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SYMPOSIUM

An Individual-Based Simulation Approach to the Evolution of Locomotor Performance

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Synopsis 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 maximal 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 and Huey 1990; Irschick and 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 and 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

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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 Marroig 2015). These simulations therefore constitute a promising alternative approach to investigating the evolution of preferred performance. Here, we present such an approach to modeling 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 uses 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 modeling 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 (Fig. 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,

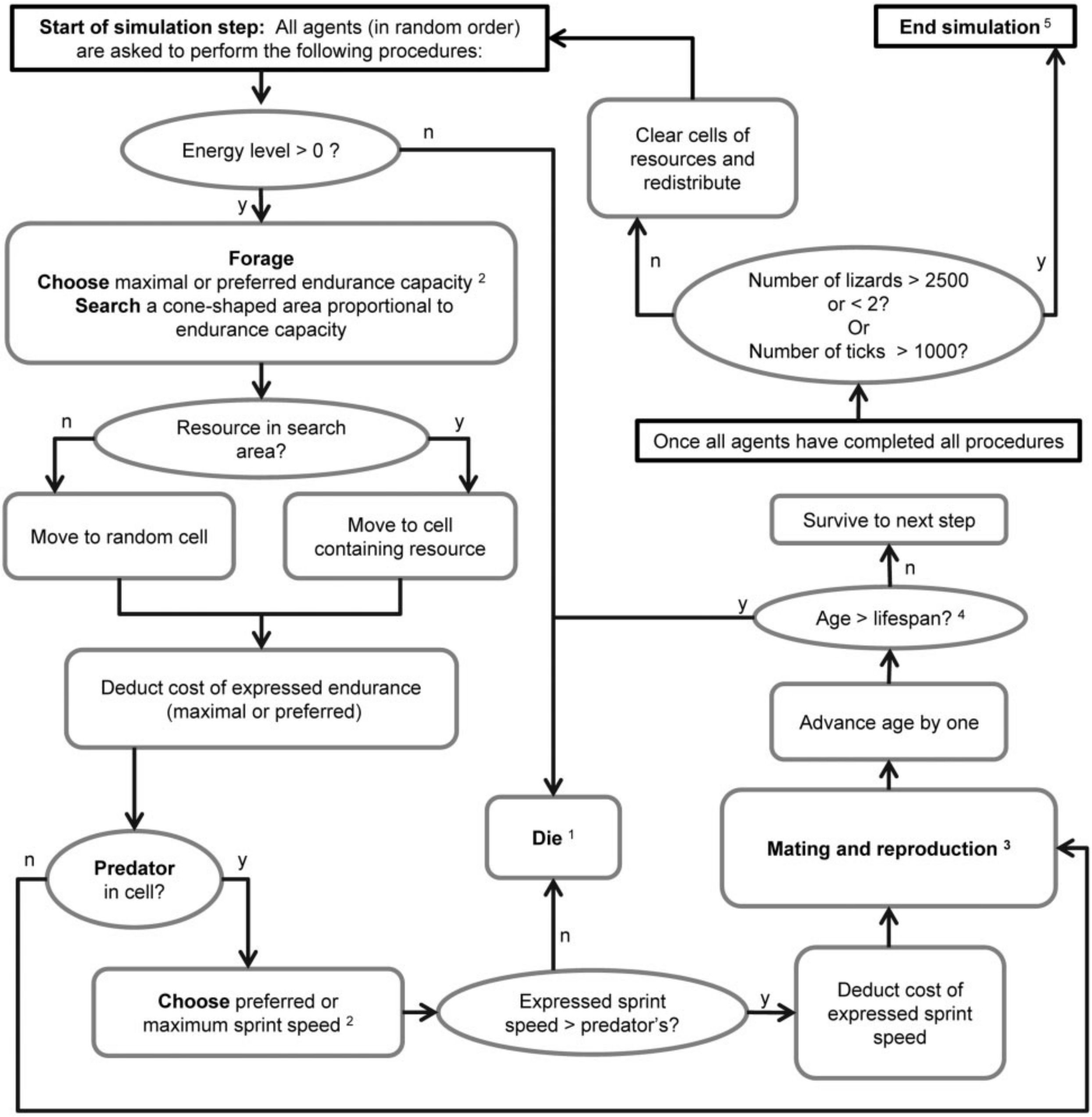

Fig. 1 Simulation processes and scheduling.

