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Evolution of maximal endurance capacity: natural and sexual selection across age classes in a lizard

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ABSTRACT

Hypothesis: One of the basic tenets of evolutionary physiology is that physical performances and fitness are tightly linked.

Question: Are phenotypes with exceptional locomotor capacity strongly favoured by natural and sexual selection?

Organism: A ground-dwelling, actively foraging and non-territorial lizard species, *Lacerta vivipara*.

Methods: We analysed the relationship between morphology (body size and condition) and maximal endurance capacity in three age classes (juveniles, yearlings, and adult males). We then tested whether morphology and endurance capacity predicted variation in annual body growth, annual survival, and reproductive success.

Results: The large variation in maximal endurance capacity observed at hatching has a genetic basis. Endurance capacity increased with body size in juveniles and with body condition in juveniles and yearlings. Endurance capacity was not correlated with annual body growth at any age class. Positive, directional viability selection on endurance capacity was detected for juveniles and yearlings, but not for adult males. Endurance capacity was weakly, positively correlated with male reproductive success. Natural selection in juveniles and sexual selection in adult males was non-linear and the strength of selection decelerated with endurance capacity.

Conclusion: In the common lizard, selection on maximal performances is non-linear and varies between age classes. This pattern of weak and inconsistent selection could explain the maintenance of considerable genetic variation of locomotor performance within populations.

Keywords: locomotor performance, microevolution, reproductive success, squamate reptiles, survival.

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INTRODUCTION

Quantitative variation in locomotor performances, like endurance capacity (time to exhaustion at fast sustainable speed) or sprint speed (maximal burst speed), has been investigated extensively over the past two decades, in particular among squamate reptiles (Bennett and Huey, 1990; Garland and Losos, 1994; Irschick and Garland, 2001). Traditionally, the evolutionary physiology approach to locomotor performances combines biomechanical studies of the proximate determinants of locomotion with ecological and evolutionary studies of the relationship between locomotor traits and fitness (Bennett and Huey, 1990; Losos, 1990). A basic tenet of evolutionary physiology is that locomotor performances can serve as proxies of whole-organism capacities at ecologically relevant tasks, such as foraging, mating or predator avoidance (Bartholomew, 1966; Huey and Stevenson, 1979; Bennett, 1980; Arnold, 1983; Pough, 1989; Irschick and Garland, 2001). Here we evaluate this hypothesis by testing for natural and sexual selection on maximal endurance capacity in three distinct age classes of the common lizard (*Lacerta vivipara* Jacquin 1787).

Maximal endurance capacity can be measured by running individuals at fast sustainable speed on a treadmill in the laboratory (Bennett and Huey, 1990). Inter-individual variability in maximal endurance capacity is ubiquitous in animals, including humans (e.g. Garland, 1984; Walker and Hill, 2003). Intraspecific variation in endurance capacity has been related to enzymatic, physiological, and morphological attributes, such as body size, muscle mass, and aerobic capacity in lizards (e.g. Garland, 1984; Garland and Else, 1987). Heritability of inter-individual variation in maximal endurance capacity has also been detected in some species, and responses to selection on endurance capacities can therefore be expected in these species (e.g. Tsuji *et al.*, 1989). Furthermore, maximal endurance capacity measured in the laboratory sets an upper limit on all field activities that require fast sustainable speed (e.g. movement patterns). Maximal endurance capacity might therefore constrain how individuals perform at ecologically relevant tasks in the field (Arnold, 1983; Garland and Else, 1987; Hertz *et al.*, 1988; Bennett and Huey, 1990; Irschick and Garland, 2001). For example, maximal endurance capacity has been used as an indicator of foraging mode (Huey *et al.*, 1984), foraging activity (Nagy *et al.*, 1984), mate search ability (Cuthill and Houston, 1997), and predator avoidance capacity (Christian and Tracy, 1981). In lizards, high endurance capacity may be required for foraging, searching for mates, courtship, male–male combats, and activities associated with social dominance like territorial defence (discussed in Huey *et al.*, 1984; Garland, 1999; Sinervo *et al.*, 2000).

