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Correspondence and requests for materials should be addressed to K.P. (buddha@ucla.edu).

Physical performance and darwinian fitness in lizards

Jean-François Le Galliard[1]*, **Jean Clobert**[1] & **Régis Ferrière**[1,2]

[1] *Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, CNRS UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05, France*
[2] *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA*

* Present address: Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1050, Blindern, 0316 Oslo, Norway

Strong evidence for a genetic basis of variation in physical performance has accumulated[1,2]. Considering one of the basic tenets of evolutionary physiology—that physical performance and darwinian fitness are tightly linked[3]—one may expect phenotypes with exceptional physiological capacities to be promoted by natural selection. Why then does physical performance remain considerably variable in human and other animal populations[1,2,4]? Our analysis of locomotor performance in the common lizard (*Lacerta vivipara*) demonstrates that initial endurance (running time to exhaustion measured at birth) is indeed highly heritable, but natural selection in favour of this trait can be unexpectedly weak. A manipulation of dietary conditions unravels a proximate mechanism explaining this pattern. Fully fed individuals experience a marked reversal of performance within only one month after birth: juveniles with low endurance catch up, whereas individuals with high endurance lose their advantage. In contrast, dietary restriction allows highly endurant neonates to retain their locomotor superiority as they age. Thus, the expression of a genetic predisposition to high physical performance strongly depends on the environment experienced early in life.

Sporting events would be exceedingly boring were there no variation in human performance; fortunately, this is not the case. For example, the distribution of finish times at international marathons has a large variance and a long tail[1], due to a variety of factors affecting the performance of individual runners[5]. Although genetic variation in locomotor performance has been documented in human and other animal populations[1,2], questions remain as to how genetic and non-genetic factors would interact with each other and what effect selection has on the resulting individual variation[1,6]. We addressed these two questions using ground-dwelling lizards, a popular model system for studies of locomotor performance[2,4,7]. Our focus here is on the endurance capacity as assayed in the laboratory (see Methods). In lizards, endurance shows considerable interindividual variation that reflects differences in tight muscle mass, heart mass and aerobic metabolism[8].

Our study species is the common lizard (*Lacerta vivipara* Jacquin 1787) for which locomotor performance and life-history traits have been routinely studied[9]. We took advantage of the populations established at the Ecological Research Station of Foljuif (Nemours, France) in the semi-natural conditions of outdoor enclosures[10] to measure the heritability of initial endurance and the age-specific strength of natural selection on this trait. In these enclosures, endurance capacity could reflect social rank[2] and abilities to compete for and exploit basking sites and prey[4], and thus influence darwinian fitness[9]. Insights into proximate mechanisms underlying the observed pattern of selection have been gained experimentally by investigating how dietary conditions early in life influence the ontogeny of endurance and the relationship between survivorship and endurance.

In 2001, initial endurance was recorded in a cohort of 447 offspring (Fig. 1). Measurements spanned a 45-fold range, from 36 s to 1,677 s (mean = 222 s ± 153.7 s.d.). The distribution is typically skewed, with a few 'champions' displaying exceptional endurance. Initial endurance increased with offspring body size and body condition, decreased with maternal body size, and increased with behavioural motivation (Table 1). Accounting for all these factors, initial endurance was highly heritable ($h^2 = 0.40$), concurring with previous studies in this species and many other reptiles[2,11]. Even in the controlled conditions of our outdoor enclosures, high heritability might have been caused by maternal effects, but no such

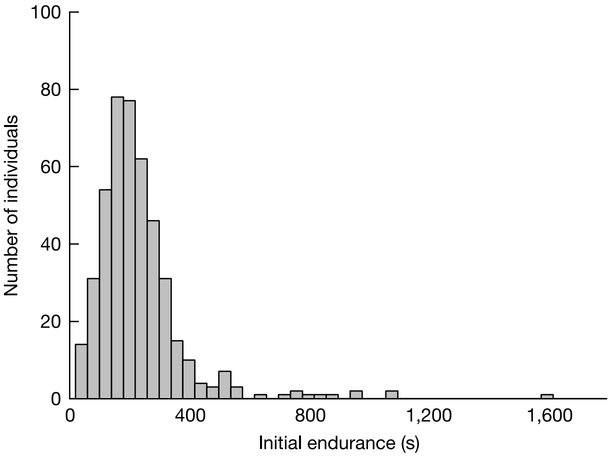

Figure 1 Individual variation in endurance capacity among 447 common lizard offspring.

