of whole-organism performance capacities, as well as for testing hypotheses regarding their evolutionary trajectories. Using a relatively simple model, we have shown that intra-individual variation in realized performance results in less intense selection on performance regardless of the extent of variation, and furthermore that the evolutionary trajectories of multiple performance traits dependent on a common pool of resources are affected by the nature of the bivariate correlation between them. Future iterations of this model will be able to test further scenarios of the evolution of performance under a variety of ecologically relevant conditions.

Funding

This work was not supported by any funding agency. Travel to this meeting was in part funded by the University of New Orleans Department of Biological Sciences.

Acknowledgements

We would like to thank J. Husak and R. Wilson for inviting us to participate in this symposium. We also thank R. Brooks for valuable discussion and L. J. Elhaj for significant technical support.

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Chapter 2:

Sex-specific multivariate morphology → performance relationships in *Anolis carolinensis*

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Abstract

Animals rely on their ability to perform certain tasks sufficiently well to survive, secure mates, and reproduce. Performance traits depend on morphology, and so morphological traits should predict performance, yet this relationship is often confounded by multiple competing performance demands. Males and females experience different selection pressures on performance, and the consequent sexual conflict over performance expression can either constrain performance evolution or drive sexual dimorphism in both size and shape. Furthermore, change in a single morphological trait may benefit some performance traits at the expense of others, resulting in functional trade-offs. For example, muscles built for fast burst speed are morphologically distinct from those which maximize oxygen delivery and can work longer before tiring. Identifying general or sex-specific relationships between morphology and performance at the organismal level thus requires a multivariate approach, as individuals are products both of an integrated phenotype and the ecological environment in which they have developed and evolved. Here I focused on the multivariate morphology → performance gradient in wild-caught, local green anoles (*Anolis carolinensis*). To determine this gradient, I used standard measurements of body morphology as well as fore- and hindlimb musculature, vital organs (heart, lungs, liver). I also measured seven performance traits that cover the broad range of ecological challenges faced by these animals (sprint speed, endurance, exertion, climbing power, jump power, cling force, and bite force). By using multivariate techniques to reduce dimensionality and still preserve the complexity inherent in an organism's phenotype, and mapping these new trait variables to performance, I describe the morphological underpinnings of the multivariate performance phenotype, demonstrate the existence of sex-specific functional trade-offs that follow from the sexes' different selective contexts, and identify classic and novel examples of trade-offs between classes of performance traits.

Introduction

Animals in nature are required to conduct a variety of ecological tasks, ranging from foraging and predator escape to reproduction, in their day-to-day existence that can have important effects on individual fitness. Many of these tasks are bolstered, if not entirely enabled, by dynamic whole-organism performance abilities, such as running, jumping, climbing or biting (Bennett and Huey 1990; Lailvaux and Irschick 2006; Husak et al. 2009). These different tasks frequently require different kinds of performance, which may place disparate and conflicting demands on the underlying individual morphology and physiology (Arnold 1983) . Consequently, an important trend throughout the animal kingdom is that excellence in a particular performance trait comes at the expense of less-than-excellent performance in others (Van Damme and Wilson 2002; Van Damme et al. 2002). For example, animals that are specialized for endurance running tend to have poor maximum sprint speeds, and vice versa (Vanhooydonck et al. 2001) because the morphological and physiological requirements for each are not concordant, and a similar functional trade-off between running and fighting has been posited between running ability and fighting (Pasi and Carrier 2003). But while investigations of bivariate functional trade-offs between pairs of performance capacities are common (e.g. Losos et al. 1993; Van Damme et al. 1996; Wilson et al. 2002; Herrel and Bonneaud 2012), studies that test for trade-offs among suites of different performance traits within the same species are less common.

The basis of functional trade-offs lies in the ecomorphological paradigm, which tells us that an individual's performance is determined by its underlying morphology and physiology (Arnold 1983). However, intraspecific variation in morphology is widespread. One of the most striking sources of such variation is sexual dimorphism, whereby males and females differ markedly in size, shape, or physiology. There exists a large literature on sexual dimorphism in size, shape, color, and behavior in animals (reviewed in Rice 1984; Hedrick and Temeles 1989; Shine 1989); but while the functional basis of sexual dimorphism in performance has been well studied in humans (e.g. Wells and Plowman 1983; Mooradian et al. 1987), it is poorly understood for the vast majority of animal species. In some cases where sex differences in performance have been reported, the causes of such differences can be obviously ascribed to factors such as sexual dimorphism in size such that the larger sex exhibits greater performance than the smaller sex, or to gravidity/pregnancy, which tends to impair performance in the sex that bears the young (Veasey et al. 2001; e.g. Shine 2003; but see Scales and Butler 2007). However, there are also several cases where males and females of a given species differ in one or more types of performance even after scaling effects are accounted for (reviewed in Lailvaux 2007), suggesting that those differences are rooted in intrinsic physiological factors.

Empirical support for such differences has been found in select species; for instance, male alligators have more active mitochondria during the breeding season than females, which has been suggested to fuel the higher seasonal demand for male locomotor performance (Seebacher et al. 2003), and the average higher basal metabolic rate in men versus women of the same size is thought to contribute to greater locomotor endurance capacities in men (Pate and Kriska 1984). From the perspective of multiple performance traits, males and females may even show sex-specific relationships between morphology and performance and, potentially, sex-specific performance trade-offs. For example, maximal jumping ability in the frog *Xenopus tropicalis* not only has different morphological determinants in males and females, but also exhibits a sex-specific trade-off whereby a negative relationship between peak jumping force and jump exhaustion was detected in females but not in males (Herrel et al. 2014). If physiological differences between males and females affect trade-offs between traits differently in each sex, and if functional trade-offs prevent individuals from maximizing performance among suites of traits, then males and females may not only exhibit differences in size-corrected performance, but may show different patterns of functional trade-offs driven by intrinsic differences in physiology as well.

The green anole lizard, *Anolis carolinensis*, is a model system for understanding both ecology and evolution and for testing hypotheses relating to whole-organism performance capacities. As such, there is a large literature investigating the relationship between morphology and performance in this and related species (e.g. Bels et al. 1992; Spezzano and Jayne 2004; Vanhooydonck et al. 2005; Foster and Higham 2012) . Previous studies on performance in green anoles specifically have detected evidence for sex-specific effects on performance beyond those explained by scaling. For example, Irschick et al. (2005) showed that adult female green anoles are always the best performers relative to size compared to both juveniles and adult males for clinging and jumping ability, and Lailvaux & Irschick (2007) found that certain aspects of jump performance do not respond similarly in male and females to changes in body temperature after controlling for body size. Adult males also exhibit significantly larger heads and higher bite forces for their size than females, likely because of the importance of relative bite force to male combat outcomes in this species (Lailvaux et al. 2004). Because of the integrative nature of the overall multivariate performance phenotype (Ghalambor et al. 2003), such differences can have implications for the expression of other performance traits in males relative to females in ways that may not be immediately apparent. In *Hemidactylus frenatus* geckos, for example, there is a male-specific trade-off between head shape and sprinting ability (driven by the likely need for high bite forces in males) that is exacerbated when males are forced to run up inclines, because larger heads require the animal to do more work against the influence of gravity (Cameron et al. 2013). There is thus a need for studies that consider not only morphology-driven trade-offs among several types of whole-organism performance, but that test for the sex-specific nature of those trade-offs as well.

We measured a suite of seven whole-organism performance traits in a sample of wild-caught adult male and female *Anolis carolinensis* lizards and tested for sex-specific trade-offs among those traits. We also measured several morphological and physiological variables, including limb dimensions, muscle size, and organ mass, in all individuals to test for functional relationships among morphology and performance beyond allometric effects (Garland 1984). We tested the following specific hypotheses: (1) That males and females are sexually dimorphic in both morphology and performance after controlling for size difference, and (2) that there will be differences in the pattern of morphology → performance relationships between the sexes.

Materials and Methods

We caught 125 adult green anoles (64 males, 61 females) from various locations in the Greater New Orleans area and measured seven different performance capacities (jumping ability, sprint speed, endurance, exertion, bite force, clinging ability, and climbing ability). We measured morphology on the same day as capture, as well as bite force, clinging ability, and climbing speed. All other performance measures were conducted within three weeks of capture. Lizards were housed in plastic cages (28.5cm x 17.5cm x 21cm) with mulch substrate and a wooden dowel perch. Each shelving rack of cages was provided with Repti-Sun 5.0 UVB 310 40 W Fluorescent Lamps to mimic natural sunlight. Animal room conditions were maintained at approximately 30^o C, 70% relative humidity, with a light:dark cycle of 12:12 hours (Kolbe and Losos 2005). Lizards were misted at least twice daily, and fed a diet of 1-2 crickets supplemented with calcium powder (Repti Calcium, Zoo Med Laboratories Inc.) every 2-3 days.

Morphology

Digital calipers were used to measure SVL, all limb segments (humerus, radius, metacarpal, longest finger, femur, tibia, metatarsal, longest toe) as well as head dimensions (head length, width, height) to the nearest 0.01mm. Body mass was measured with a digital balance (Mettler Toledo PR8002 DeltaRange) to the nearest .01g. Toe-pad size was measured by placing the lizard inside a flatbed scanner (HP Scanjet G3110), scanning the toe-pad area at 600 dpi, and then digitally measuring toe-pad size with tpsDIG (Rohlf 2010).

At the end of all performance trials, lizards were euthanized with Tricaine methanesulfonate (MS222, IACUC protocol #14-005; Conroy et al. 2009), fixed in formalin, and stored in 70% ethanol. Vital organs were removed (heart, liver, lungs), patted dry, and weighed on an analytical balance (Mettler Toledo XS105) to the nearest 0.001 mg. For a subset of 31 males and 31 females chosen at random, ten muscles related to locomotor performance were also removed and weighed to the nearest 0.001 mg. The muscles and their proposed functions (from Herrel et al. 2008) are found in Table 1.

Forelimb	Function	Hindlimb	Function
M. biceps	Elbow flexion	M. ambiens	Knee extension
M. triceps brachii	Elbow extension	M. puboischiotibialis	Knee flexion and femoral adduction
M. latissimus dorsi	Humeral retraction	M. iliofibularis	Knee flexion
Trapezius	Shoulder rotation and stability	M. gastrocnemius pars fibularis	Ankle extension
M. pectoralis par superficialis	Humeral retraction	M. caudofemoralis longus	Femoral retraction

Table 1. Muscles chosen for analysis and their proposed function and information on function taken from Herrel et al. (2008).

Bite Force

We measured bite force using an isometric Kistler force transducer (type 9023, Kistler, Winterthur, Switzerland) connected to a type 5058a Kistler charge amplifier (see Herrel *et al*. 1999, 2001 for a detailed description). Lizards were induced to bite a force plate by tapping their cheek until their mouth opened, then lining up the mouth with the center of the force plate until the lizard bit forcefully. Bite trials were repeated every hour for a total of five trials per animal, and the largest bite force obtained was taken as the maximal bite force for that animal (Adolph & Pickering, 2008; Losos, Creer, & Schulte, 2002). All lizards were placed in an incubator at 33°C (approximately the preferred field body temperature for both species; see Huey & Webster, 1976; Lailvaux & Irschick, 2007) for one hour prior to trials, and during rest periods in between trials.

Clinging Ability

Lizards were warmed in an incubator for one hour at 33°C, then dragged backwards with both fore-limbs in contact with a sheet of acetate taped to the top of a Kistler Z17097 piezoelectric force plate connected to a Kistler 9685 charge amplifier (Bloch & Irschick 2004; Elstrott & Irschick 2004). Digital traces were read from a Kistler 5691 DAQ-book into a Windows computer using Bioware software version 4.1.02. Because the force plate measures forces exerted in the x, y, and z planes, clinging force was measured as the force trace on the y-axis. Each trial was repeated 4-5 times, with the highest recorded score considered the maximum for clinging ability.

Sprint Speed

Sprint trials were conducted in a small room 33^{o}C using similar methods to those of Losos and Irschick (1996). Lizards were given at least one hour to acclimate before each trial. A custom-made track consisting of a cork substrate inside a wooden structure with fitted infrared sensors placed every 25 cm was used to track sprint speed. When the beams are interrupted by the lizard running past, the time is recorded (SCL Timer, Trackmate Racing, Surrey BC, Canada). Thus consecutive beam interruptions allow for accurate measurement of the time it takes for each lizard to traverse each 25 cm interval. The track was placed at a forty-five degree angle to encourage lizards to run up rather than hop, as is typical behavior on level ground (Perry et al. 2004). Lizards were placed at the beginning of the track, and encouraged to run with a gentle tap on the tail. For each trial, the highest speed measured for a 25 cm distance was recorded. Each trial was also given a score of “good” (continuous, fast sprint across multiple 25 cm sections), “fair” (at least one 25 cm section was continuously sprinted across), or “poor” (failure to continuously sprint across a 25 cm section). Lizards were given five opportunities to yield at least one “good” sprint trial.

Climbing

Climbing was measured using a custom-built, vertical track with a cork substrate. Lizards were warmed in an incubator for one hour at 33^{o}C before climbing trials. Acetate walls bound either side of the track to prevent escape and to maintain a straight path upwards. Trials were recorded with a high-speed camera (TroubleShooter TS1000MS, Fastec Imaging Corporation, 2007) at 250 fps. Lizards were placed near the bottom of the track and encouraged to run up with gentle tap using a wooden dowel. Once they reached the top, they were collected and placed back in the incubator. Trials were scored as good (continuous strides across the field of view), fair (at least two strides without interruption), or poor (less than two strides of continuous motion, or pausing between steps), and each lizard was given at most five attempts. A 1 cm x 1 cm grid was placed in view of the camera for calibration, and motion-tracking software was used to analyse the climbing data (ProAnalyst, Xcitex Inc. 2006). The tip of the snout was digitized frame by frame, and average climbing speed was measured by finding 2-3 full footsteps and taking the average speed across this distance. This was converted to a measurement of climbing power by multiplying by the acceleration of gravity.

Endurance

Endurance was measured using a treadmill modified to operate at roughly 0.4 km/hr. To prevent lizards from escaping the treadmill setup, plastic walls were erected and lizards were encouraged to stay within the center of the treadmill belt by hand. Lizards were trained on the treadmill at least a day before trials were recorded, and were also made to fast for a day before the trial to control for the differences in stomach contents during the trials. The room was heated to 33°C. Endurance was measured as the time the lizard maintained a relatively constant speed while being lightly tapped on the tail for motivation (Le Galliard et al. 2004). If the lizard stopped, they were inspected for signs of exhaustion by placing them on their backs. Exhaustion was determined as failure to right themselves. If they were not fully exhausted, the trial continued. Timing stopped when the lizard was determined to be fully exhausted. As endurance is taxing for the animals, only one trial per lizard was conducted.