There are still few animal populations for which the strength of selection on endurance capacities has been documented (for a review of field studies that examined selection on locomotor performances, see Irschick *et al.*, 2008). For example, Miles *et al.* (2000) increased endurance capacity in gravid female side-blotched lizards (*Uta stransburiana*) by decreasing their reproductive effort and found that viability selection favoured experimentally increased endurance capacity in gravid females. However, the strength of natural selection on stamina was low in other species (Le Galliard *et al.*, 2004). With regard to sexual selection, endurance capacity predicts the intensity of agonistic behaviours and threat displays, as well as social dominance and field territorial activities in some, but not all, lizard species investigated to date (Garland *et al.*, 1990; Robson and Miles, 2000; Brandt, 2003; Perry *et al.*, 2004). Dominance during male–male competition may not necessarily translate into higher male reproductive success since female choice can select for performance capacities unrelated to male–male competition (Lailvaux and Irschick, 2006). More data on male reproductive success in the wild are needed to assess whether whole-organism performances like endurance capacity are involved in sexual selection (Husak *et al.*, 2006; Lailvaux and Irschick, 2006).

The lack and inconsistency of fitness data on endurance capacities might reflect technical difficulties inherent to most studies of selection in natural populations. In addition, several factors could reduce the strength of selection on locomotor performances. Endurance capacity may trade off with other fitness traits, like reproductive effort, sprint speed, or body condition (Ghalambor *et al.*, 2003; Le Galliard *et al.*, 2004). When energy acquisition is limited, the presence of physiological trade-offs between endurance capacity and other fitness traits means that individuals that allocate more energy to endurance traits will suffer from reduced energy allocation to other relevant fitness traits. Hence, putative advantages to perform better at tasks requiring high levels of stamina in the field may be cancelled out by costs of reduced performances in other ecologically relevant tasks (e.g. Clobert *et al.*, 2000; van Damme *et al.*, 2002). In addition, behaviour might play an important role since selection on maximal locomotor performances depends on how individuals make use of their performance capacities in the field (Hertz *et al.*, 1988; Irschick, 2003; Irschick *et al.*, 2005). Animals may compensate for their low locomotor performances by using their maximal physiological capacities more often in the field (e.g. Husak and Fox, 2006). Another possibility is that individuals compensate for their poor locomotor performances by adjusting their behavioural strategies (Brodie, 1989). For example, the burden of gestation in female lizards is often associated with diminished locomotor capacities that compromise escape abilities and sensitivity to predation in gravid females. Consequently, pregnant female lizards rely more on crypsis than boldness to compensate for their greater susceptibility to natural predators (Bauwens and Thoen, 1981).

We evaluated the relationship between morphology, endurance capacity, and fitness in three age classes (male and female juveniles, male and female yearlings, and adult males aged 2 or more years) of the common lizard, a ground-dwelling and actively foraging lizard species with poor sprinting abilities relative to other Lacertidae (Bauwens *et al.*, 1995). Our study focuses on endurance capacity because this trait is important in nature for predator–prey interactions, foraging, and social interactions in the common lizard (Clobert *et al.*, 2000; Le Galliard *et al.*, 2004). The study was conducted in outdoor enclosures that mimic the natural microhabitats used by common lizards and the social setting where selection takes place in the wild (Le Galliard *et al.*, 2004). This protocol avoids some shortcomings of selection studies in natural populations by standardizing environmental conditions and controlling for heterogeneity in detection probability among individuals. We present analyses of the relationship across three age classes (juveniles, yearlings, and adult males) between morphology (body size and body condition), maximal endurance capacity, and three fitness components: annual body growth, annual survival, and male reproductive success. This is done by running multivariate selection analyses on both endurance capacity and morphological traits and measuring standardized selection gradients (Lande and Arnold, 1983). We also complement the sexual selection analyses with results from staged encounters designed to test whether endurance capacity predicts dominance during male–male competition. Our analyses are aimed at testing three hypotheses:

1. Endurance capacity should be a strong predictor of annual body growth and survival probability.
2. Natural selection on maximal endurance capacity should decline with age if younger

animals make more use of their maximal capacities and are more susceptible to mortality factors than adults (Husak and Fox, 2006).