Table 1 **Proximate factors of initial endurance**

	Test statistics	Parameter estimates (±s.e.)	Partial regression r^2
Fixed effects			
Offspring body size	$F_{1,355} = 14.6$*	0.098 ± 0.026	0.041
Offspring body condition	$F_{1,355} = 40.4$†	8.725 ± 1.373	0.070
Behavioural motivation	$F_{1,355} = 86.1$†	−0.031 ± 0.012	0.233
Maternal body size	$F_{1,355} = 7.1$*	−0.953 ± 0.103	0.046
Random effects			
Family	$\chi^2 = 105.1$†	0.125 ± 0.026	–

Behavioural motivation was measured by the number of stimulations per unit distance. Endurance was log-transformed to ensure normality and homoscedasticity. The final model was obtained after a stepwise multivariate linear regression. Fixed factors included offspring characteristics, that is body size (snout–vent length), residual tail size (relative to body size), condition (residual body mass) and sex; maternal characteristics, that is body size, residual fecundity (relative to maternal body size) and post-partum body condition. Family was included as a random effect, and the broad-sense heritability was calculated from variance components[27]. Statistical tests are type III F tests for fixed effects and likelihood ratio tests for random effects.
*$P < 0.01$, †$P < 0.001$.

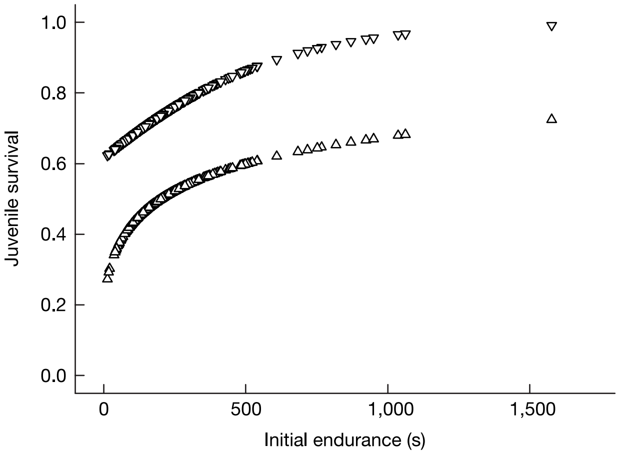

Figure 2 Fitness functions of initial endurance during the first summer (triangles pointing down) and the whole year (triangles pointing up) following birth. Data have been back-transformed from values predicted by the models (see Table 2). Each triangle corresponds to a single individual.

effect (maternal age or population density, see Methods) was detected (analysis of variance (ANOVA) with family included as a random factor nested within age and density effects; age effect: $F_{2,45} = 0.88$, NS; density effect: $F_{1,45} = 0.10$, NS; age × density effect: $F_{2,45} = 0.17$, NS).

Juvenile survival is an important component of darwinian fitness in the common lizard[12]. Among the 447 offspring scored at birth, 16 individuals died before release, 316 survived during the summer and 192 survived after one year. Natural selection acted independently on morphology and endurance (non-significant patterns of correlational selection among body size, body condition and endurance; $P > 0.13$). Directional selection for greater endurance and larger body size at birth was detected over the first summer and over the whole year following birth, with most selection taking place shortly after birth (Table 2; end of summer to next year selection on initial endurance: $F_{1,234} = 0.01$, NS; on initial body size: $F_{1,234} = 2.86$, NS). However, juvenile survival selection on endurance was highly sensitive to the few lizards with lowest initial endurance (Table S1 in Supplementary Information), which agrees with the shape of the fitness function (Fig. 2). Thus, natural selection acted predominantly against very low initial endurance and was nearly neutral at intermediate and high levels of endurance.