Exertion

Exertion was measured as the distance a lizard could run at maximum speed while being chased around a circular track (Mautz et al. 1992). The track was built out of a flexible acrylic sheet fastened together and attached to a wooden base. The track was divided into 10cm segments with a marker and each segment was numbered consecutively. At the start of a trial, the lizard was placed on the first numbered segment and encouraged to run using a soft paintbrush. Once a lizard began showing signs of exhaustion, they were checked for righting ability and either quickly returned to the track, or the trial ended. A stopwatch was used to measure the time each trial lasted, and the distance was measured by counting how many times around the track the lizard traveled, plus the number of segments away from the starting segment the lizard was when the trial ended. Number of segments was converted to total centimeters (10 cm/ segment). The room was heated to 33°C, and only one trial per lizard was conducted.

Jumping

Jumping was measured again using high speed video at 500 fps. As jumping involves a three-dimensional trajectory, a mirror was placed at a 45-degree angle above the jumping arena to capture movement in the directions parallel to ground, while the camera was placed to the side, capturing both vertical and forward movement. 1cm grid paper was placed both on the wall perpendicular to the camera view, as well as on the jumping platform, in view of the mirror for calibration of all planes. In order to automatically track motion over many frames, and to aid calibration between the two fields of view, six white-out dots were applied to the lizards (Wite-Out® Brand Quick Dry Correction Fluid, Bic USA Inc.). Three dots were evenly spaced on the dorsal side: one near the neck, one near the center of mass, and one near the base of the tail. Three corresponding dots were placed on the lateral side of the lizard facing the camera.

A perch was placed at a distance far enough away from the jumping platform to encourage the lizards to employ their maximal jump capacity. Once filming began, the lizard was placed at the edge of the platform and encouraged to jump with a loud, startling clap (Toro et al. 2003)

Statistical Analyses

For all analyses, morphological and performance variables were standardized to a mean of zero and a standard deviation of 1. Statistical outliers were removed, and data were checked for violations of assumptions for multivariate tests. Bite force was log-transformed. When size-correcting data, residuals were extracted from a linear model of the trait regressed onto snout-vent length (SVL).

Sexual Dimorphism

To test for sexual dimorphism between morphology and performance variables, we performed a MANCOVA for each group of multivariate dependent variables: head dimensions, limb segment factors, muscles (all ten muscle mass measurements), residual organ weights, and finally all seven performance variables. The morphological variable sets were created to handle differences in sample sizes, as muscles and organs were not dissected from all lizards. Sex and snout-vent length were used as dependent terms, and we included the interaction between sex and size. To determine the best-fit MANCOVA we sequentially dropped terms from the full model and compared fits using partial F tests.

Construction of the F-matrix

To map the contributions of our many morphological variables to the suite of performance traits, we use an F-matrix model (Ghalambor et al. 2003; Walker 2007; Bergmann and McElroy 2014). Arnold (1983) suggested the use of standardized partial regression coefficients to estimate performance gradients, allowing one to partition the variation in performance due to separate traits despite their being integrated into a single phenotype. Placing these performance gradients into a matrix allows for mapping many phenotypic traits to many performance traits and will aid in identifying functional trade-offs associated with our morphological traits. By creating sex-specific F-matrices we are able to identify differences in morphology → performance relationships as well as compare between sexes the amount of functional constraint each phenotypic or performance trait is under (Bergmann and McElroy 2014).

Results

Sexual dimorphism in morphology and performance

Sexual dimorphism in all morphological trait sets was apparent. Separate MANCOVAs revealed significant differences in trait means between the sexes. In Table 2, results are presented for the best-fit MANCOVA models (significant results from model comparison tests). Head dimensions were significantly different between sexes. Size also significantly contributed to this variation. Variation in limb segments was also significantly different between sexes, and size also contributed to this variation. Sex and size were similarly significant in terms of muscle mass variation, as well as an interaction term between sex and size.

	Pillai's Trace	Approximate F	Df	p
Head				
Sex	0.43	30.47	3, 121	< 0.005
SVL	0.74	114.29		< 0.005
Limb				
Sex	0.39	9.48	8, 117	< 0.005
SVL	0.74	24.42		< 0.005
Muscles				
Sex	0.33	2.31	10, 48	< 0.005
SVL	0.74	13.72		< 0.05
Sex:SVL	0.38	2.91		< 0.05

Table 2. Results from best-fit MANCOVA for each set of morphological variables. "Head" includes head width, length, and height. Limb includes all fore- and hindlimb segments. Muscles include all ten muscle masses.

Performance data also significantly differed between the sexes (Table 3). Terms for sex, size, and the interaction between them were all significant. This indicates that variation among the suite of performance trait expression while controlling for size differs between the sexes beyond differences due to allometry. Univariate tests showed a significant effect of sex on jumping, sprinting, clinging, and exertion. Sex, size, and their interaction had significant effects on bite force. Differences in endurance were only significantly affected by size. Consequently, the data for males and females was divided, and all raw performance and morphology variables were size-corrected separately for each sex.

Performance	Pillai's Trace	Approximate F	Df	p
Sex	0.231	3.989	7, 93	< 0.005
SVL	0.66	25.82		< 0.005
Sex:SVL	0.314	6.095		< 0.005

Table 3. Results from best-fit MANCOVA for all seven performance variables.

Male morphology

To reduce the dimensionality of our limb segment data, I performed a principal components analysis followed by orthogonal rotation of the size-corrected data (varimax, Kaiser, 1958). Inspection of the principal components analysis indicated retention of three factors using the Kaiser-Guttman criterion of retaining all factors with eigenvalues greater than one. The resulting factors (Table 4) described the major axes of residual limb variation. Residual tibia length had the greatest loading, with tibia and all other hindlimb segments loading positively on Factor 1. Factor 2 consisted of high, positive loadings for residual humerus length, with intermediate loadings for other forelimb segments (radius, and longest digit). A small negative loading for metatarsals was also observed. Residual metacarpal length loaded most highly on Factor 3. Thus, high scores for each of our factors represent: (1) relatively longer tibia length (and other hindlimb components), (2) relatively longer humerus (and other arm components) and smaller metatarsal length, and (3) relatively longer metacarpals.

Male muscle morphology analysis resulted in the retention of four muscle factors (Table 5). M. caudofemoralis longus and M. latissimus dorsi are the muscles with the highest loadings on Factor 1. Factor 2 includes high loadings for M. iliofibularis and trapezius muscles. M. biceps is the greatest contributor to Factor 3, and M. ambiens to Factor 4.

We computed the geometric means from each of the three head dimensions to produce a single head variable, which we size-corrected using only male data for all traits and SVL. Heart, liver, and lung masses were similarly size-corrected.

	Factor 1: Tibia	Factor 2: Humerus	Factor 3: Metacarpal	
Femur	0.470	0.116		
Tibia	0.673			
Metatarsals	0.562	-0.207		
Longest Digit (hindlimb)	0.434			
Humerus		0.774		
Radius	0.312	0.421		
Metacarpals		0.133	0.986	
Longest Digit (forelimb)		0.4		
				Cumulative variance (%)
Proportion of Variance (%)	16.1	28.9	12.7	41.5

Table 4. Loadings for each size-corrected limb segment on each factor for males. Loadings < 0.2 are not shown.

	Factor 1: M. caudofemoralis longus	Factor 2: M. iliofibularis	Factor 3: M. biceps	Factor 4: M. ambiens	
M. ambiens				0.979	
M. puboischiotibialis	0.543			0.220	
M. iliofibularis	0.417	0.802			
M. gastrocnemius pars fibularis	0.537				
M. caudofemoralis longus	0.841			0.203	
M. biceps			0.965		
M. triceps brachii	0.319	0.421	0.299	0.436	
M. latissimus dorsi	0.703		0.408		
Trapezius		0.724			
M. pectoralis pars superficialis	0.559	0.396	0.306	0.210	
					Cumulative variance (%)
Proportion of Variance (%)	24.6	15.5	13.3	13.2	66.7

Table 5. Loadings for each size-corrected muscle mass on each factor for males. Loadings < 0.2 are not shown.

Female morphology

Factor analysis of size-corrected female limb segments yielded three factors (Table 6). The trait with the highest positive loadings on Factor 1 was tibia length, with intermediate positive loadings for humerus and femur length. For Factor 2, metatarsal length loaded positively, followed by femur length. Radius length loaded positively on Factor 3, but this loading was relatively small.

For female muscle morphology, we retained three factors (Table 7). M. iliofibularis had the highest loading on Factor 1. Factor 2 had similarly high loadings for three muscles: M. pectoralis pars superficialis, M. latissimus dorsi, and M. biceps. Thus, we refer to this factor as "Upper Body," as it refers to a collection of muscles related to upper body movement. M. ambiens contributed highly positively to Factor 3.

As with males, we computed geometric means for head size, and size-corrected head and organ traits using only female trait and SVL data.

	Factor 1: Tibia	Factor 2: Metatarsals	Factor 3: Radius	
Femur	0.417	0.559		
Tibia	0.946	0.296		
Metatarsals		0.793	-0.233	
Longest Digit (hindlimb)		0.280		
Humerus	0.463		0.374	
Radius	0.344		0.543	
Metacarpals	0.327			
Longest Digit (forelimb)			0.448	
				Cumulative variance
Proportion of Variance	19.2%	14.5%	9.2%	43.0 %

Table 6. Loadings for each size-corrected limb segment on each factor for females. Loadings < 0.2 are not shown.

	Factor 1: M. iliofibularis	Factor 2: Upper body	Factor 3: M. ambiens	
M. ambiens	0.290		0.954	
M. puboischiotibialis	0.580	0.262	0.236	
M. iliofibularis	0.978			
M. gastrocnemius pars fibularis	0.394	0.286	0.580	
M. caudofemoralis longus	0.637	0.360	0.278	
M. biceps		0.711		
M. triceps brachii	0.483		0.323	
M. latissimus dorsi	0.351	0.713	0.427	
Trapezius	0.435			
M. pectoralis pars superficialis		0.757	0.368	
				Cumulative variance
Proportion of Variance	25.3%	19.2 %	18.7 %	63.1 %

Table 7. Loadings for each size-corrected muscle mass on each factor for females. Loadings < 0.2 are not shown.

Morphology → Performance relationships

For each sex, we constructed three separate F-matrices using standardized partial regression coefficients from multiple regression models. The first F-matrix relates limb, head, and toepad traits to each of the seven performance variables. Because of different sample sizes for muscle and organ data, separate F-matrices were constructed from multiple regressions with each separately. All trait data were standardized to a mean of zero and standard deviation of one, and therefore all regression coefficients are themselves standardized.

From these F-matrices we can see both similarities and differences between male and female morphology → phenotype relationships. For example, the head variable in both males and females correlates positively with increasing bite force, indicating that this trait influences performance similarly in both sexes (Table 8). However, male relative tibia length (limb Factor 1) correlates negatively with climbing ability, while for females, the opposite is true. The differences in Factors between males and females must also be taken into account when interpreting the F-matrices. Residual toepad size also shows opposite sign relationships with cling force between males and females.

The F-matrix for each sex's muscle mass factors (Table 9) are not as comparable due to differences in factors, however relative M. iliofibularis mass does appear as a main factor in both, and we do see differences in how these similar factors relate to performance in males and females as evidenced by the change in sign between coefficients for sprinting and climbing.

Finally the F-matrices for vital organ and their relationship to performance are presented in Table 10.

Males	Bite	Climb	Cling	Endurance	Exertion	Jump	Sprint	Row sum	Row var
F1 Tibia	-0.014	-0.034	0.118	0.049	0.079	-0.127	0.075	0.146	0.007
F2 Humerus	-0.201	-0.131	-0.012	0.290	-0.332	0.093	0.053	-0.239	0.043
F3 Metacarpals	-0.005	0.085	-0.227	0.068	0.150	0.057	-0.102	0.025	0.017
Toepad	0.196	0.224	-0.088	-0.107	0.371	0.102	-0.108	0.590	0.036
Head	0.586	-0.163	0.130	0.212	0.002	-0.001	-0.089	0.678	0.062
Column sum	0.562	-0.018	-0.079	0.513	0.269	0.124	-0.171		
Column var	0.090	0.026	0.022	0.024	0.065	0.009	0.008		

Females	Bite	Climb	Cling	Endurance	Exertion	Jump	Sprint	Row sum	Row var
F1 Tibia	-0.015	0.256	0.169	0.005	0	-0.088	0.222	0.550	0.018
F2 Metatarsals	0.011	-0.060	-0.180	-0.022	0.104	-0.151	0.006	-0.291	0.010
F3 Radius	0.019	-0.117	0.122	0.002	-0.005	0.089	0.103	0.212	0.007
Toepad	-0.110	0.113	0.296	0.185	0.114	0.051	-0.113	0.537	0.022
Head	0.656	-0.138	-0.057	-0.031	-0.066	0.084	-0.241	0.206	0.086
Column sum	0.561	0.054	0.351	0.139	0.148	-0.016	-0.023		
Column var	0.095	0.029	0.035	0.008	0.006	0.012	0.033		

Table 8. F-Matrix mapping phenotypic traits to performance traits. All data are size-corrected or factors derived from size-corrected data. Values in cells are standardized regression coefficients from multiple regression models of each performance trait on all morphology variables. Row sums denote functional constraint on each morphological trait, while row variances (abbreviated 'var') measure the variation in the influence of different variables.