3. Maximal endurance capacity should constrain dominance and mate searching abilities in the common lizard, and thus predict male mating success.

STUDY SPECIES AND WORKING HYPOTHESES

The common lizard *Lacerta vivipara* inhabits cool and humid habitats across Eurasia. Natural populations include three main age classes (juveniles; yearlings, 1 year old; adults, ≥2 years old) that differ among each other in patterns of body growth, survival, and reproduction. The first stage is characterized by strong viability selection (~20–30% annual survivorship) and rapid somatic growth (approximately five-fold annual increase in body mass), and therefore corresponds to a critical stage to investigate natural selection in this species. The second stage has higher average survival probability (~30–40% annual survivorship) together with reduced somatic growth but pronounced growth of reproductive tissues and sexually dimorphic traits. Some females may start reproduction at the age of one year in lowland areas. The third stage is characterized by high average survival (~40–50% annual survivorship) and poor body growth but intense sexual activity. Adults are also socially dominant over yearlings and juveniles during competition for space (Lecomte *et al.*, 1994). In our study site, the reproduction mode is ovoviviparous. Mating occurs in April and May each year. Parturitions start from the beginning of June through the end of July. Females lay on average five transparent, soft-shelled eggs (range 1–12). Offspring hatch shortly after parturition and are autonomous. All sex and age classes share overlapping territories of a few hundred square metres where routine movements and competition take place (Lecomte *et al.*, 1994). The natural structure of the peat bogs, heathlands, and humid grasslands inhabited by this species is typically heterogeneous. Basking sites and shelters (rock shoulders and trees) are interspersed with foraging areas (mostly herbaceous and heather layer). Thus, common lizards must adjust their microhabitat use to optimize foraging and basking activities according to seasonal and diurnal changes in thermal conditions. We hypothesize that ability to shift between microhabitats, to acquire basking sites and retreats, as well as foraging success, will be constrained by maximal endurance capacity in this actively foraging species.

Natural predators documented in the wild are generalist birds and mammals (e.g. crows, magpies, foxes) and two specialized snake species (the adder *Vipera berus* and the smooth snake *Coronella austriaca*). All these predators were excluded from our enclosures. However, the density and impact of natural predators in the wild is poorly documented (Strijbosch, 1981) and common lizards are most often found in habitats with few predators (personal observations). Furthermore, competition with other lizard species is rare in nature. Population densities are among the highest recorded for lizards (>1000 adults and yearlings per hectare) and social selection is therefore intense. Social selection takes the form of competition between congeners to acquire and defend critical basking sites, shelters, and foraging sites, as well as competition for food (Massot *et al.*, 1992; Lecomte *et al.*, 1994; Le Galliard *et al.*, 2005). Experimental manipulations of population density show strong density-dependent feedback through juvenile mortality and body growth, adult fecundity, and immigration (Massot *et al.*, 1992; Meylan *et al.*, 2007). We therefore hypothesize that maximal endurance capacity sets a physiological limit to the level of social dominance directly relevant to social selection.

The mating system of the common lizard is polygynandry and females mate with one to five different males (Fitze *et al.*, 2005). Males emerge earlier than females by an average of 3–4 weeks and therefore face conditions where food availability is more limited and thermal conditions are sub-optimal. Early emergence of males allows maturation of spermatozoa and completion of a spring moult after which males become sexually active. The mating season lasts for 2–4 weeks after females emerge. Males patrol their home range in search of receptive females. Males can also chase away other males to ensure access to females and adult males use social dominance to access basking sites during the mating season (Lecomte *et al.*, 1994). Mating lasts from a couple of minutes up to several hours. During mating attempts, a male grasps the female on the posterior abdomen with his mouth, and twists his body around the female to introduce his hemipenis into the female's cloacae. Mating attempts do not always result in successful copulations. If, as stated above, endurance constrains foraging success and habitat use in adult males, we first predict that endurance capacity should be critical for their survival and sexual activity in spring. We also hypothesize that the reproductive success of a male should be limited by its maximal endurance capacity. Maximal endurance capacity may be important for exploitation competition to locate receptive females, for social dominance and interference competition among males, and for the ability to copulate with a female.