Weak selection for elite endurance is at odds with the common assumption that performance and darwinian fitness are tightly correlated. One explanation for our findings might have been that endurance reflected motivational factors in the laboratory more than physiological capacities (Table 1), but behavioural motivation did not correlate with survival probabilities, and factoring motivation out of the selection analyses had no effect on our main results (Table S2 in Supplementary Information). Moreover, the pattern of selection demonstrated by this experiment is concordant with two previous correlative studies of initial endurance and survival in natural populations[9,13]. Our analysis also found a strong positive effect of selection on body size at birth, which is similar to the effect detected in natural populations of the same species[14], and in other vertebrates[15]. The overall coherence of these observations suggests that our results are not an artefact of measuring selection in the semi-natural conditions of our enclosures (see Discussion in Supplementary Information).

In 2002, we tested the hypothesis that rapid ontogenic shifts in endurance under favourable conditions could explain this unexpected pattern of selection. We measured the change in endurance over the month following birth in two samples subjected to different dietary conditions, and then assessed the relationship between initial endurance and annual survival by releasing these individuals in two outdoor enclosures (see Methods). The treatments were carefully calibrated to mimic full feeding and dietary restriction compared with the favourable conditions of our enclosures (see Table S3 in Supplementary Information). Overall, individuals gained endurance as they grew up (paired Student's t-test, $P < 0.001$; average individual change: 158 s ± 19.4 s.e.). The ontogenic change in endurance was affected by an interaction between diet and initial endurance ($F_{1,90} = 10.9$, $P < 0.01$): under dietary restriction, initial endurance had no effect on the change in endurance ($F_{1,28} = 1.34$, NS); in contrast, the performance of fully fed juveniles with low initial endurance rose markedly, whereas the performance of individuals with high initial performance dropped ($F_{1,29} = 58.9$, $P < 0.001$; Fig. 3). Thus, individual differences in endurance were

Table 2 **Natural selection on initial endurance, body size and body condition**

	Summer survival			Annual survival		
	Test statistics	Estimates (±s.e.)	Gradient	Test statistics	Estimates (±s.e.)	Gradient
Fixed effects						
Endurance (linear)	$F_{1,344} = 6.42$†	0.465 ± 0.183	0.104	$F_{1,343} = 4.43$†	0.268 ± 0.127	0.120
Body size (linear)	$F_{1,344} = 7.17$‡	0.341 ± 0.127	0.077	$F_{1,343} = 7.45$‡	0.335 ± 0.123	0.150
Condition (linear)	$F_{1,344} = 3.3$*	0.249 ± 0.137	0.056	$F_{1,343} = 1.27$	0.146 ± 0.130	0.065
Condition (quadratic)	NS	NS	NS	$F_{1,343} = 5.92$†	0.228 ± 0.094	0.102
Random effects						
Enclosure	$\chi^2 = 39.39$§	0.491	–	$\chi^2 = 60.83$§	0.743	–
Family	$\chi^2 = 52.56$§	0.531	–	$\chi^2 = 52.63$§	0.441	–

Natural selection was studied over the summer following birth (summer survival), and over the first year of life (annual survival). Endurance, body size and body condition were standardized (zero mean, unit variance) for 431 lizards (9 enclosures, 84 families). Survival probability was modelled with mixed-effects logistic regressions using the GLIMMIX macro in SAS[28]. The final models were obtained after stepwise multivariate analyses. We used linear terms to test for patterns of directional selection on single traits, quadratic terms to test for patterns of stabilizing or disruptive selection on single traits, and mixed polynomial terms to test for correlational selection on pairs of traits. Enclosure effects and family effects nested within enclosures were modelled as random effects. Models adequately fitted the data[28], and qualitatively matched non-parametric, cubic spline regressions of fitness functions[29]. Parameter estimates are given on a logistic scale. Standardized selection gradients are obtained from the slope terms of the logistic regression[30].
*$0.05 < P < 0.10$, †$P < 0.05$, ‡$P < 0.01$, §$P < 0.001$.