Males	Bite	Climb	Cling	Endurance	Exertion	Jump	Sprint	Row sum	Row var
F1 M. caudofemoralis longus	0.170	-0.166	0.217	-0.276	0.123	-0.229	-0.176	-0.337	0.044
F2 M. iliofibularis	0.180	-0.005	-0.184	0.156	-0.089	0.050	-0.083	0.025	0.018
F3 M. biceps	-0.252	-0.319	-0.172	0.004	0.108	-0.215	0.022	-0.825	0.026
F4 M. ambiens	0.040	0.098	0.058	-0.290	0.409	-0.252	-0.256	-0.193	0.065
Column sum	0.137	-0.392	-0.081	-0.406	0.551	-0.646	-0.493		
Column var	0.041	0.033	0.037	0.048	0.042	0.020	0.014		

Females	Bite	Climb	Cling	Endurance	Exertion	Jump	Sprint	Row sum	Row var
F1 M. iliofibularis	0.224	0.282	-0.124	0.372	-0.188	0.041	0.072	0.678	0.043
F2 Upper Body	0.416	-0.041	0.334	-0.050	0.144	0.096	0.128	1.028	0.031
F3 M. ambiens	0.456	0.549	0.016	0.085	0.265	-0.067	-0.293	1.011	0.089
Column sum	1.096	0.790	0.225	0.407	0.221	0.070	-0.093		
Column var	0.015	0.087	0.055	0.046	0.055	0.007	0.052		

Table 9. F-matrix for performance traits and muscle morphology for males and females.

Males	Bite	Climb	Cling	Endurance	Exertion	Jump	Sprint	Row sum	Row var
Lungs	0.155	0.091	-0.069	0.177	-0.210	0.068	0.062	0.273	0.0184
Liver	-0.312	-0.102	0.158	-0.249	0.082	-0.362	-0.069	-0.856	0.039
Heart	0.155	-0.142	0.188	0.171	-0.059	-0.040	-0.103	0.170	0.020
Column sum	-0.003	-0.154	0.276	0.099	-0.188	-0.334	-0.110		
Column var	0.073	0.015	0.020	0.060	0.021	0.050	0.008		

Females	Bite	Climb	Cling	Endurance	Exertion	Jump	Sprint	Row sum	Row var
Lungs	0.171	-0.168	0.049	0.045	0.001	-0.035	-0.044	0.019	0.011
Liver	0.185	-0.033	0.166	0.191	0.098	0.038	-0.044	0.601	0.010
Heart	0.073	-0.028	0.008	-0.045	-0.142	0.011	0.087	-0.035	0.006
Column sum	0.429	-0.228	0.223	0.191	-0.042	0.014	-0.001		
Column var	0.004	0.006	0.007	0.014	0.015	0.001	0.006		

Table 10. F-matrix for performance traits and vital organs for males and females.

Discussion

Our results clearly show differences in both morphology and performance between the sexes as well as many differences in how morphological traits map to performance traits. While sexual size dimorphism is apparent in *Anolis carolinensis* and is a feature widely distributed in *Anolis* lizards (Butler et al. 2007), there is little known about dimorphism beyond differences related to size, and less known about differences in performance between sexes (but see Lailvaux & Irschick 2007; Irshick et al 2005). Male and female multivariate analyses of limb segments and muscle morphology revealed differences in inter-trait correlations between sexes as evidenced by the different loadings of traits onto factors. While these axes of variation are particular to the multivariate phenotypic space of each sex, the differences in patterns of morphological variation reveal real information about how males and females occupy their respective phenotypic spaces, and that there are real differences that presumably correlate with specific ecological demands. Differences in male and female muscle morphology revealed by MANCOVA as well as differences in the factor analysis results between the sexes imply differences in functional and performance demands as well.

Many of the relationships between morphology and performance we observed are intuitive. Larger head size correlates with higher bite forces in both males and females, even after size correction, and increased toepad area correlates with higher clinging ability. Some of the more surprising relationships may indicate functional contraints on the phenotype wherein deviance away from normal scaling relationships could lead to decreased performance. For example, while biomechanical models predict longer hindlimbs would yield increased jumping ability, this was not the case for either sex in these lizards. While jumping does scale with overall size, and thus with longer leg lengths, having longer legs relative to body size does not necessarily increase performance beyond that range (Losos, Papenfuss, and Macey 1989), but these results differ from a previous study of jumping ability in *A. carolinensis* (Toro, et al 2003).

Inspection of the F-matrix reveals apparent trade-offs whenever the sign of the effect of a morphological trait on two different performance traits oppose each other (i.e., different signs for effects in the same row). For example, female radius length contributes positively to clinging ability, while having an opposite effect of similar magnitude on climbing ability. No such trade-off was evident in males. In both males and females, head size correlates with increased bite force, but decreased sprint speed and climbing, indicating that perhaps larger heads pose a significant burden on locomotion (e.g., Vanhooydonck & Van Damme, 1999; Herrel et al. 2001; but see also Kohlsdorf, et al 2008)

It is also important to note that some phenotypic correlations with performance may not indicate a causal relationship, but rather a correlation between the trait and other, unmeasured, morphological or physiological traits. For example, toepad area was estimated to correlate with bite force in males, but there is little reason to suspect toepads themselves are contributing to increased bite force. Rather, increased toepad area may be related to individual condition or investment, or a plastic response to the environment that may relate to increased bite force. We do see that male M. caudofemoralis longus muscle size relates to both bite and cling force (Table 9), which supports the idea that perhaps some aspect of quality or investment is altered in males leading to both increased muscle mass, toepad area, and biting and clinging performance.

In terms of male and female morphology → performance relationships, there are some notable differences between the F-matrices. For example, the iliofibularis factor for males correlates positively with bite force and endurance, but negatively with clinging and sprinting. In females, there is a similar pattern, with positive influences of iliofibularis size on bite force and endurance, and negative influence on clinging, but indeed this female muscle factor loads positively for sprint speed. In the vital organs F-matrix (Table 10), we see that residual heart size has a positive influence on male endurance and exertion, yet the opposite is true for females. Heart size also negatively influences male sprint speed, while positively influencing female sprint speed.

Further investigation of the F-matrix also yields insight into redundancies in phenotypes. While some traits have negative effects on performance, there may be other traits that can “rescue” the performance trait. Looking at the column sums, most of our performance traits have net positive values in these cells, indicating redundancy (Bergmann and McElroy 2014). Besides redundancy, trade-offs themselves can rescue a phenotype from being adversely affected by a single trait as that trait may positively influence another ecologically relevant trait. Thus, approaching functional trade-offs from a multivariate perspective gives us much more insight than investigating only two traits, as complexity and redundancy in the phenotype may mask phenotypic correlations.

In conclusion, our investigation of the multivariate morphological and performance phenotype in a common lizard species revealed distinct differences between males and females. Indeed sexual differences go beyond scaling effects, and reflect sex-specific ecological and functional contexts. Furthermore, we have uncovered these differences only because of the complexity and range of the traits measured, and these differences in traits and intertrait relationships would not have been recognized without preserving the broader phenotypic context.

Acknowledgments

Would like to thank J. Jusak for valuable comments on this manuscript. I also thank L. Birke and J. Edwards for their invaluable animal care support. All experimental procedures were approved under University of New Orleans IACUC protocol 14-005.

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Chapter 3

Conflict and the evolution of sexual dimorphism in whole-organism performance: an individual-based simulation approach

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Abstract

Intralocus sexual conflict arises when males and females experience divergent selection pressures and, due to their shared genome, the response to selection pushes one or both sexes away from their respective fitness optimum. Sexual conflict is resolved when the sexes express separate optimal phenotypes, resulting in sexual dimorphism. Whole-organism performance traits are integrated morphological and physiological phenotypes and are often subject to sex-specific selection. Selection for male performance in combat, for example, affects the evolutionary trajectories of both sexes. As performance traits rely on the additive effects of many genes necessary for development and survival, sexual dimorphism in performance may be constrained due to correlated expression between males and females. Furthermore, performance traits are typically subject both to competing selection pressures and to trade-offs with other types of performance that rely on conflicting physiological and skeletomuscular phenotypes. Finally, animals do not always perform at their maximum capacity, which can alter the effects of selection. Yet sexual conflict in performance is not given much attention. In this study, we created an individual-based simulation to test how multiple performance traits evolve in response to sex-specific selection pressures under various constraints. By imposing fixed energy budgets and performance costs as well as functional and genetic trade-offs on performance traits, and by manipulating the intersexual genetic correlation of a performance trait and sex-specific selection, we show how balancing performance demands, energy requirements, and sex-specific selective paradigms alters the direction, shape, and intensity of selection, and ultimately drives separate trajectories of performance evolution in males and females.

Introduction:

The interests of males and females during reproduction seldom align. The resulting conflict can affect the evolutionary trajectories of traits that either are involved in male-female reproductive interactions directly, or of shared traits that are expressed differently in males and females. The latter form of conflict arises because males and females of a species share a genome, such that selection on a given phenotype in one sex necessarily affects expression of that same phenotype in the other. This intralocus sexual conflict can lead to suboptimal expression of a trait or traits in one sex if selection acts strongly and oppositely on the other (Arnqvist and Rowe 2005; Parker 1979).

Because the fitness consequences of intralocus sexual conflict can be negative and significant for the sex that is displaced from its selective optimum by antagonistic selection, selection can also act to mitigate or resolve intralocus sexual conflict. Several mechanisms exist for the resolution of intralocus conflict. For example, in species with XY sex determination systems, genetic variation for secondary characters such as male ornaments or weapons might be associated with the Y chromosome such that traits are expressed only in male (e,g, Postma et al. 2011). In cases where sexual conflict is completely resolved, each sex may maintain separate fitness optima resulting in sexual dimorphism for the trait or traits in question. While the literature (and nature) is rife with examples of sexual dimorphism in morphology, there is less attention paid to sexual differences in performance traits, despite the fact that performance capacities do often differ between males and females and may experience sex-specific divergent selection. Furthermore, exaggerated morphological traits often evolve due to selection acting directly on performance capacities causing changes to the underlying morphology, and sexual dimorphism in morphology may thus be a consequence of sex-specific selection on performance as well. While mechanisms driving the resolution of sexual conflict have received empirical attention (Bonduriansky and Chenoweth 2009) the extent to which dimorphism is able to evolve within the constraints imposed by intralocus sexual conflict is poorly understood.

Whole organism performance traits such as sprinting and endurance are integrated morphological and physiological traits (Ghalambor, Walker, and Reznick, 2003), and thus the additive effects of many genes contribute to any one performance trait. As such, performance traits are often highly correlated with each other (Ghalambor, Reznick, and Walker 2004), and should also be correlated between the sexes. In a species that depends on locomotor performance to survive, both sexes must derive their performance capacities from similar architecture and physiology, and completely sex-limited performance expression is unlikely. However, performance requirements between males and females may often differ. For example, wild great reed warbler males with longer, pointed wings that confer efficient migratory flight have increased fitness due to earlier arrival at breeding grounds and consequent increased reproductive success. However females need robust wings for maneuverability in dense vegetation to feed their young and ensure survival of their own reproductive output. This difference in locomotor needs puts males and females in conflict (Tarka et al., 2014). Beyond differences in locomotor behavior, male-male combat can put demands on the male phenotype that come at a cost to females with no benefits for survival or reproduction.

While sexual conflict in performance is likely common, there are many complicating factors that hinder our understanding of how performance traits respond to selection in general, as well as how sexual differences in performance capacities can evolve (reviewed in Lailvaux 2007; see also Lailvaux et al., 2003; Kaliontzopoulou, Bandeira & Carretero, 2013). First, there are issues with studying performance in general. Performance traits do not exist or evolve within a vacuum and are typically correlated with each other (as noted above). They may be positively correlated, as when the underlying traits facilitate multiple performance capacities. They may also be negatively correlated, as in the case of functional trade-offs, wherein optimal morphological or physiological traits required for one performance traits decrease another performance trait, e.g. power output versus speed (Pasi and Carrier, 2003). Thus the evolution of performance traits may be constrained by both genetic and functional correlations between traits.

Furthermore, trait expression requires energetic investment and should be optimized by selection with respect to need, cost, and ability. Individuals must perform a careful balancing act: one needs to perform well enough to survive multiple challenges (catching prey, escaping predators, attracting mates) and still have enough energy to survive and reproduce. Performance traits differ from morphological traits in the respect that the extent of performance expression has an energetic basis, such that it is more expensive to express higher levels of performance (e.g. to run at a higher speed) than it is to express lower performance levels. Performance traits are thus dynamic, and organisms can choose to use all of their available performance capacities or only some percentage of their maximum performance in any ecological context. Given a performance trait's cost-to-benefit ratio, the optimal strategy for an individual may be to perform suboptimally to conserve energy while still performing adequately well, and yet maintaining a higher, maximal capacity in the long run, as a reservoir for meeting future challenges (either at the individual level or the population level) (Wilson & Husak, 2015; Cespedes & Lailvaux 2015 and refs. therein).

Such a strategy of employing suboptimal levels of performance trait expression can decrease the intensity of or dampen the response to selection (Cespedes and Lailvaux 2015). When individuals only use their maximum capacities, selection on these traits proceeds deterministically on traits, and the response is straightforward. When individuals vary performance, selection is acting on the range of performance capacities and the probability of surviving an encounter does not only depend on the maximum capacity, but also a given probability of employing "preferred performance".

As all of these factors contribute to a sexual population's response to selection, including sex-specific or divergent selection, on multiple performance traits, the scale of the challenge of understanding selection on the multivariate performance phenotype becomes clear. It is not feasible to expose natural populations of –for example- most vertebrate species with long lifespans to artificial selection on performance traits and measure fitness. Here, individual based simulation models offer an opportunity to understand performance evolution under different experimentally-imposed scenarios (Peck 2004) Using an individual-based simulation approach, we can create a population wherein individuals possess multiple performance traits with experimenter-imposed phenotypic, genetic, and intersexual genetic variances and covariances. We can then apply selection to create intralocus sexual conflict and measure the responses to selection, and the intensity of selection for both sexes and the population as a whole.

In this paper we simulate a sexually-reproducing population that experiences selection on three performance traits: sprint speed, endurance, and bite force. Males are subject to combat with rival males, and winning a bout depends on who has the higher bite force. As male bite force increases in response to this selection, this comes with a cost in terms of both increased energetic expenditure of biting (during feeding), and decreased sprint speed and endurance. The rationale behind this trade-off is that larger head and muscle mass required for higher bite force would necessarily affect the costs of locomotion as this increases the work done by the animal in moving that additional load (Cameron, et al. 2013). In males, the benefits of winning and thus surviving combat bouts outweigh these costs. However, if female phenotypes are highly correlated with male phenotypes, as female bite forces increase, they are incurring both energetic costs and decreased locomotor abilities without receiving any fitness benefits.