Notes: 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.

depending on the environmental parameter values. An overview of the simulation is presented in Fig. 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

Table 1 Parameters and settings for simulations investigating intra-individual variation in sprint speed.

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 × 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 (SR)	$SR_{max} = 20$ $SR_{min} = 1$	Translates expressed endurance capacity into a −distance that defines the radius of the cone-shaped foraging area. For agent *i*: $SR_i = \frac{endurance_i - endurance_{min}}{endurance_{max} - endurance_{min}} (SR_{max} - SR_{min}) + SR_{min}$
Cost of endurance	$a = 2$, $b = 0.5$, $c = 0$	$C_{endurance} = a^{(b * SR - c)}$
Cost of sprint	Mean = 100 SD = 20	$C_{sprint} = P(X < sprint_{agent}) *$ energy budget, where X is a random variable drawn from a normal distribution with mean and SD parameters

Notes: All combinations of preferred sprint speed and covariance (sprint, endurance) were run multiple times (Supplementary Information S2). 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.

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.

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 toward 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 (Bennett 1982; Biewener 2003), 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's output. Data recorded during a simulation is outlined in Fig. 1, and we used customized R (R Core Team 2014) 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 the traits' 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 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 both by 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} 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 2, A) and for the subset of all simulations, excluding populations that never vary in sprint performance (Table 2, B), 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 maximal 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 3, A). When we excluded simulations in which individuals used only their maximum, the best model was the saturated model, with all terms and interactions (Table 3, B). To compare with the previous model (Table 3, A), we also fit the model without the three-way interaction, and there was a sign change for all terms involving preferred speed (Table 3, C).

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 4, A). 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

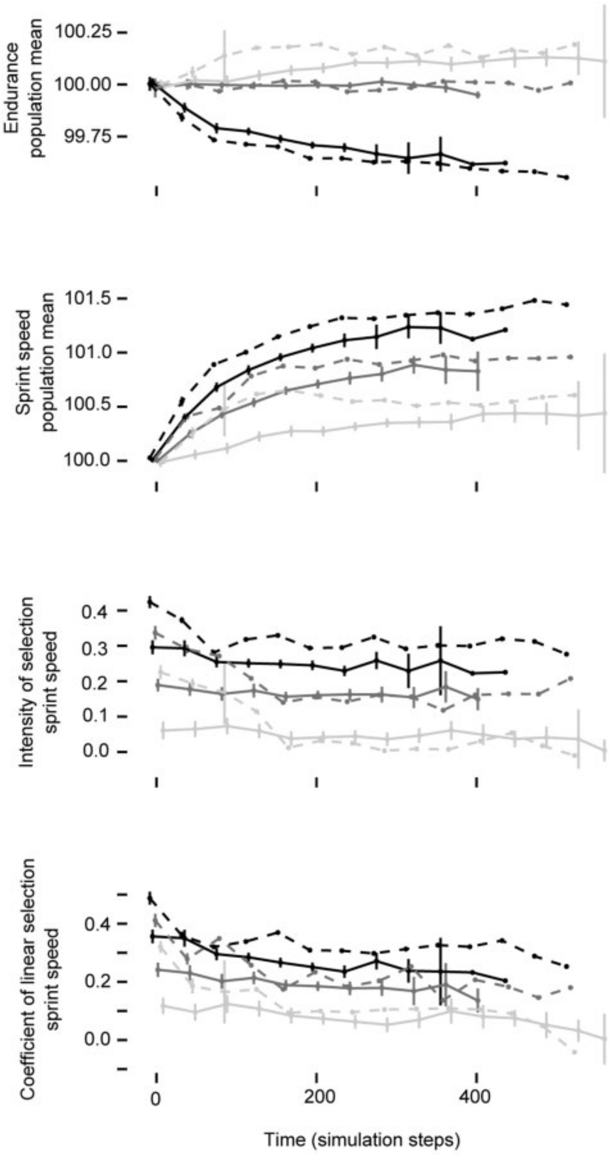

Fig. 2 Correlation between traits affects the trajectory of phenotypic change in simulated populations. For each type of correlation between sprint and endurance (negative—black; none—dark gray; positive—light gray) and performance strategy (individuals only use maximum sprint—dashed line; sprint speed 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.

speed over time within this subset (Table 4, B). 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 that 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).