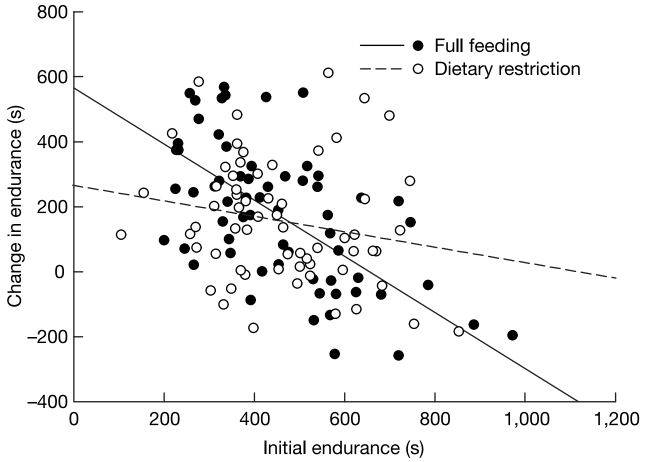

Figure 3 Ontogenic change in endurance depending on diet and initial endurance. Straight lines are regression lines in full feeding conditions (solid line) and under dietary restriction (dashed line). The one-month change in endurance was modelled as a function of diet, sex, initial endurance and interactions between these factors. Blocks (trays, see Methods) and family within blocks were treated as random effects. The Pearson product-moment correlation coefficient between initial endurance and endurance at the age of one month was higher under dietary restriction ($r = 0.57$) than in the full feeding treatment ($r = 0.21$, Student's t-test on z-transformation, $P = 0.018$).

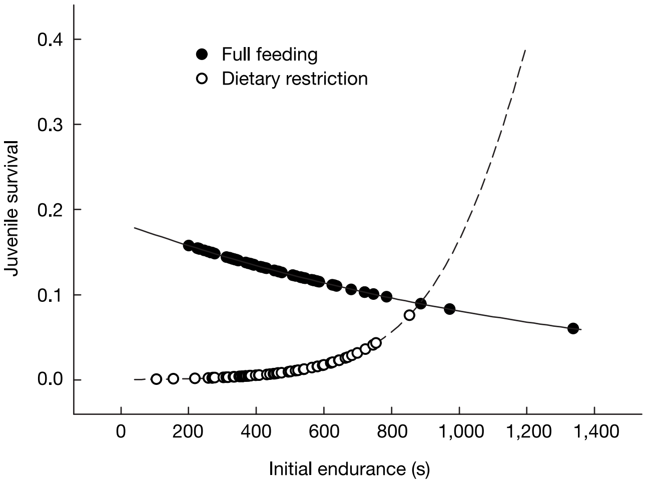

Figure 4 Fitness functions of initial endurance depending on dietary conditions experienced during the first month following birth (filled circles and solid line, full feeding; open circles and dashed line, dietary restriction). Data have been back-transformed from values predicted by the logistic regression; each circle corresponds to a single individual. The annual survival probability was significantly affected by dietary conditions ($F_{1,92} = 7.29$, $P = 0.0083$) and by an interaction between dietary conditions and initial endurance ($F_{1,92} = 2.98$, one-tailed test of the directional hypothesis, $P = 0.04$), while controlling for differences between enclosures and amongst families.

consistent across ontogeny only under dietary restriction (ANOVA on subject effect, $F_{63,64} = 2.17$, $P < 0.01$, intra-class correlation coefficient $r = 0.37$; with rich diet, $F_{62,63} = 0.99$, NS). We therefore expected that after releasing both groups of lizards in field enclosures, the effect of natural selection on initial endurance would be stronger in the dietary restricted group than in the fully fed group, and found support for this prediction (Fig. 4). Thus, dietary conditions experienced early in life influence both the ontogenic consistency of endurance and the predictability of natural selection on variation in initial endurance.