We use this simulation approach to perform multiple replicate experiments imposing the same selection pressures on simulated populations drawn from the same parameters, and measure the form and intensity of selection as well as male and female responses to selection and the evolution of sexual dimorphism and how these metrics are altered by the amount of intersexual genetic correlation of bite force, which is the trait we are exposing to sex-specific selection. By extracting data on individual traits and reproductive output, we can estimate the form and intensity of selection as well track the response to selection over multiple generations. We expect that (1) while the whole population should respond to selection on sprint speed and endurance, males will also respond to selection on bite force. (2) We expect that the intersexual genetic correlation of bite force will determine the extent to which females respond to this selection via indirect effects. (3) We expect that higher intersexual genetic correlations of bite force in conjunction with male-specific selection on bite force will cause a greater phenotypic shift in female bite force, with consequent negative effects on the two locomotor performance traits due to intertrait correlations, and that this will manifest as decreased female fitness and a shift away from their fitness optima. (4) Finally we expect that sexual dimorphism will evolve more easily when intersexual genetic correlations are low, and male bite performance may vary while their female offspring will not inherit the phenotypic shift.

Materials and methods:

Simulation parameters and procedures

The basic mechanics and flow of procedures in this simulation are outlined in Cespedes and Lailvaux 2015. We use the Java-based, programmable modeling environment NetLogo (Wilensky 1999) to build the environment and run simulations. We employ the R-extension (Thiele and Grimm 2010) to access the broader range of R’s computing ability, packages, functions, and matrix calculations. Below, we outline all procedures that are new or specific to the current simulation model.

A starting population of individual males and females is created at the beginning of each simulation. Performance traits are pulled from multivariate normal population determined by a user-defined phenotypic variance-covariance matrix (P-matrix) and population means (mvrnorm function in R package MASS, R core development team 2014). For this experiment, each simulation starts with no sexual dimorphism—male and female means are the same for all three traits. Also, we have imposed a functional trade-off between bite force and endurance and between bite force and sprint speed by assigning the negative covariances for these pairs of traits in the P-matrix. The sex ratio at the start of the simulation is exactly 0.5 (250 males, 250 females). Individuals are also all assigned a maximum lifespan of 400 ticks or steps of the simulation as well as a maximum energy budget of 100 arbitrary units of energy.

Performance demands and costs of performance

Individuals are assigned a cost for each performance value based on assigned cost functions (Table 1). Preferred performance capacity for each trait (as a percent of the individual's maximal capacity, set at 80%), and its associated cost are also calculated and stored as agent variables. For sprint speed, we used a cumulative distribution function for a normal distribution with a mean equal to that of the mean sprint speed of the starting population. The shape of this distribution is roughly linear near the mean, as the costs increase or decrease as one moves away from the mean or 'optimal' speed, and eventually plateau at extremely high or low values (Biewener 2003). Extremely high sprint speeds are thus very costly, but ensure survival in the face of predation events requiring speedy escape, while extremely low sprint speeds have negligible energetic costs, but will mean certain death when faced with a predator.

Selection against low sprint speeds is thus imposed by predators that "chase" individuals over a short distance at high speed, killing those that are too slow. These predators are distributed at a given density (Table 1) randomly throughout the environment. When an individual encounters a patch with a predator, the individual will either use its maximal or preferred performance capacity (0.5 probability of either), and if this is greater than the predator's capacity, the individual survives. The predator trait capacities are normally distributed with a mean equal to one standard deviation less than that of the starting population's, and with a standard deviation equal to the starting population's. The variation in predator speed ensures that there selection pressures are sufficiently great to eliminate individuals in the lower end of the sprint speed trait distribution, but also that selection is not so great that it causes extinction too rapidly for the population to respond.

The costs of endurance and bite force are both modeled using exponential functions. This ensures that at the low end of trait values there are low costs, but that costs increase dramatically for higher values. This mimics a physiological upper limit on these performance traits. Endurance capacity is realized in the simulation as (1) the maximum distance one can travel to acquire resources or (2) distance traveled to escape a predator. Across the range of the starting population's endurance values, energetic costs of endurance are tolerable, but costs increase dramatically when increasing endurance above this range, becoming prohibitive, as endurance is constrained by physiology and aerobic capacity (Bennett 1982; Biewener 2003).

Global Parameter	Value(s)	Description
Preferred performance	80	Percent of maximal sprint capacity an individual can use in a simulation
Genetic variances Genetic covariances	0.5 0	Diagonals of the G-matrix, additive genetic variance of each trait Off-diagonals of the G-matrix, no covariances between traits
Bm_1f_1, Bm_2f_2 Bm_3f_3	1 {0, 0.1, 0.5, 1}	Intersexual genetic correlations of sprint and bite force, respectively
Trait means	100	Population means for all three traits
Phenotypic variances (P_{ii}) P_{12} P_{13} P_{23}	50 0 -20 -20	Trait variances for all traits Phenotypic covariances between: Sprint and endurance Sprint and bite force Endurance and bite force
Size of environment	40,401 cells	
Maximum Lifespan	400 (steps)	
Initial lizard population density	~0.012	% of area (500 individuals)
Sprint predator density	0.05	% of available area
Endurance predator density	0.01	% of available area
Rival male, bite force	0.05	% of available area
Resource density	50% of area	
Resource quality	50	Units of energy added to an individual's energy budget when a resource is consumed
Cost of Reproduction	2	Amount of energy deducted per offspring
Threshold for 'surplus energy'	80	Minimum amount of energy an individual can have in order to reproduce during a reproductive event
Energy budget	100	Maximum energy an individual can have at one time
Initial energy	80	Amount of energy assigned to an individual at birth defined as a constant or function of parental investment
Sex ratio	0.5	Determined by probability of being assigned female
Probability of using preferred trait	0.5	Governs agent's decision to use preferred versus maximal capacity
Search Radius	10% of endurance	Translates expressed endurance capacity into a distance that defines the radius of the cone-shaped foraging area.
Cost of endurance		$C_{endurance} = 2^{(0.45 * \text{search radius})}$
Cost of Bite		$C_{bite} = 2^{(0.05 * \text{bite})}$
Cost of sprint		$C_{sprint} = P(X < sprint_{\text{agent}}) * 100$ Where X is a random variable drawn from a normal distribution with mean and SD parameters

Table 1: Simulation Parameters.

We used a similar curve for bite force, not because it reflects the true energetic costs of bite force per se, but that it accounts for the high energetic costs of combat relative to the low cost of using bite performance when eating prey, for example. As with endurance, the exponential cost curve is also chosen to impose an upper limit to how much the trait can ultimately increase in response to selection.

Similar to sprint speed, predators are distributed randomly at a given density (0.01 %, Table 1) that, if encountered, chase an individual for a certain distance. These endurance predators are assigned an endurance capacity pulled from distribution that is parameterized the same as sprint speed. Again, individuals may employ either their maximal or preferred endurance capacity (0.5 probability of either). If their performance in this scenario is greater than that of the predator, they survive and incur the associated costs. If not, they die. Variable endurance in foraging, however, manifests not as 80% preferred performance, but rather as variable distance traveled to a nearby resource. An individual searches within their maximum range, and if any resources are present in this area, the individual moves to one patch with food at random, incurring the cost associated with the distance traveled. If no resource is present, it is as if the individual searched the entire search area, thus incurring the maximum cost with no resource reward. So during foraging, how far they must travel for food is random, but bounded by their maximum endurance capacity.

Bite force costs also follow an exponential curve. Again, bite force costs near the mean of the starting population are tolerable, but as one increases beyond this range, costs become prohibitive. Individuals rely on bite force in two ways: (1) during eating, both males and females use 50% of maximal bite force and incur the associated cost, which is small), and (2) during male-male combat.

In the simulation, male agents are not actually fighting each other; rather they encounter bite challenges using a similar procedure as predators. “Rival males” are distributed randomly at a given density throughout the environment (Table 1), and they are assigned bite force capacities drawn from the same normal distribution as the starting population. In not having actual males fight each other, we remove any fluctuating density effects that would occur. If a male arrives at a patch that has a rival male present, the male can use either his maximum or preferred bite capacity (0.5 probability of either), which must be higher than the rival’s to survive the event. While individual males may vary bite force, their “rival males” are always using their maximum capacity. However, the traits of all types of predators vary from the high end to the low end of the actual male agent trait distributions (at the start of the population), and therefore there exist individuals whose preferred performance traits are higher than the maximal capacities of other individuals.

Given these selection pressures, we expect sprint speed to increase due to positive selection from predators, endurance to remain relatively stable, as selection against low endurance from predators is low, while costs of high endurance are high, and we expect bite force in males to increase. Bite force in females should either decrease in response to negative correlation with sprint speeds, which are under positive selection, or bite force may increase due to correlated evolution with males, despite the increased costs.

Mating and Reproduction

Every forty ticks or steps of the simulation, individuals mate and reproduce. An individual must have sufficient energy to mate and reproduce (at least 80% of their maximum energy budget). Females are randomly paired with a male that also has sufficient energy (≥ 80%), and the female's excess energy reserve is translated into the clutch size. Both the male and female incur a small cost per offspring.

Offspring traits are calculated using a quantitative genetics approach. For this we employ the G, P, and B matrices defined before the start of the simulation and the three trait values for both parents. The G-matrix is the matrix of additive genetic variances and covariances between traits (Lande 1980, Falconer 1960), while the P-matrix is the phenotypic variance-covariance matrix . For this simulation model we have constrained the G- and P- matrices to be the same for both sexes (Gm = Gf, Pm = Pf). The B-matrix is the matrix of covariances between the additive genetic effects of traits when expressed in the opposite sex (Lande 1980). Using the "Lande equation" in Lande (1980):

$$\begin{pmatrix} \Delta\overline{\boxed{?}} \\ \Delta\overline{\boxed{?}} \end{pmatrix} = \frac{1}{2}\begin{pmatrix} \boxed{?}_{\boxed{?}} & \boxed{?} \\ \boxed{?}^{\boxed{?}} & \boxed{?}_{\boxed{?}} \end{pmatrix}\begin{pmatrix} \boxed{?}_{\boxed{?}}{}^{-1}\boxed{?}_{\boxed{?}} \\ \boxed{?}_{\boxed{?}}{}^{-1}\boxed{?}_{\boxed{?}} \end{pmatrix}$$

where $\boxed{?}_{\boxed{?}}$ is the matrix of differences of the father's trait values and the mean trait values of all males in the population at the time of reproduction, and $\boxed{?}_{\boxed{?}}$ is the same matrix but for the difference between the mother's phenotype and that of the population of females. The resulting vectors $\Delta\overline{\boxed{?}}$ and $\Delta\overline{\boxed{?}}$ determine the shift in male offspring and female offspring means, respectively. Thus, male offspring traits are randomly drawn from multivariate normal population, with mean trait values centered on the new means for males with variances and covariances determined by the P-matrix, and females are drawn from a multivariate distribution using the new vector of female trait means. This allows male and female offspring to resemble their parents, and allows the population to respond to selection on many traits at once.

For this simulation, we constrained all off-diagonals of B to zero (no correlation between, for example, the value of male sprint speed and the expression of female endurance). Instead we constrain sprint speed and endurance to have intersexual genetic covariances of one. The intersexual genetic covariance of bite force (Bm_3f_3), which is under sex-specific selection, has one of four values for our four treatments {0, 0.1, 0.5, 1}.

Analyses of population dynamics

At the end of every simulation, all individuals born during the simulation run are recorded along with their phenotypic values, total number of offspring, age at death (or age at the end of the simulation), cause of death or whether they were alive when the simulation ended, as well as a list of all mates and offspring. With this output, for each simulation, we extracted the population size at time of reproduction (before reproduction) and male and female trait means and variances for each generation (born every 40 ticks/ steps). We also calculate the univariate selection differentials $\boxed{?}_{\boxed{?}}$ (change in trait means after selection, but before reproduction) for each trait, standardized by the trait variance (Lande and Arnold 1983). Using the trait means for males and females, we calculated sexual dimorphism for each trait as the ratio of mean male values to mean female values. All output processing and statistics were performed in R version 3.1.2 (R core team, 2014) and RStudio Version 1.0.136.

To determine changes in the form and intensity of selection, we performed a formal selection analysis on all traits and fitness for both sexes using pooled data from all simulations within each intersexual genetic covariance of bite force treatment. Using separate multiple regressions (Lande and Arnold 1983), we first estimated the vector of linear selection gradients (β) and then the matrix of quadratic and correlational selection gradients (γ). We doubled the coefficients for the quadratic terms from the regressions to get the correct gradients (Hall, Bussière, Hunt, et al, 2008; Stinchcombe et al., 2008). As our fitness data were overdispersed, we used absolute fitness rather than relative fitness, and fit generalized linear models using a quasipoisson error distribution reference saying this is ok here. All regressions were performed using standardized trait data, scaling each variable to a mean of zero and standard deviation of one (Lande & Arnold 1983).

To investigate nonlinear selection, we performed a canonical analysis of the γ matrices (Phillips and Arnold 1989; Blows and Brooks 2003; Hall, Bussière, Hunt, et al, 2008), yielding new eigenvectors that allow for clarification of nonlinear selection by having rotated the data along the canonical axes to essentially remove the correlational selection terms, which can confound interpretation of fitness surfaces (Blows and Brooks 2003; Walsh unpublished, Phillips and Arnold 1989). Using these new eigenvectors (m_i), we performed another regression, again using a generalized linear model with quasipoisson errors and absolute fitness, and included all linear (m_i) and quadratic (m_i^2) terms. We compare the estimates of all six terms and their significance in the full model across the 4 treatments for each sex.

To estimate the total selection intensity (*V)*, we calculated the expected fitness for each individual from the full regression model including all linear, quadratic, and correlational terms (before canonical analysis). *V* is then calculated as the squared coefficient of variation of the expected fitness (Schluter 1988).

In order to visualize fitness surfaces, we picked the two major axes (out of three) as indicated by their eigenvalues (the two axes with eigenvalues of greatest magnitude), and created a three-dimensional fitness surface. We used thin-plate splines estimated by the Tps function of the fields package in R (ver. 3.1.2 R Development Core Team, 2014). As our pooled datasets were too large to estimate these splines (required matrix calculations yield integers beyond the capacity of R), we instead used smaller subsets of the data and fit multiple surfaces, and representative plots are presented for each sex and each treatment.

Results

After performing a number of parameter sweeps to check the behavior of the simulation model and debug, we chose constant parameters for environmental variables, as well as G and P (Table 1). We ultimately ran at least 136 simulations per treatment (Bm_3f_3 = 0, n = 138; Bm_3f_3= .1, n = 136; Bm_3f_3= 0.5, n = 137; Bm_3f_3= 1, n= 137), with all other variables held constant. In all treatments, approximately one third of all simulations resulted in a population that expanded or remained stable, while two thirds went extinct. In terms of population trait means and sexual dimorphism over generations, there were no differences in how these fluctuated over time, but as expected, bite force increased in males relative to females (Figure 1).