METHODS

Source and study populations

Individuals in this study were source-, first- or second-generation lizards captured in natural populations located in an upland area (Lozère, 1500 m above sea level, 44°27′N, 3°44′E) of southern France. Source-generation lizards were transferred directly from the upland area to the experimental area, while first- and second-generation lizards were progeny of the source generation born in the experimental site (for more details on translocation procedures, see Boudjemadi *et al.*, 1999). More details on the source populations are given for each analysis reported below. All lizards were given a unique code by toe-clipping, which has no effect on survival or endurance capacity in this species (unpublished results). Juveniles and yearlings of both sexes and adult males were measured for their endurance capacity in the laboratory (see below) and maintained for one year after the endurance measurements inside outdoor enclosures. This allowed us to investigate the relationship between endurance capacity and fitness in the three age classes. Outdoor enclosures are located at the Research Centre in Experimental and Predictive Ecology at Saint-Pierre-lès-Nemours (Seine et Marne, 60 m above sea level, 48°17′N, 2°41′E; www.foljuif.ens.fr). The enclosures consist of enclosed patches (10 × 10 m) of natural grassland enhanced with basking sites and refuges (rock and wood piles). Food is not supplemented artificially – only natural prey (mostly insects and spiders) are available in the enclosures. Enclosed populations are protected from terrestrial predators by plastic fences and from avian predators by nets. The design therefore mimics the natural microhabitats encountered by common lizards and the demographic conditions (density, age and sex structure) under which social selection takes place in nature.

Endurance trials

Circular racetracks and motorized treadmills are two common techniques to measure endurance capacity (Garland, 1984; Bennett and Huey, 1990). Here, maximal endurance capacity was measured by the same person with juveniles, yearlings, and adult males on a circular racetrack (external diameter: 60 cm) covered with cork to ensure traction. Lizards were warmed up to 31–32°C before trials and the racetrack was maintained at 30–32°C. This choice of temperature matched the average body temperature in the field (modal range: 30–33°C) and the preferred body temperature of this species (~32°C). Lizards were stimulated to run at a constant speed by gently tapping the base of their tail with a soft paintbrush. The speed was chosen based on other studies with similarly sized lizard species and relevant movement rates in the natural habitat (Garland, 1994; Sorci *et al.*, 1995; Clobert *et al.*, 2000). The speed was set at $0.36\ \mathrm{km \cdot h^{-1}}$ for juveniles and at $0.66\ \mathrm{km \cdot h^{-1}}$ for yearlings and adults. Each trial was stopped upon exhaustion of the individual, estimated by the loss of a righting response after 10 consecutive taps on the tail (Huey *et al.*, 1984). Endurance capacity was measured as the time to exhaustion (to the closest second). The probability distribution of endurance data was skewed with many low-performance individuals and a few champions (Le Galliard *et al.*, 2004). We therefore log-transformed the endurance values to ensure a more symmetric and homogeneous distribution. However, results are reported on the original measurement scale for the sake of easier interpretation.