Previous evidence of ontogenic consistency of physical performance was mainly restricted to post-growth life-history stages[4], and as far as we know, no study so far has tested the hypothesis that ontogenic consistency could be sensitive to environmental conditions. The pattern of ontogenic change reported here suggests that low- and high-performance juveniles utilize different resource allocation strategies when resources are abundant. Low-performance individuals might allocate resources to muscles and aerobic metabolism resulting in enhanced locomotor performance, whereas high-performance individuals would either reallocate resources towards growth and maturation, or direct more energy to fat reserves with impaired locomotion as a side effect[16,17]. Our finding of a positive correlation between change in endurance and growth in body size under full feeding conditions ($F_{1,29} = 7.37$, $P = 0.01$), whereas no correlation arose under dietary restriction ($F_{1,28} = 1.71$, NS), lends weight to this allocation trade-off hypothesis.

Evolutionary physiologists have assumed ontogenic consistency of locomotor traits and a strong, positive relationship between locomotor performance and darwinian fitness[3]. Our results challenge these basic tenets of evolutionary physiology: ontogenic consistency depends upon environmental conditions, thus limiting the predictability of natural selection on performance at birth. Variation in food availability occurs in wild populations of the common lizard[18]; our experimental results predict that natural selection on initial endurance is ineffective in high-food years or locations. Under unfavourable conditions, other mechanisms such as behavioural compensations (for example, active versus sit-and-wait foraging strategies[7]) or trade-offs (for example, differential exposure to predators or parasites[9]) might also weaken selection on initial endurance. Lack of ontogenic consistency should further cause low heritability of endurance at the yearling and adult stages, and therefore contribute to the maintenance of individual variation for physical performance at all life-history stages.

There are other contexts in which the paradox arises of a trait measured at birth being a positive influence of darwinian fitness early in life, but having little effect on fitness at later stages or over the whole life[15,19]. Persistently high heritability for such a trait was previously explained by changes during the life cycle in how selection operates[19]. Our study emphasizes that locomotor traits are embedded in a more complex, dynamic phenotype, and provides evidence for the role of ontogeny to loosen the link between the initial value of the trait and darwinian fitness[20]. As a consequence, specific conditions applied early in life would seem necessary to counter developmental effects on endurance and to ensure the expression of a genetic predisposition to high physical performance. ☐

Methods

Species

The common lizard is viviparous (modal clutch size: 5–6 eggs) and offspring are autonomous at birth. Lizards used in this study were monitored in enclosed populations located at the Ecological Research Station of Foljuif (60 m above sea level, 48°17′ N, 2°41′ E). Our selection study avoids the limitations of previous works[2] by using multivariate selection analysis on both performance and morphological traits[3]; by controlling survival estimates for capture and movement heterogeneity; and by using outdoor enclosures to limit environmental heterogeneity.

Maternal effects

To evaluate the effects of maternally experienced population density on offspring performance, a sub-sample of our populations (257 offspring from 51 families) was manipulated in 1999 so that reproductive females experienced two levels of population density[10]. During the gestation interval for the young born in 2001, the population size was 9.6 individuals (±3.6 s.e.) in the low-density and 21.3 individuals (±4.4 s.e.) in the high-density enclosures ($\chi^2 = 9.0$, $P < 0.01$). We also defined three age classes of mothers: 2-year-old, 3-year-old, and older.

Sampling protocol

In June 2001, 89 gravid females were removed from outdoor enclosures and maintained in the laboratory. Females were measured (snout–vent length) and weighed regularly during gestation. After parturition, females were weighed and offspring were sexed, sized (snout–vent length, tail length, mass), individually marked (toe-clipping) and isolated in individual terraria. Endurance was measured on the day following birth.