Selection Analyses

For both sexes in all treatments, there was significant nonlinear selection, and the model containing all linear (⍰), quadratic, and correlational terms (γ) performed better than the model with only linear terms (Table 2). We present the estimates from the full models for each sex in each treatment in Table 3. For each sex, the treatment had little effect on the estimated coefficients with some notable exceptions involving the nonlinear terms. In all treatments, males experienced significant positive directional selection on bite force only. Females experienced significant positive directional selection on all three traits.

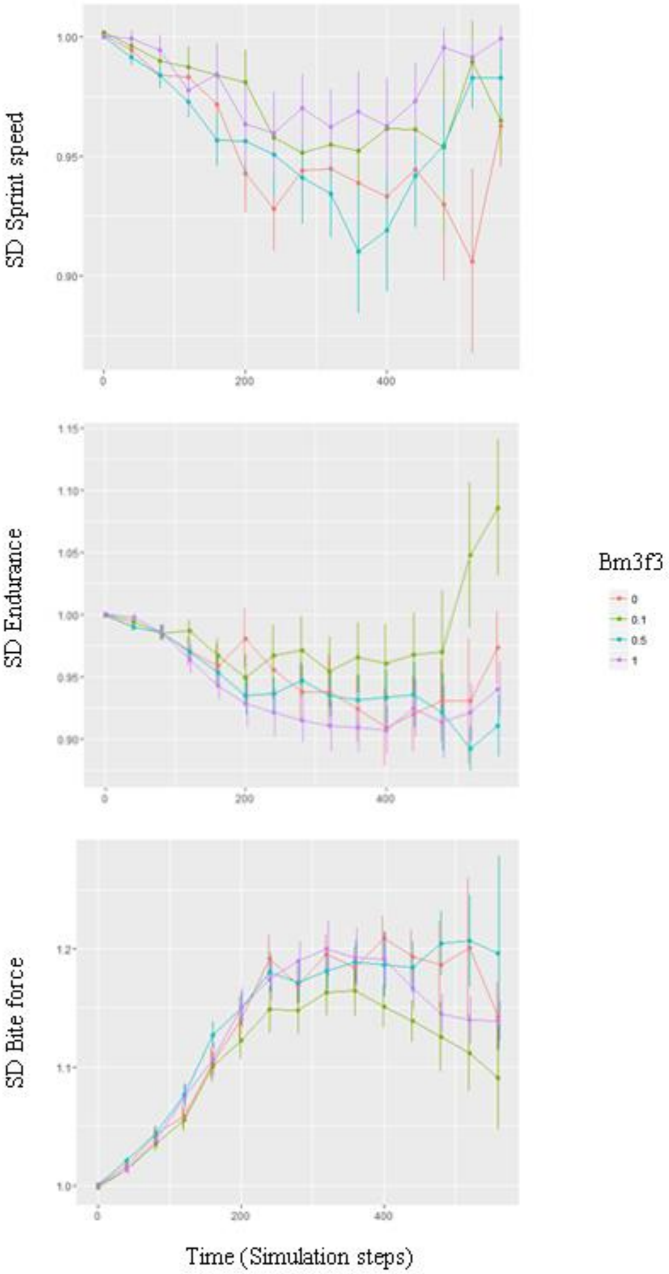

Figure 1. Mean sexual dimorphism in three performance traits over time, colored by treatment. Values greater than 1 indicate mean male traits are higher than females. Bite forces for males increase in all treatments, while sprint speed and endurance, which are both negatively correlated with bite force, typically increase in females relative to males. Error bars represent ± standard error of the mean.

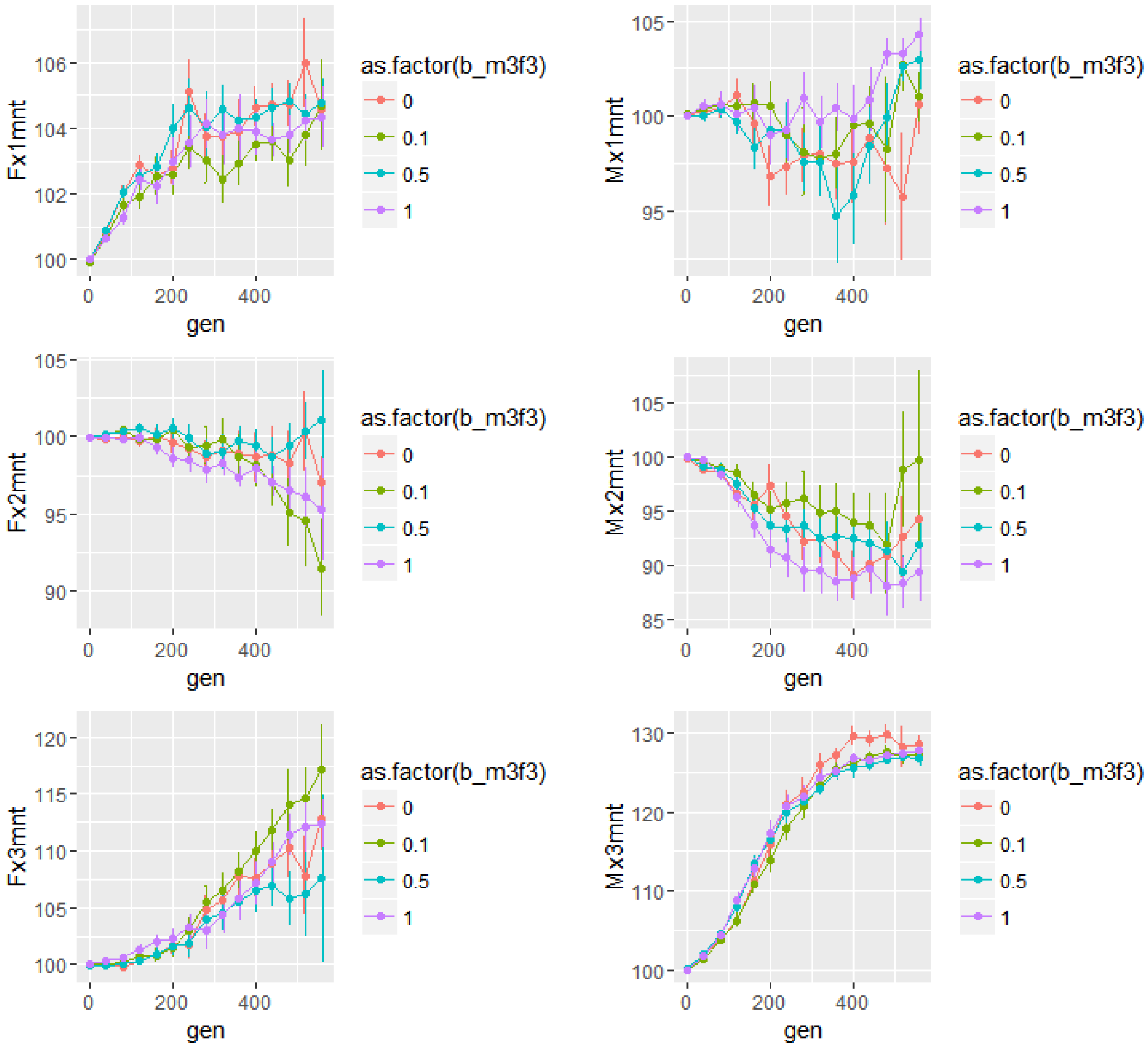

Figure 2. Changes in trait means over time. While sexual dimorphism maybe evolving, both sexes are responding to selection in the same direction across all treatments. “Fx” refers to female traits, while “Mx” refers to male traits. The term “x1” denotes sprint speed, “x2” denotes endurance, and “x3” denotes bite force.

Treatment	Sex	Deviance (df = 6)	p-value
$Bm_3f_3 = 0$	M	30142	< 2.2e-16 ***
	F	16415	< 2.2e-16 ***
$Bm_3f_3 = 0.1$	M	26976	< 2.2e-16 ***
	F	13039	< 2.2e-16 ***
$Bm_3f_3 = 0.5$	M	30097	< 2.2e-16 ***
	F	16553	< 2.2e-16 ***
$Bm_3f_3 = 1$	M	33073	< 2.2e-16 ***
	F	14001	< 2.2e-16 ***

Table 2. Log-likelihood ratio test results comparing selection model with only linear terms versus full model with all linear, quadratic, and correlational terms. In all cases, there was significant nonlinear selection and the full model was selected.

	Males					Females			
$Bm_3f_3=$	0	0.1	0.5	1		0	0.1	0.5	1
Intercept	0.800	0.801	0.803	0.819		0.686	0.647	0.670	0.691
z1 (Sprint)	0.004	0.014	0.003	-0.009		0.094	0.112	0.084	0.086
z2 (Endurance)	.007	-0.003	-0.001	-0.007		0.045	0.043	0.037	0.031
z3 (Bite)	0.168	0.214	0.182	0.181		0.135	0.122	0.100	0.130
ɣ11	-0.074	-0.094	-0.091	-0.099		-0.148	-0.154	-0.156	-0.144
ɣ22	-0.008	-0.014	-0.003	-0.007		-0.004	-0.003	-0.004	-0.0002
ɣ33	-0.225	-0.240	-0.218	-0.235		-0.033	-0.009	-0.006	-0.032
ɣ12	-0.018	-0.026	-0.017	-0.011		-0.015	-0.030	-0.024	0.003
ɣ13	-0.016	-0.037	-0.004	-0.013		-0.101	-0.099	-0.092	-0.097
ɣ23	-0.010	-0.020	0.001	-0.009		-0.050	-0.034	-0.042	-0.019

Table 3. Coefficients from full models of selection with all directional, quadratic and correlational terms for each of the three performance traits. Separate regressions were performed for each sex in each treatment. Bold indicates significance ($p < 0.05$). (Bm_3f_3 is the intersexual genetic correlation for bite)

For males in all treatments, sprint and bite capacities experience apparent convex selection. Significant convex selection on male endurance is only estimated for the Bm_3f_3= 0.1 treatment. For females, there is significant convex selection on sprint speed across all treatments. In no treatment was there convex selection on female endurance. However, for bite force, there is significant convex selection in the “extreme treatments” (Bm_3f_3= 0, 1), and not when Bm_3f_3= 0.1 and 0.5, or the “intermediate” intersexual genetic correlation treatments.

For males and females, there is always selection for a negative correlation between sprint speed and endurance force except for when Bm_3f_3= 1, in which case the term is not significant for either sex. A negative correlation between male sprint and bite force is only significant when Bm_3f_3= 0.1. There is no significant selection on the correlation between male bite force and endurance in any treatment. For females, there is selection for negative correlations between all pairs of traits across all treatments with one exception. In the Bm_3f_3= 1 treatment, the correlation term between sprint and bite is not significant.

Canonical analyses of the γ matrices helped clarify these differences. Across treatments, the new eigenvectors (m_i) for each sex were similar. However, the eigenvalues (λ_i), whose magnitudes indicate the importance of each new axis, differed for females across the treatments. Again, we see differences between extreme and intermediate values of Bm_3f_3 (Table 4).

The estimates of selection coefficients for the *m* eigenvectors (Table 5) reveals subtle differences in selection across treatments, as well as the differences in selection on males and females. It is important to note that opposite signs for linear selection coefficients do not necessarily indicated dramatic reversals in selection. Inspection of the signs of the eigenvectors themselves is necessary for interpretation, as these are arbitrary. Unless otherwise noted, for most eigenvectors the magnitude and relative directions of each trait with these eigenvectors are similar across treatments, while the entire axis may be flipped. Thus, a change in sign of the coefficient is to be expected when the eigenvector itself has the opposite sign.

	Males					Females				
Treatment	m_i	λ_i	SPR	END	BIT	m_i	λ_i	SPR	END	BIT
0	m_1	-0.013	0.129	-0.991	0.018	m_1	0.027	-0.148	-0.796	0.587
	m_2	-0.150	0.990	0.128	-0.058	m_2	-0.059	0.345	-0.597	-0.724
	m_3	-0.450	0.055	0.026	0.998	m_3	-0.337	0.927	0.096	0.363
0.1	m_1	-0.023	0.147	-0.987	0.031	m_1	0.031	-0.177	-0.594	0.785
	m_2	-0.187	0.981	0.142	-0.132	m_2	-0.019	0.268	-0.796	-0.542
	m_3	-0.487	-0.126	-0.050	-0.991	m_3	-0.343	0.947	0.115	0.300
0.5	m_1	-0.005	0.098	-0.995	-0.002	m_1	0.039	-0.162	-0.610	0.776
	m_2	-0.183	0.995	0.098	-0.015	m_2	-0.029	0.252	-0.786	-0.565
	m_3	-0.436	0.015	-0.001	1.000	m_3	-0.342	0.954	0.104	0.281
1	m_1	-0.014	0.059	-0.998	0.019	m_1	0.010	0.153	0.885	-0.440
	m_2	-0.198	0.997	0.058	-0.021	m_2	-0.037	-0.314	0.466	0.827
	m_3	-0.470	-0.049	-0.050	-0.999	m_3	-0.325	0.937	0.011	0.349

Table 4. The M matrices of the eigenvectors from the canonical analyses of γ. The first column is the eigenvalue (λ_i) of each eigenvector (m_i). The eigenvectors describe how each trait contributes to the new rotated axis. Traits are abbreviated (SPR = Sprint speed; END = Endurance; BIT = Bite force). Eigenvectors with the two largest eigenvalues are in bold. The traits with the largest magnitude, or the two largest magnitudes of opposite signs, are underlined to aid interpretation of selection estimates on these axes.

	Males					Females			
Bm_3f_3 treatment	0	0.1	0.5	1		0	0.1	0.5	1
Intercept	0.643	0.801	0.803	0.819		0.686	0.647	0.670	0.691
m_1	-0.024	0.011 ns	3.99×10^{-4} ns	0.010 ns		0.029	0.051	0.041	-0.017
m_2	0.076	-0.15 ns	1.42×10^{-4} ns	-0.019		-0.091	-0.070	-0.064	0.094
m_3	0.118	-0.123	0.182	-0.181		0.141	0.148	0.112	0.126
m_1^2	0.009	-0.011	-0.002 ns	-0.007 ns		0.013	0.015	0.020	0.005
m_2^2	-0.102	-0.094	-0.092	-0.099		-0.029	-0.010 ns	-0.015	-0.018
m_3^2	0.017	-0.243	-0.218	-0.235		-0.168	-0.172	-0.171	-0.163

Table 5. Coefficients from second order polynomial with new eigenvectors, m_i . Separate regressions were performed for each sex in each treatment. Bold indicates significance ($p < 0.05$). Note that sign changes across treatments do not necessarily signal a reversal in the direction of selection, as the signs of the eigenvectors may be switched.