Assessment of social dominance

We assessed the relationship between maximal endurance capacity and social dominance following a protocol designed by Garland *et al.* (1990). In spring 2001, we ran 100 staged encounters in the laboratory with 90 adult males measured for their endurance capacity one week before. Pairs of adult males were introduced in a large cage (130 × 47 × 35 cm) heated in its centre with an incandescent bulb (40 W). Adult males within a pair were matched for their body size to the nearest 2 mm to avoid confounding effects of body size on agonistic interactions. The cage was fenced with plastic walls and littered with peat. Live food (cricket larvae) and water were provided *ad libitum*. The thermal gradient ranged from room temperature (19–20°C) at each end of the cage to 35°C under the bulb in the centre of the cage. Males were in visual contact throughout each staged encounter and competed for the limiting heating resource located at the centre of the cage. After an initial period of 5 min, a naive observer watched each encounter through a blind for 15 min. For each male, the observer measured the time spent basking (to the nearest second) and counted aggressive approaches, tail quivers (rapid movement of the tail at the approach of the other lizard), foot stomps (rapid stomp of the front feet at the approach of the other lizard), retreats (movements away from the other lizard), and escape attempts (scratching and climbing behaviours to escape the cage). We were also able to identify a ‘winner’ based on subjective observation of aggressive and submissive behaviours and assessment of domination for the basking site.

Assessment of natural and sexual selection

We measured three components of natural and sexual selection: the annual body growth in each age class, the annual survival in each class, and the reproductive success of adult males.

For body growth, we calculated for each age class the difference in body size (snout-to-vent length, SVL) and body condition between capture occasions one year apart. Body condition was assessed by using the residuals from a linear regression of body mass on SVL since there was no indication of non-linearity within a given age class. We analysed the relationship between body growth in outdoor enclosures and endurance capacity using a mixed-effect linear model with endurance capacity as a fixed effect and enclosure identity as a random effect. Initial size was included as a covariate since change in size decreases with initial SVL in the common lizard. More details on additional covariates are given for each analysis below.

For each lizard, we assessed survival status (dead or alive) from the time of measurement to the following year (see Results section for more detail). For the analysis of survival probabilities, we used both an exploratory method and a multivariate logistic regression. Models were run with survival status (dead or alive) as a response variable. Endurance capacity, body size, and body condition before selection were treated as explanatory covariates and all models included a logit link function and binomial error terms. The exploratory method was used to detect non-linearity in the fitness function. Generalized additive models (GAM) were fitted to the survival data using a linear term, cubic spline smoothing terms for each covariate, and a generalized cross-validation to select the degrees of freedom of the cubic spline smoothers (Hastie and Tibshirani, 1990; Schluter and Nychka, 1994). We also ran a mixed effect multivariate logistic regression to test the significance of linear and quadratic terms of selection (Littell *et al.*, 1996). Enclosure identity was added as a random effect in these models. For each age class, the multivariate logistic regression included additive linear and quadratic terms for endurance capacity, body size, and body condition. We standardized all covariates prior to analyses and calculated standardized selection gradients following Janzen and Stern (1998). Standardized selection gradients provide a standardized measure of the strength of selection acting on a trait and are useful for comparisons across study systems (Lande and Arnold, 1983; Kingsolver *et al.*, 2001). Since quadratic terms were not significant here, we report only on the linear selection gradients (termed β thereafter).

Sexual selection on endurance capacity in adult males was investigated by counting the number of offspring sired by each male in the next breeding season. A tissue sample (tip of the tail) of each adult male was collected before release and stored in ethanol 70° for subsequent DNA extraction. Furthermore, all pregnant females from the same enclosures and recaptured during the next breeding season were kept in individual cages in the laboratory until they gave birth. A sample of the tip of the tail of each offspring born from those females was taken at hatching for DNA extraction. The DNA of all offspring and putative fathers was amplified at 5–6 microsatellite markers. The siring success of all adult males measured for their endurance capacity was then scored unambiguously by comparing microsatellite data of offspring and all candidate fathers (see Fitze *et al.*, 2005, for greater methodological detail). The number of offspring sired by each male (siring success) was strongly correlated with the number of mating partners, or mating success (Pearson's correlation coefficient $r = 0.80$, $P < 0.0001$, $n = 71$). Thus, both siring success and mating success provided relevant metrics to measure the strength of sexual selection acting on endurance capacity (Arnold and Wade, 1984). For the analysis of mating and siring success of adult males, we proceeded as for survival analysis. However, since both mating and siring success data conformed to a Poisson distribution, all models were run with a loglink function and Poisson error terms. The procedure MIXED of SAS v8.2 was used for analysis of endurance and body growth, and the procedure GLIMMIX was used for analysis of viability and sexual selection

(Littell *et al.*, 1996). Model selection was performed backwards with a type I error risk $\alpha = 0.05$ until all non-significant terms were removed from the starting model.