Endurance trials

Endurance was measured on a circular treadmill[21]. Lizards (warmed up and maintained at a temperature close to their field optimum) were stimulated to run at a constant speed by gently tapping the base of their tail with a soft paintbrush. Endurance capacity was measured as the time to exhaustion (to the closest second), signalled by the lack of response after 10 consecutive taps[22]. There was a highly significant correlation between first and second measurements ($r = 0.78$) (ANOVA on 70 offspring from 14 families measured two days apart, log-transformed endurance, $F_{69,70} = 10.18$, $P < 0.001$).

First analysis of natural selection

In July 2001, all offspring were released in nine enclosures, each receiving 10 families, 21 adults (including mothers) and 16 yearlings. Two recapture sessions took place in August 2001 (average age = 33 days ± 7.7 s.d.) and June 2002 (average age = 311 days ± 9.9 s.d., all individuals were then removed to the laboratory). Capture probabilities in August 2001 were estimated by fitting probabilistic models of individual capture-recapture histories[23]. Estimates were very close to one, allowing us to assume that individuals not seen in August 2001 had died before that census.

Dietary effects on ontogenic consistency and second analysis of natural selection

In 2002, we performed a laboratory manipulation of rations during the four weeks following birth. Two food treatments were designed on the basis of our unpublished growth data (used to calibrate a realistic distribution of postnatal growth rates), and physiological data[24] (to translate growth rates into expected food intakes in the laboratory). Dietary restriction was set to a delivery of 15 mg day^{-1} of house cricket larvae (*Acheta domesticus*, 3–5 mm size) during the first week, and raised each subsequent week to match the pattern of individual growth (see Table S4 in Supplementary Information). The full feeding treatment followed a parallel pattern in a 1:3 ratio. Over the entire manipulation, average food provision was 20.5 mg day^{-1} in the low-food treatment and 61.5 mg day^{-1} in the high-food treatment. To compare siblings, we selected two males and two females from 32 families and allocated one individual of each sex to each treatment. We recorded endurance at the age of one day and at the end of the manipulation (age 33 days). Siblings were then released at random in one of two outdoor enclosures where populations of 13 adults, 30 yearlings and 10 juveniles had been established two months earlier. All individuals were removed from the enclosures in late May of the following year. The difference in annual survival probabilities between this and the first analysis of natural selection is likely to reflect costs of settlement in already populated enclosures and costs of translocation from the laboratory[25]. The directional prediction that dietary conditions should affect the relationship between endurance and survival probability was tested with a mixed-effects logistic regression using a one-tailed test[26].

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Correspondence and requests for materials should be addressed to J.-F.L.G. (j.f.l.galliard@bio.uio.no).

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Predator-induced behaviour shifts and natural selection in field-experimental lizard populations

Jonathan B. Losos[1], **Thomas W. Schoener**[2] & **David A. Spiller**[2]

[1] *Department of Biology, Campus Box 1137, Washington University, St Louis, Missouri 63130, USA*
[2] *Section of Ecology and Evolution and Center for Population Biology, University of California, Davis, California 95616, USA*

The role of behaviour in evolutionary change has long been debated. On the one hand, behavioural changes may expose individuals to new selective pressures by altering the way that organisms interact with the environment, thus driving evolutionary divergence[1–3]. Alternatively, behaviour can act to retard evolutionary change[4–6]: by altering behavioural patterns in the face of new environmental conditions, organisms can minimize exposure to new selective pressures. This constraining influence of behaviour has been put forward as an explanation for evolutionary stasis within lineages[4,7–9] and niche conservatism within clades[10,11]. Nonetheless, the hypothesis that behavioural change prevents natural selection from operating in new environments has never been experimentally tested. We conducted a controlled and replicated experimental study of selection in entirely natural populations; we demonstrate that lizards alter their habitat use in the presence of an introduced predator, but that these behavioural shifts do not prevent patterns of natural selection from changing in experimental populations.

Caribbean *Anolis* lizards are ideal subjects for examining the evolutionary role of behaviour. Comparative and experimental studies indicate that populations alter their habitat use in response to the presence of competing or predatory species[12–14]; observations reveal that individuals change their behaviour over short periods of