Form of selection on males

As expected, in males, the largest linear term coefficients indicate selection for high bite force in all treatments (*m_3*). Interestingly, there is clear convex selection, or selection against extremely high or low bite forces, in all treatments except for when $Bm_3f_3 = 0$. In this treatment there is a small, positive estimate, indicating weak concave selection. There is much greater variation across treatments in the other linear terms. For the m_1 term, there is a small but significant coefficient in the $Bm_3f_3 = 0$ treatment, indicating selection for high endurance. In all treatments, the coefficients for nonlinear selection on this axis are very small or not significant.

The *m2* term on the other hand shows interesting variation across treatments. While there is no significant selection on this term in either of the intermediate treatments, the terms are significant in the extreme treatments, but have opposite signs. This indicates that for $Bm_3f_3 = 0$, there is positive selection for sprint speed, while in the $Bm_3f_3 = 1$ treatment, there was weak selection against high sprint speeds. In all treatments, there was significant convex selection on sprint speeds.

Form of selection on females

In females, across all treatments, the largest coefficients relate to the eigenvector associated with increasing sprint speed (m_3 for females). Females experience the strongest selection for higher sprint speeds, with significant convex selection indicating selection against the most extreme values for sprint speed (high or low).

The m_2 eigenvector itself differed between treatments. In the extreme ($Bm_3f_3 = 0, 1$) treatments, the trait with the largest contribution to the axis is bite force, with endurance the second largest contributor. The opposite is true for the intermediate treatments ($Bm_3f_3 = 0.1, 0.5$), where endurance has the largest magnitude and bite force is second. In both, however, these two traits load in the same direction, indicating correlated selection. The selection estimates for this term indicate selection for high bite force and endurance in all treatments, although higher endurance is the more important trait on this axis in the intermediate treatments. We also see higher coefficients in the extreme treatments relative to the intermediate treatments. Again, we see convex selection, or selection against extreme values of endurance and bite force in females.

Finally the m_1 term reveals significant selection for high bite force and against high endurance values. The coefficients for this term are twice as large in the intermediate treatments. While bite force and endurance load in the same direction on m_2, the opposite is true of m_1. Interestingly, the coefficients for the quadratic term all indicate concave selection on m_1. Thus, high bite force or high endurance contribute to fitness, while mean values for both do not (holding sprint speed constant).

Visualizing fitness surfaces

Representative fitness surfaces drawn from subsets of the pooled data of all individuals from all simulations within each treatment are shown in Figure 3. In males, high fitness always correlates with higher bite forces (positive values on the y-axis for Bm_3f_3= 0 and 0.5; negative values on the y-axis for Bm_3f_3 = 0.1 and 1). In the Bm_3f_3 = 0 treatment, the surfaces shows increasing fitness for high bite force, and intermediate values for sprint, indicating the strongest selection is on bite force, but selection against extremely low or high sprint speeds. For higher levels of intersexual correlations of bite force, we see similarly high fitness for high bite forces, with the high fitness area extending into areas of lower bite force and higher sprint speeds. For the Bm_3f_3 = 1 treatment, we see that at mean bite force values there is a wide ridge shape across intermediate to high sprint speeds, and second peak in an area of high bite force. The effects of convex selection on sprint and bite are also apparent as low fitness areas appear away from trait means, causing a ridge shape along the axis of of increasing bite force and sprint speed.

In the female fitness surfaces, we see very clear ridge-shaped functions. Positive values on the y-axis for all surfaces correspond to increasing sprint speeds above the mean. When Bm_3f_3 = 1, the peak is more constrained to high high bite force (on the x-axis) and intermediate-to-high sprint speeds. For the intermediate treatments, the x-axis corresponds to higher bite force at the positive end and higher endurance at lower values. The ridge corresponds to convex selection on sprint speed, showing lower fitness for extremely high or low values of sprint speeds. In the Bm_3f_3 = 0 treatment, we again see a very clear peak spanning intermediate-to-high sprint speeds as well as high bite force areas, with a similar ridge extending out towards decreasing bite forces.

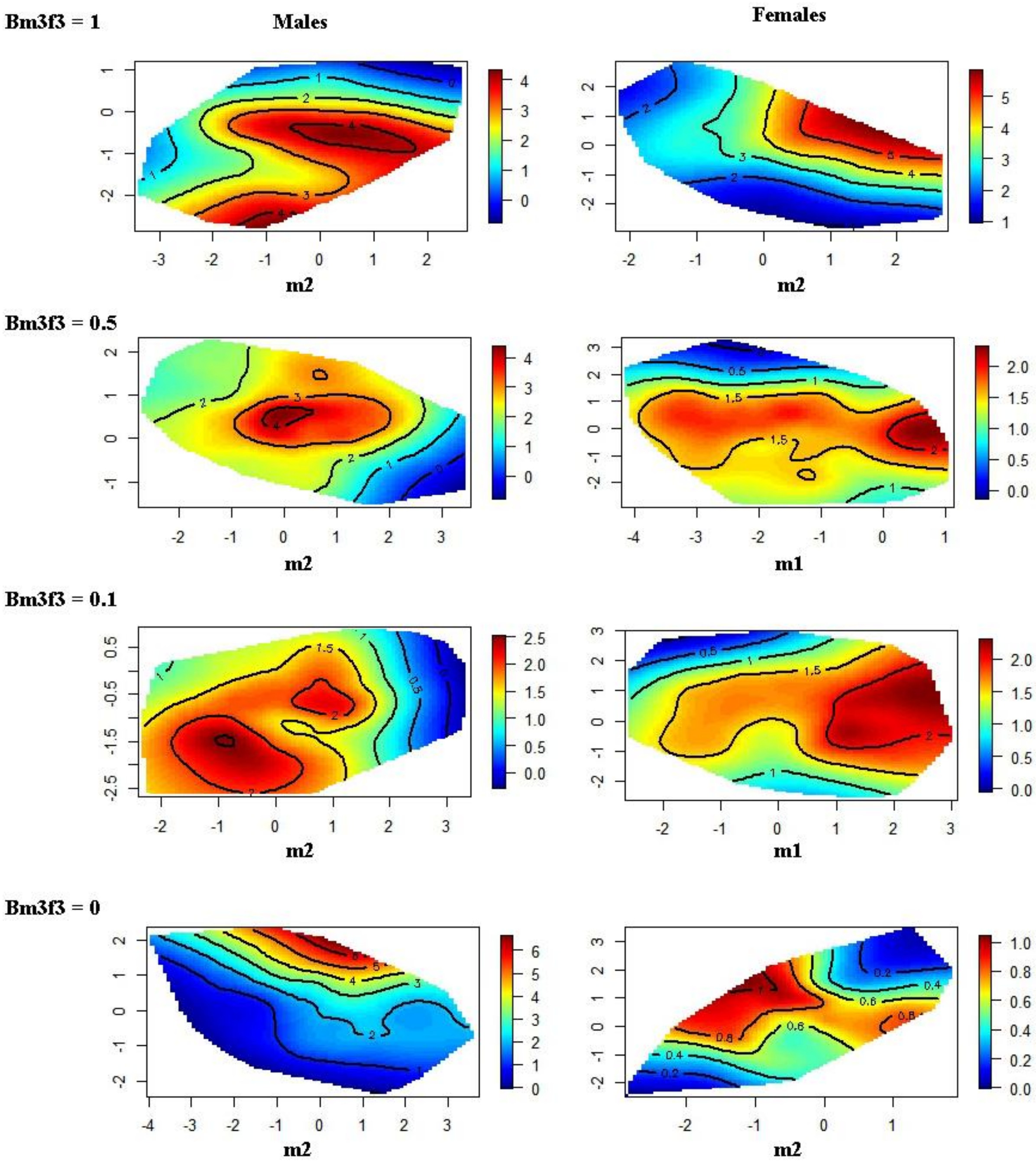

Figure 3. Fitness surfaces for the major axes from each canonical analysis of selection. All y-axes are m_3 from the respective sex and treatment. Warmer colors indicate higher fitness, as depicted in the color scales to the right of each graph. Fitness is measured as total offspring.

Total intensity of selection

Table 6 shows that while males do experience higher selection intensity than females, there are no differences across treatments in the total intensity of selection. This is to be expected, however, as there was no difference in the amount of selection imposed on individuals between treatments, only the correlation of bite force expression between sexes was altered.

Bm3f3 Treatment	V_m	V_f
0	0.08718518	0.03808416
0.1	0.1054277	0.03896186
0.5	0.09390939	0.03596051
1	0.1002586	0.03688448

Table 6. Total intensity of selection V for both sexes in each treatment.

Discussion:

Our simulation model demonstrated the expected response to imposed selection on (1) sprint and endurance in both sexes and 2. on male bite force. Mean sprint speeds for both sexes increased relative to the start of the simulation in all surviving populations (Figure 2), and selection on male bite force increased mean bite force capacities in both sexes, with higher mean bite forces for males. Furthermore, higher bite forces correlated with higher male fitness in all treatments.

However, the intersexual genetic correlation of bite force did not significantly alter the dynamics of the response to selection in females, and female fitness tended to correlate with higher bite force as well. Across all treatments, populations went extinct more often than not, and female fitness always tended to correlate with high bite force. If bite force is not contributing directly to female survival, and females only experience increased energetic costs and lower sprint and endurance speeds, then the benefits of high bite forces in females must be stemming from the indirect genetic benefits of the selection for high bite force on males (Kotiaho and Puurtinen 2007).

First, the intertrait correlations—the negative phenotypic correlations between sprint speed and bite force, and between endurance and bite force—combined with the high intersexual correlations of these two traits cause the intersexual genetic correlation of bite force to be nearly redundant. If bite force is free to vary, but is negatively correlated with another trait under selection such as sprint speed, individuals that survive will be contributing to lower sprint speeds in the next generation. Since sprint speed is constrained between both sexes, males with higher bite force and lower sprint speeds will pass those lower sprint speeds onto both male and female offspring.

A second possibility that would explain these results is that female inheritance of higher bite force from their fathers contributes to the stability of the male response to selection. In other words, when females share the additive genetic variance of a trait under selection only in males, they too pass this on to their sons, which serves to further push the mean male phenotype away from a lower fitness area, accelerating the response to selection. More importantly, this contribution to male fitness probably helps to account for female fitness being correlated with higher bite forces in our simulation runs. If the male population fails to respond to selection, or if not enough males are surviving the intense selection pressure, the decreased density of males decreases the probability of a female finding a mate and reproducing, thus lowering her reproductive output. In this case, shared genetic correlations in performance between males and females could be a buffer against “evolutionary suicide” (Kokko and Brooks 2003), whereby sexual selection like sexual selection, and the associated costs compromise the survival of individuals to the point of deterministic extinction (Kokko & Brooks, 2003; Matsuda & Adams, 1994)

Despite differences in amount of intersexual genetic correlation of bite force, sexual dimorphism always evolves. While bite force becomes male-biased as males increase to meet selection demands, sprint speed becomes female-biased (Figure 1). However, in both traits, population means are both increasing (Figure 2), but each sex increases one more relative to the other. Similarly, endurance traits decrease across the whole population, due to the combination of lower selection pressures for high endurance; high costs of for higher endurance; and the negative relationship between endurance and bite force. While both sprint speed and bite force are negatively correlated with bite force, selection for higher sprint speeds is strong enough to maintain higher sprint speeds in the population.

There were also differences in the form of selection across treatments. First, there was only positive selection for male sprint speed when there was no intersexual correlation on bite force, and negative selection on high sprint speeds when the intersexual genetic correlation of bite force is one. Since high sprint speeds correlate with lower bite force, it makes sense that when males are more free to vary relative to females, or are less constrained, then bite forces are increasing rapidly enough that higher sprint speeds are manageable. In the opposite case, when males are completely constrained, selection against sprint speed (a contributor to lower bite force) may result.

Also notable is a difference in the nonlinear selection on male bite force across treatments. In all cases where there is some intersexual genetic correlation on bite force, there is convex selection, or decreased fitness for extreme values of male bite force. However, when there is no intersexual genetic correlation for bite force, there is concave selection, indicating higher fitness for more extreme values of bite force.

The fitness surfaces (Figure 3) reveal important differences between selection on males and females. While females fitness forms a ridge, male selection was more often multiple peaks. This indicates that the female performance phenotype can move along an axis while not decreasing fitness. Males however can descend into a valley of lower fitness if they move away from one of two peaks corresponding to either very high bite force, or moderate bite force and moderately high sprint speed. Interestingly, for males and females there are both scenarios where there appears to be a single fitness peak, and these occur in opposite treatments. When Bm_3f_3 is 1, female fitness is highest in a single area of moderate sprint and high bite force, and a similar single peak for males exists when Bm_3f_3 is zero. Thus, the intersexual correlation is affecting the form of selection, and high or low values for this correlation place higher constraints on what constitutes a “fit” individual.

From these data, we show that intersexual correlation alone is not enough to drastically alter the response to selection, and that the cumulative effects of inter-trait correlations, the selection pressures on these traits, and the intersexual correlations among other traits affect the response of the multivariate performance phenotypes to selection in both sexes. We also found differences in the form and intensity of selection across our intersexual genetic correlation of bite force treatments, demonstrating that the correlation between sexes does affect how selection proceeds on performance traits, albeit in counter-intuitive and surprising ways. This simulation framework can be extended and modified for use in generating hypotheses or predictions for natural or theoretical populations.

Acknowledgments

I would like to thank J. Husak, N. Anthony, and J. G. Howard for valuable input on this manuscript.