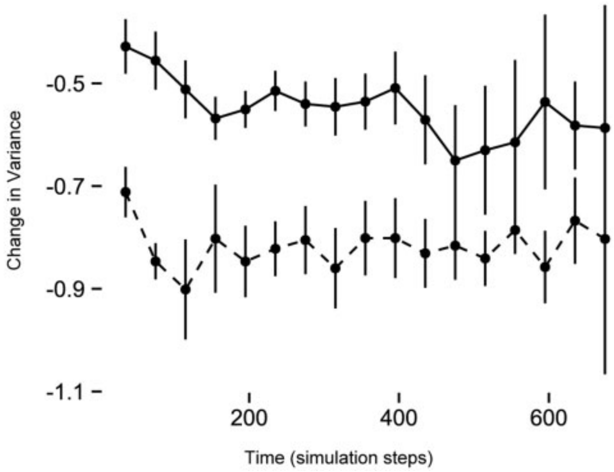

Fig. 3 The change in variance between reproductive events for sprint speed (individuals only use maximum sprint—dashed line; sprint speed variable—solid line). Initially the variance decreases, as directional selection on the first generation truncates the distribution of phenotypes in a population, 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 on the costs of sprint speed 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

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)

	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:Cov	8.3×10^{-5}	2.1×10^{-5}		Gen:Cov	6.2×10^{-5}	2.0×10^{-5}
	Gen:Preferred	-1.7×10^{-6}	6.1×10^{-7}		Gen:Preferred	9.8×10^{-7}	5.7×10^{-7}

Notes: (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.

Table 3 Best-fit model β_{sprint} at each generation of each simulation

	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:Cov	2.9×10^{-4}	7.6×10^{-5}
	Gen:Preferred	2.5×10^{-6}	9.0×10^{-7}
	Cov:Preferred	2.3×10^{-4}	1.7×10^{-4}
	Gen:Cov:Preferred	-2.1×10^{-6}	1.0×10^{-6}

	Model term	Coefficient	SE		Model term	Coefficient	SE
A	Intercept	0.21	0.010	C	Intercept	0.25	0.010
	Gen	-2.3×10^{-4}	6.0×10^{-5}		Gen	-3.8×10^{-4}	5.9×10^{-5}
	Cov	−0.12	0.009		Cov	−0.11	0.008
	Preferred	6.7×10^{-4}	1.2×10^{-4}		Preferred	-2.0×10^{-4}	1.3×10^{-4}
	Gen:Cov	1.5×10^{-4}	2.6×10^{-5}		Gen:Cov	1.4×10^{-4}	2.6×10^{-5}
	Gen:Preferred	-2.2×10^{-6}	7.6×10^{-7}		Gen:Preferred	1.6×10^{-6}	7.7×10^{-7}
	Cov:Preferred	1.5×10^{-4}	1.0×10^{-4}		Cov:Preferred	-3.4×10^{-5}	1.0×10^{-4}

Notes: 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).

Table 4 Best-fit model for the change in variance during each interval between reproductive events for (A) simulations with variable and nonvariable sprint speed included together and (B) variable sprint speed only

	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

Notes: 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 with its standard error. Thus, within the variable sprint group there is little difference between simulations with differing preferred speeds.

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 2, A) to just those simulations in which individuals had variable sprint speeds (Table 2, B) 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 did 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.

The behavior of our simulation when individuals varied sprint speed may stem from multiple sources. While varying performance introduces stochasticity to predator/prey 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 and 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).

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 if selective 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 modelers, 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 toward 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 modeled 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.

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Supplementary data

Supplementary data available at *ICB* online.

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