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Appendix:
Chapter 1 Simulation Code and Results

Supplementary File S1: Chapter 1 Simulation Code

The following code is Netlogo and R code for the simulations run in Chapter 1. For the Netlogo file, including graphical user interface, contact the author. Two or more semicolons and hashes at the beginning of a line indicate comments to the user that are not read by the program.

```
;; Simulation Performance Evolution: NetLogo Code
;; Author: Ann Cespedes
;; email: acespede@uno.edu
;;
;; Supplementary material S1 to "An individual-based simulation approach to the evolution of locomotor performance"
;; Integrative and Comparative Biology


;; Below is the code to paste into the NetLogo Code Tab, and will perform the simulations as presented in the manuscript.
;; Changing parameters may require changing the R scripts (below) for processing output!
;;
;; You will need to install the R-extension create buttons and sliders!
;; Get started with NetLogo here: http://ccl.northwestern.edu/netlogo/docs/
;;
;; You must also specify the path to the directory you want your output to go to.

extensions [r]
globals [
  X1 X2
  traitmax traitmin searchmax searchmin
  lifespan
  clutch-size
  mp
  filename]

breed [females female]  ;; turtles differentiate into sexes
breed [males male]

directed-link-breed [mate-links mate-link]
directed-link-breed [parent-links parent-link]

turtles-own [
  perf1
  perf2
  srchradius

  varyX1       ;; means = 100 for both traits
  varyX2
  vary-srchradius

  cost-X1
  search-cost

  cost-varyX1
  cost-varyX2
  vary-search-cost

  eaten
  hungry

  energy

  offspring
  age
  mate

  cause
  birth
```

```
  death
]

patches-own [
  pperf1
  pperf2

]

to setup
  clear-all
  reset-ticks

  set lifespan 400


  crt (population)
  R-setup
  scale-endurance-search
  set-turtle-traits
  setup-df

  setup-patches
  set-filename

  let file (word "c:/Path2Folder/" filename "links.csv")
  file-open file
  file-print (word "tick,type,end1,end2")

  ask turtles [srchradius-check]

end

to set-filename
  set filename date-and-time
  set filename remove ":" filename
  set filename remove "-" filename
  set filename remove " " filename
  set filename remove "." filename
  set filename (word  filename ".txt" )


end

to go
  ;carefully [
  ask turtles [
    energy-check
    forage
  ]

  if npred1 > 0 [ask turtles [check4pred1]]
  if npred2 > 0 [ask turtles [check4pred2]]

  ;; make switch between selfing and sexual reproduction
  if (ticks > 1) [if ticks mod 40 = 0 [
    ask females [
      if energy >= 80 [ pairup ]
    ]
  ]
  ]

  write-to-file
```

```
 ask turtles [
   set mate nobody
   set age (age + 1)
 ]

  ask patches [
   set pcolor black
   if random 1000 < resource-density [set pcolor blue]
 ]



 if (ticks > 1) and ((ticks mod 50) = 0) [ask turtles [lifespan-check]]

 if (count turtles <= 1) [ end-sim
   stop]
 if (count turtles >= 2500) [ end-sim
   stop ]
 if (ticks = 1000) [end-sim
   stop]
 if (min [perf1] of turtles > max [pperf1] of patches) [show "minimum X1 for lizards is greater than highest predator requirement"]

 tick
 ;; LOG STUFF
 ;;ask lizards with [age = 1] [show (word "offspring at " ticks " x1 " perf1 " x2 " perf2)]
 ;;export-output (word "Path2Folder" ticks "_" random-float 1.0 ".csv")

 ;]
 ;[print error-message
 ;end-sim]


end


to R-setup
 r:clear
 ;; comment out unused path, uncomment path to this computer's R packages

 r:eval ".libPaths(c('C:/Path2Folder'))"      ;; path to folder

 r:eval "library(mvtnorm)"  ;; load packages
 r:eval "library(MASS)"
 r:eval "library(nlme)"
 r:eval "library(matrixcalc)"
 r:eval "library(psych)"
 r:eval "library(truncnorm)"
 r:eval "setwd( 'Path2Folder' )"
;; read user input into R (mean and variance for trait 1 (x1); mean and variance for trait 2 (x2))
 r:put "muX1" 100
 r:put "muX2" 100
 r:put "varX1" varX1
 r:put "varX2" varX2
 r:put "covX1X2" covX1-X2
 r:put "hsq" h-squared

;; standard deviations for each trait
;; for defining distributions from which to sample offspring traits
 r:eval "sdX1<- sqrt(varX1)"
 r:eval "sdX2<- sqrt(varX2)"

;; for defining trait regressions (midparent-offspring for X1, X2~X1)
 r:put "intX1" 100 - h-squared * 100
 r:put "intX2" 100 - (covX1-X2 / varX1) * 100
 r:put "slopeX2" covX1-X2 / varX1
```

```
;; get normally distributed trait values for X1 for the starting population
;; no more matrix algebra

  r:put "start" population
  r:eval "startPopX1 <- rnorm(start, mean = muX1, sd = sdX1)"

  set X1 r:get "startPopX1"           ;; make netlogo list of X1
end

to scale-endurance-search
  set searchmax 20
  set searchmin 0
  set traitmax (100 + (3 * sqrt varX2))
  set traitmin (100 - (3 * sqrt varX2))

  ;; appears later in:
  ;; " set srchradius round (((( perf2 - traitmin ) / ( traitmax - traitmin )) * ( searchmax - searchmin )) + searchMin )  "
  ;; in "set-turtle-traits" procedure & set-offspring-traits

end

to setup-patches
  ask patches [
    if random 1000 < resource-density [set pcolor blue]
    if (npred1 > 0) and (random-float 1000 < npred1) [set pperf1 r:get "rnorm(1, mean = ( muX1 - sdX1 ), sdX1)" ]
    if (pperf1 = 0) and (npred2 > 0) and (random-float 1000 < npred2 ) [set pperf2 r:get "rnorm(1, mean = (muX2 - sdX2) , sdX2)" ]
  ]

  ;; changed npred1 & npred2 from random-float 100 < npred to random-float 1000 < npred

end


to setup-df
  ( r:putagentdf "df" turtles "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")


end

to set-costX1
  r:put "myX1" perf1
  r:eval "blip <- round((pnorm(myX1, mean=muX1, sd=20)), digits = 3)"
  r:eval "costX1 <- 100*blip"
  set cost-X1 r:get "costX1"
end

to comp-varyX1
  set varyX1 ((percent-of-max-X1 / 100) * perf1)
  r:put "varyX1" varyX1
  r:eval "blip <- round((pnorm(varyX1, mean=muX1, sd=20)), digits = 3)"
  r:eval "costvaryX1 <- 100*blip"
  set cost-varyX1 r:get "costvaryX1"
end



to set-srchradius
  set srchradius round (((( perf2 - traitmin ) / ( traitmax - traitmin )) * ( searchmax - searchmin )) + searchmin )
  set search-cost ( base ^ (( a * srchradius) + c ))
end

to comp-varyX2
  ;set varyX2 (percent-of-max-X2 * perf2)
  ;set vary-srchradius round (((( varyX2 - traitmin ) / ( traitmax - traitmin )) * ( searchmax - searchmin )) + searchmin )

  set vary-srchradius (round ((percent-of-max-X2 / 100) * srchradius))
```

```
  if vary-srchradius < 1 [ set vary-srchradius 1 ]

  set vary-search-cost ( base ^ (( a * vary-srchradius) + c ))
end

to set-sex
  ifelse random 2 < 1 [
    set breed females ]
  [ set breed males ]
end


to check4pred1
  if [pperf1] of patch-here > 0 [

    ifelse (percent-of-max-X1) = 100 [

      ifelse (perf1 >= [pperf1] of patch-here) [
        fight1]
      [ update-my-row-pred1
        die ]]

    [ ifelse perf1 >= [pperf1] of patch-here [
      ifelse random 2 > 0 [vary-fight1][fight1]]
    [ update-my-row-pred1
            die ]]
    ]
end

to check4pred2
  if [pperf2] of patch-here > 0  [

    ifelse percent-of-max-X2 = 100 [

      ifelse perf2 >= [pperf2] of patch-here [
        fight2]
      [ update-my-row-pred2
        die ]]


      [ ifelse srchradius >= [pperf2] of patch-here [
        ifelse random 2 > 0 [vary-fight2][fight2]]
      [ update-my-row-pred2
            die ]]
  ]


end

to fight1
  set energy (energy - cost-X1)
end

to vary-fight1
  ifelse varyX1 >= [pperf1] of patch-here [
    set energy (energy - cost-varyX1)]
  [ update-my-row-pred1
    die ]       ;;  if no then die
end


;; fight 2 needs work ;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
to fight2
  set energy (energy - search-cost)
end
```

```
to vary-fight2
  ifelse vary-srchradius >= [pperf2] of patch-here [
    set energy (energy - vary-search-cost)]
  [ update-my-row-pred2
    die ]       ;;  if no then die
end




to lifespan-check
  if age >= lifespan [ update-my-row-lifespan
    die]
end

to energy-check
  if energy <= 0 [ update-my-row-energy
    die]
end

to srchradius-check
  if srchradius < 1 [ update-srchradius
     die ]
end

to forage

  ifelse vary-search-effort? and (percent-of-max-X2 < 100)[
    ifelse (random 2 < 1 ) [vary-search][max-search] ]
  [max-search]

end


to vary-search

     ifelse (any? patches in-cone vary-srchradius 75 with [pcolor = blue]) [

    move-to one-of patches in-cone vary-srchradius 75 with [pcolor = blue]
    set color orange
    set eaten (eaten + 1)
    ifelse exponential? [set energy (energy - (vary-search-cost))]
    [set energy (energy - vary-srchradius)]
    if energy <= 100 [set energy (energy + food-benefit)]
    if energy > 100 [set energy 100]
    energy-check
    set hungry 0
    if finite-resources [if random 2 < 1 [ask patch-here [set pcolor black]]   ; .5 probability that patch resource is locally extinct
    ]
  ]


  [
    set color yellow
    set hungry (hungry + 1)
    ifelse exponential? [set energy (energy - (vary-search-cost))]
    [set energy (energy - vary-srchradius)]
    energy-check
    rt random 360
    fd vary-srchradius]
end



to max-search
```

```
   ifelse (any? patches in-cone srchradius 75 with [pcolor = blue]) [

    move-to one-of patches in-cone srchradius 75 with [pcolor = blue]
    set color orange
    set eaten (eaten + 1)
    ifelse exponential? [set energy (energy - (search-cost))]
    [set energy (energy - srchradius)]
    if energy <= 100 [set energy (energy + food-benefit)]
    if energy > 100 [set energy 100]
    energy-check
    set hungry 0
    if finite-resources [if random 2 < 1 [ask patch-here [set pcolor black]]   ; .5 probability that patch resource is locally extinct
    ]
  ]


  [
    set color yellow
    set hungry (hungry + 1)
    ifelse exponential? [set energy (energy - (search-cost))]
    [set energy (energy - srchradius)]
    energy-check
    rt random 360
    fd srchradius]
end

to pairup
  set mate one-of males with [mate = nobody and energy >= 80 and age > 1]
  if mate != nobody [create-mate-link-to mate               ;; is this right?
  reproduce]

end

to reproduce
  set mp ((perf1 + [perf1] of mate)/ 2 )
  set clutch-size round(((energy - 80) / 2))
  r:put "mp" mp

  hatch (round( ((energy - 80) / 2 ))) [                  ;; having max # of babies with the one mate, not optimizing # of matings !!
    ifelse truncate? [                               ;; if "truncate" switch is on, draw traits from a truncated normal distribution
      r:eval "ExpMn1 <- (hsq*mp + intX1)"                 ;; expected X1 mean from parent-offspring regression
      r:eval "baby1 <- rnorm(1, mean = ExpMn1, sd = sdX1)"  ;; draw perf trait value from distribution with mean at the expected value
      r:eval "ExpMn2 <- (slopeX2 * baby1 + intX2)"         ;; expected X2 mean
      r:eval "baby2 <- rnorm(1, mean = ExpMn2, sd = sdX2)"  ;; draw trait value from
      set perf1 r:get "rtruncnorm(1, a = (muX1-3sdX1), b = (muX1 + 3sdX1), mean= ExpMn1, sd = sdX1)"    ;; a is lower bound,  b is upper bound
      set perf2 r:get "rtruncnorm(1, a= (muX2-3sdX2), b = (muX1 + 3sdX1), mean = ExpMn2, sd = sdX2)"
      create-parent-link-to myself
      create-parent-link-to mate
      set-offspring-traits]

   [ r:eval "ExpMn1 <- (hsq*mp + intX1)"                  ;; if "truncate" off, same procedure as above but use non-truncated normal
      r:eval "baby1 <- rnorm(1, mean = ExpMn1, sd = sdX1)"
      r:eval "ExpMn2 <- (slopeX2 * baby1 + intX2)"
      r:eval "baby2 <- rnorm(1, mean = ExpMn2, sd = sdX2)"
      set perf1 r:get "baby1"
      set perf2 r:get "baby2"
      create-parent-link-to myself
      create-parent-link-to mate
      set-offspring-traits
       ]

  ] ;set mate nobody     ;; set all other variables, otherwise they are one of the parent's clones!
     ; set energy 80       ;; energy starts at 50, comment this out to set energy level the same as one of the parents
      ;set age 0
      ;set color green   ;; starting population is yellow, all progeny are orange
```

```
     ;set offspring_count 0]

  set offspring (offspring + clutch-size)
  set energy (energy - (clutch-size * 2))
  ask mate [set energy ( energy - (clutch-size * 2))
    if energy < 75 [set energy 75]
    set offspring ( offspring + clutch-size )
  ]



end

to set-turtle-traits
  foreach sort turtles [
     ask ?[set perf1 item who X1]]

  ask turtles [
    r:put "ownX1" perf1
    r:eval "ownX2 <- slopeX2 * ownX1 + intX2"
    set perf2 r:get "rnorm(1, mean = ownX2, sd = sdX2)"

    setxy random-xcor random-ycor
    set color red
    set energy 80  ;; start at 80, max is 100.
    set-sex
    set-srchradius
    set-costX1
    set birth ticks
    set cause "NA" ]


  if (percent-of-max-X1 < 100) [ask turtles [comp-varyX1]]
  if (percent-of-max-X2 < 100) [ask turtles [comp-varyX2]]


end

to set-offspring-traits
  setxy random-xcor random-ycor
  set-sex
  set color green
  set energy 80  ;; start at 80, max is 100.
  set-srchradius
  set eaten 0
  set hungry 0
  set offspring 0
  set age 0
  set birth ticks
  rt random 360
  fd 10
  set-costX1
  set cause "NA"

  if (percent-of-max-X1 < 100) [comp-varyX1]
  if (percent-of-max-X2 < 100) [comp-varyX2]

  add-me2df
  srchradius-check
end


;; ================================================================
;; ================================================================
 ;; Output ;;
```

```
to add-me2df
  r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
 ; r:eval "rownames(dfadd) <- dfadd$who"
  ;r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"

end

to update-srchradius
  set death ticks
  set cause "zerosrch"


  r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
 ; r:eval "rownames(dfadd) <- dfadd$who"
  ;r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"
end

to update-my-row-lifespan
  set death ticks
  set cause "old.age"

  r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
 ; r:eval "rownames(dfadd) <- dfadd$who"
  ;r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"
end

to update-my-row-pred1
  set death ticks
  set cause "pred1"

  r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
 ; r:eval "rownames(dfadd) <- dfadd$who"
 ; r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"
end

to update-my-row-pred2
  set cause "pred2"
  set death ticks

    r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
 ; r:eval "rownames(dfadd) <- dfadd$who"
 ; r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"
end

to update-my-row-energy
  set cause "energy"
  set death ticks

  r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
 ; r:eval "rownames(dfadd) <- dfadd$who"
 ; r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"
end
```

```
to update-my-row-end
  r:put "me" who + 1
( r:putagentdf "dfadd" self "who" "perf1" "perf2" "srchradius" "age" "offspring" "cause" "birth" "death")
  ;r:eval "rownames(dfadd) <- dfadd$who"
  r:eval " dfaddv <- as.vector(dfadd) "
  r:eval " df[me, ] <- dfadd"

end

to write-to-file
  ask mate-links [file-print (word ticks ",mate," end1 ","end2 )]
  ask parent-links [file-print (word ticks ",parent," end1 "," end2 ",")]
  ;;export-output (word "C:/Users/Simon/Desktop/AMC performance simulation/links" ticks "_" random-float 1.0 ".csv")
  ;;clear-output


  clear-links
end



to end-sim
  ask turtles [
    set cause "alive"
    update-my-row-end
  ]
  ;r:eval "rownames(df) <- df$who"
  outout
  export-all-plots (word "c:/Path2Folder/" filename "plots.csv")
  ; export-output (word "c:/Path2Folder/" filename "output.csv")
  file-close
end

to outout
  r:put "filename" filename
  r:eval "df$who <- unlist(df$who)"
  r:eval "df$perf1 <- as.numeric(df$perf1)"
  r:eval "df$perf2 <- as.numeric(df$perf2)"
  r:eval "df$srchradius <- as.numeric(df$srchradius)"
  r:eval "df$age <- as.numeric(df$age)"
  r:eval "df$offspring <- as.numeric(df$offspring)"
  r:eval "df$cause <- as.character(df$cause)"
  r:eval "df$birth <- as.numeric(df$birth)"
  r:eval "df$death <- as.numeric(df$death)"

  r:eval "write.table(df, filename, sep='\t') "


end

;; END OF NETLOGO CODE!

######################################
#
#                The following is an R script for processing simulation output and is not NetLogo code!
#
#
## Script for computing trait means, variance, intensity of selection, and univariate and multivariate selection coefficients
## Any change to the NetLogo code, including most global parameters (e.g. lifespan) will necessitate changes to this script.
## This also pulls all parameters from a separate NetLogo output file for each simulation and combines everything into one dataset.
##
## You may wish to run small batches at a time, or comment out what you do not wish to calculate to improve computation time.
##
## Notes on method for fitting multivariate selection models:
## These coefficients are estimates of the direct and indirect effects of selection on the first (ß1, ß2) and second
## (gamma11, gamma22) moments of the distribution of phenotypes in the population, while the bivariate nonlinear term
```

```
## (gamma12) estimates the effect of selection on the correlation between traits (Lande and Arnold 1983; reviewed by
## Brodie et al. 1995). We obtained these estimates from the best-fit multiple regression model of relative fitness
##(number of offspring divided by the mean number of offspring) (Lande and Arnold 1983) and both traits (Lande and Arnold 1983).
## We then fit a fully saturated model (including all selection terms) and then chose the minimum adequate model using
## stepwise selection based on AIC values (stepAIC; R package: MASS) (Venables and Ripley 2002).
##


library(nlme)
library(MASS)
library(car)
library(plyr)

## DIRECTORY MUST CONTAIN ONLY FILES CONTAINING SIMULATION OUTPUT!
path2dir <-"C:/Path2Folderofoutput"  ## Don't put a forward slash at the end


## get all filenames in directory

## only want the .txt file with individual data (for selection analyses)


files <- list.files(path=path2dir, pattern= "*.txt$", full.names=T, recursive=F)

## for "parfiles"  we want plot files (containing parameter settings for each simulation run)
parfiles <- list.files(path=path2dir, pattern= "*plots.csv$", full.names=T, recursive=F)


# function: suck in individual trait & fitness (#offspring) data (file read in by function calling arrangefile)
# and arrange into format for performing selection
# returns: data.frame

arrangefile <- function(x,y) {
   dat <- x
   dat <- data.frame( y, dat$who, dat$offspring, dat$perf1, dat$perf2, dat$birth, dat$age )
   names(dat) <- c("sim.id", "ID", "relfit", "trt1", "trt2", "birth", "age") #relfit isn't actually relative fitness yet, that happens in linfun (calc for
               each gen)
   dat <- dat[(as.numeric(as.character(dat$birth)) <= 600),]   #shave off anyone born too late (bc censored RO (sim ended before death))

   check4endofsim<- function(x){
   sum(x$relfit)}
   checkfor0 <- ddply(dat, "birth", check4endofsim)
   dat <-subset(dat, birth != checkfor0$birth[checkfor0$V1 == 0])
   dat
}


#get simulation id from filename (date and time of run)

crt.sim.id <- function(x) {
   readstrt <- (nchar(path2dir) + 2)
   readstop <- (readstrt + 19)
   sim.id <- substr((x), readstrt, readstop)
   return(sim.id)
}


linfun <- function(x) {

   datlin <- x
   datlin$relfit <- datlin$relfit/mean(datlin$relfit)

               noobst<- noobst<-dim(datlin)[1]
```

```
 sprint_mod<- try(lm(datlin$relfit ~ scale(datlin$trt1), data = datlin), silent = T)
          if(is(sprint_mod, "try-error")){
           int_sprint <- NA
           Bsprint <- NA
           Rsq_sprint <- NA} else {
            co1 <-data.frame(sprint_mod$coeff)
            int_sprint  <- co1["(Intercept)",]
            Bsprint <- co1["scale(datlin$trt1)",]
            Rsq_sprint <- summary(sprint_mod)$adj.r.squared}

          end_mod<- try(lm(datlin$relfit ~ scale(datlin$trt2), data = datlin), silent = T)
          if(is(end_mod, "try-error")){
           int_end <- NA
           Bend <- NA
           Rsq_end <- NA} else {
            co2 <-data.frame(end_mod$coeff)
            int_end  <- co2["(Intercept)",]
            Bend <- co2["scale(datlin$trt2)",]
            Rsq_end <- summary(end_mod)$adj.r.squared}

 both_mod<- try(lm(datlin$relfit ~ scale(datlin$trt1) +  scale(datlin$trt2), data = datlin), silent = T)
          if(is(both_mod, "try-error")){
           int_both <- NA
           B1both <- NA
  B2both <- NA
           Rsq_both <- NA} else {
            co3 <-data.frame(both_mod$coeff)
            int_both  <- co3["(Intercept)",]
            B1both <- co3["scale(datlin$trt1)",]
   B2both <-  co3["scale(datlin$trt2)",]
            Rsq_both<- summary(both_mod)$adj.r.squared}



          x1mntry<- try(mean(datlin$trt1))
          if(is(x1mntry, "try-error")){
          x1mnt<- NA} else {
          x1mnt<- x1mntry}

 x1VARtry<- try(var(datlin$trt1))
 if(is(x1VARtry, "try-error")){
 x1VARt<- NA} else {
  x1VARt<- x1VARtry}

          x2mntry<- try(mean(datlin$trt2))
          if(is(x2mntry, "try-error")){
          x2mnt<- NA} else {
          x2mnt<- x2mntry}

x2VARtry<- try(var(datlin$trt2))
if(is(x2VARtry, "try-error")){
 x2VARt<- NA} else {
  x2VARt<- x2VARtry}





          full<-try(lm(datlin$relfit ~ scale(datlin$trt1) * scale(datlin$trt2) + I(scale(datlin$trt1^2)) + I(scale(datlin$trt2^2)), data=datlin),
          silent=T)
  if(is(full, "try-error")){
          intrcpt <- NA
          B1t <- NA
  B2t <- NA
```

```
   y11t <- NA
   y22t<- NA
   y12t <- NA} else {
            winstep <- try(stepAIC(full, direction = "both", trace=F), silent = T)
            if(is(winstep, "try-error")){
            intrcpt <- NA
            B1t <- NA
   B2t <- NA
   y11t <- NA
   y22t<- NA
   y12t <- NA
            Rsqt <- NA} else {
   co <-data.frame(winstep$coeff)
   intrcpt <- co["(Intercept)",]
            B1t <- co["scale(datlin$trt1)",]
   B2t <- co["scale(datlin$trt2)",]
   y11t <- co["I(scale(datlin$trt1^2))",]
   y22t<- co["I(scale(datlin$trt2^2))",]
   y12t <- co["scale(datlin$trt1):scale(datlin$trt2)",]
            Rsqt<- summary(winstep)$adj.r.squared}}



            S1try<-try(mean(datlin$trt1[datlin$age > 40]) - mean(datlin$trt1))
            if(is(S1try, "try-error")){
            S1t<-NA} else {
            S1t<-S1try}

            S2try<-try(mean(datlin$trt2[datlin$age > 40]) - mean(datlin$trt2))
            if(is(S2try, "try-error")){
            S2t<-NA} else {
            S2t<-S2try}

            i1try <- try(S1t / sd(datlin$trt1))
            if(is(i1try, "try-error")){
            i1t<-NA} else {
            i1t<-i1try}

            i2try <- try(S2t / sd(datlin$trt2))
            if(is(i2try, "try-error")){
            i2t<-NA} else {
            i2t<-i2try}


   data.frame(sim.id = datlin$sim.id[1], gen = datlin$birth[1], noobs<-noobst,
            x1mnt = x1mnt, x1VAR = x1VARt, x2mnt = x2mnt,x2VAR = x2VARt, S1 = S1t, S2 = S2t, i1 = i1t, i2 = i2t,
            intrcp = intrcpt, B1 = B1t, B2 = B2t, y11 = y11t, y22 = y22t, y12 = y12t, Rsq = Rsqt, sprnt_int = int_sprint, sprnt_B = Bsprint, sprnt_rsq
            = Rsq_sprint,
   end_int = int_end, end_B = Bend, end_rsq = Rsq_end,
   both_int = int_both, both_B1 = B1both, both_B2 = B2both, both_rsq = Rsq_both)


}

linfunIndSim <- function(x) {
   sim.id <- crt.sim.id(x)
   t <- read.table(x, header=T) # load file
   t$birth <- as.factor(t$birth)

   n <- arrangefile(t, sim.id)

   sim.sum <- ddply(n, "birth", linfun)

   sim.sum
}
```

```
sel.output<- ldply(files, linfunIndSim)



# extract parameter settings from parfiles

parfun <- function(x) {

sim.id <- crt.sim.id(x)

par.f <- read.csv(x, header=F) # load file
par.rows <-par.f[5:6,]

pctx1<-which(sapply(par.rows, function(x) any(x == "percent-of-max-x1")))
pctx1p<-as.numeric(paste0(par.rows[2,pctx1]))
pctx2<-which(sapply(par.rows, function(x) any(x == "percent-of-max-x2")))
pctx2p<-as.numeric(paste0(par.rows[2,pctx2]))
npred1<-which(sapply(par.rows, function(x) any(x == "npred1")))
npred1p<-as.numeric(paste0(par.rows[2,npred1]))
npred2<-which(sapply(par.rows, function(x) any(x == "npred2")))
npred2p<-as.numeric(paste0(par.rows[2,npred2]))
fdben<-which(sapply(par.rows, function(x) any(x == "food-benefit")))
fdbenp<-as.numeric(paste0(par.rows[2,fdben]))
hsq<-which(sapply(par.rows, function(x) any(x == "h-squared")))
hsqp<-as.numeric(paste0(par.rows[2,hsq]))
cov1.2 <- which(sapply(par.rows, function(x) any(x == "covx1-x2")))
cov1.2p <-as.numeric(paste0(par.rows[2,cov1.2]))
varx1 <- which(sapply(par.rows, function(x) any(x == "varx1")))
varx1p <- as.numeric(paste0(par.rows[2,varx1]))
varx2<- which(sapply(par.rows, function(x) any(x == "varx2")))
varx2p <- as.numeric(paste0(par.rows[2,varx2]))
fddens<- which(sapply(par.rows, function(x) any(x == "resource-density")))
ffdensp<-as.numeric(paste0(par.rows[2,fddens]))
inpop<- which(sapply(par.rows, function(x) any(x == "population")))
inpopp<-as.numeric(paste0(par.rows[2,inpop]))
# add cost function vars later


data.frame(sim.id = sim.id, pctx1 = pctx1p, pctx2 = pctx2p, npred1 = npred1p,
npred2 = npred2p, fdben = fdbenp, hsq = hsqp, cov1.2 = cov1.2p, varx1 = varx1p,
varx2 = varx2p, fddens = ffdensp, inpop = inpopp)}

par.output <- ldply(parfiles, parfun)

dundundun <- merge(sel.output, par.output, by = "sim.id")


write.table(sel.output, paste0(path2dir,"/SelOut.txt"), sep = "\t", row.names=F, col.names =T, append =F)
write.table(par.output, paste0(path2dir,"/ParOut.txt"), sep = "\t", row.names=F, col.names =T, append =F)
write.table(dundundun, paste0(path2dir,"/dundundun.txt"), sep = "\t", row.names=F, col.names =T, append =F)
```

Supplementary File S2: Chapter 1 Parameter sweep

Results of a parameter sweep to determine the behavior of the simulation model. Replicate simulations are summarized. This file can be found at https://academic.oup.com/icb/article/55/6/1176/2363701 .

Supplementary File S3: Chapter 1

Results of selection analyses on 267 simulations. This file can be found at https://academic.oup.com/icb/article/55/6/1176/2363701 .

Vita

The author was born in Metairie, Louisiana. She completed her undergraduate studies at the University of New Orleans in 2008, and returned there to pursue her doctorate two years later. She began her PhD career under the mentorship of Dr. Philip J. DeVries, and in 2014, she joined the laboratory of Dr. Simon P. Lailvaux.