RESULTS

Natural selection in juveniles

In June–July 2001, we studied endurance capacity of 447 hatchlings of 90 families. Hatchlings were born in the laboratory from gravid females captured in a natural upland population ($n = 190$) and from gravid females captured in lowland outdoor enclosures ($n = 257$). These gravid females had been maintained for 2 years in the outdoor enclosures for the purpose of investigating the mechanisms of population regulation (for more details, see Le Galliard *et al.*, 2003). In 1999, population density was manipulated by releasing 20 adults and a mean (± standard error) of 36.5 ± 2.4 offspring in eight enclosures, or 40 adults and a mean of 71.2 ± 3.9 offspring in eight enclosures. In 2001, the estimated population size was 9.6 ± 3.6 individuals in the low-density enclosures and 21.3 ± 4.4 individuals in the high-density enclosures, a significant difference (log-linear model: $\chi^2 = 9.0$, d.f. = 1, $P < 0.01$). This design allowed us to classify the lowland females in a low-density or a high-density group.

Gravid females were kept in individual cages in the same laboratory room until they laid their eggs. After completion of hatching, hatchlings were isolated from their mother and their sex was determined by counting ventral scales (Lecomte *et al.*, 1992). We measured hatchling SVL to the nearest millimetre and hatchling body mass to the nearest milligram. Endurance capacity was measured on the day following birth. The repeatability of the endurance measurements was estimated on 70 hatchlings from 14 families measured 2 days apart and was highly significant (ANOVA, log-transformed endurance capacity, $F_{69,70} = 10.18$, $P < 0.001$; intra-class correlation coefficient, $r = 0.78$). We released 431 hatchlings one day after the endurance measurements in outdoor enclosures maintained at similar population densities for one year (Le Galliard *et al.*, 2005).

Endurance capacity at hatching varied from 36 s to 1677 s (mean ± standard deviation: 222 ± 154 s). Results of an investigation of proximate factors of endurance capacity at hatching and of natural selection on endurance capacity at the juvenile stage are reported elsewhere (Le Galliard *et al.*, 2004). We summarize these results briefly here. First, the analysis of interfamilial variation in endurance capacity of hatchlings showed significant broad-sense heritability ($h^2 = 0.40$). Heritable variation was not caused by the presence of few families characterized by poor or champion performances, but resulted from systematic interfamilial variation along the performance axis. In addition, endurance capacity increased with body condition and body size at hatching, and decreased with maternal body size. Endurance capacity was not influenced by maternal condition and birth date. Second, over the entire first year of life, there was additive directional selection on body size and endurance capacity at hatching and additive quadratic selection on body condition. None of the quadratic selection coefficients for endurance capacity and body size was significant, and none of the correlational selection coefficients was significant. Third, selection on endurance capacity at hatching was highly sensitive to the few individuals with the lowest endurance capacities at birth, as suggested by the shape of the fitness function (Fig. 1A, $\beta = 0.120$). Thus, natural selection acted independently on morphology and performance, but selection was nearly neutral for intermediate and higher levels of locomotor performance.

We also measured body growth at the juvenile stage and tested for the relationship between endurance capacity and body growth when controlling for sex, hatching date, and initial body size. Body size more than doubled during the first year of life (mean ± standard deviation: size at hatching = 22.8 ± 1.06 mm, growth = 27.5 ± 11.75 mm). Endurance capacity did not predict body growth ($F_{1,105} = 0.30$, $P = 0.59$). Females grew more than males ($F_{1,105} = 8.55$, $P = 0.004$; contrast = 1.16 ± 0.39 mm [standard error]) and hatchlings born later in the season grew less than early born hatchlings ($F_{1,105} = 59.93$, $P < 0.0001$).

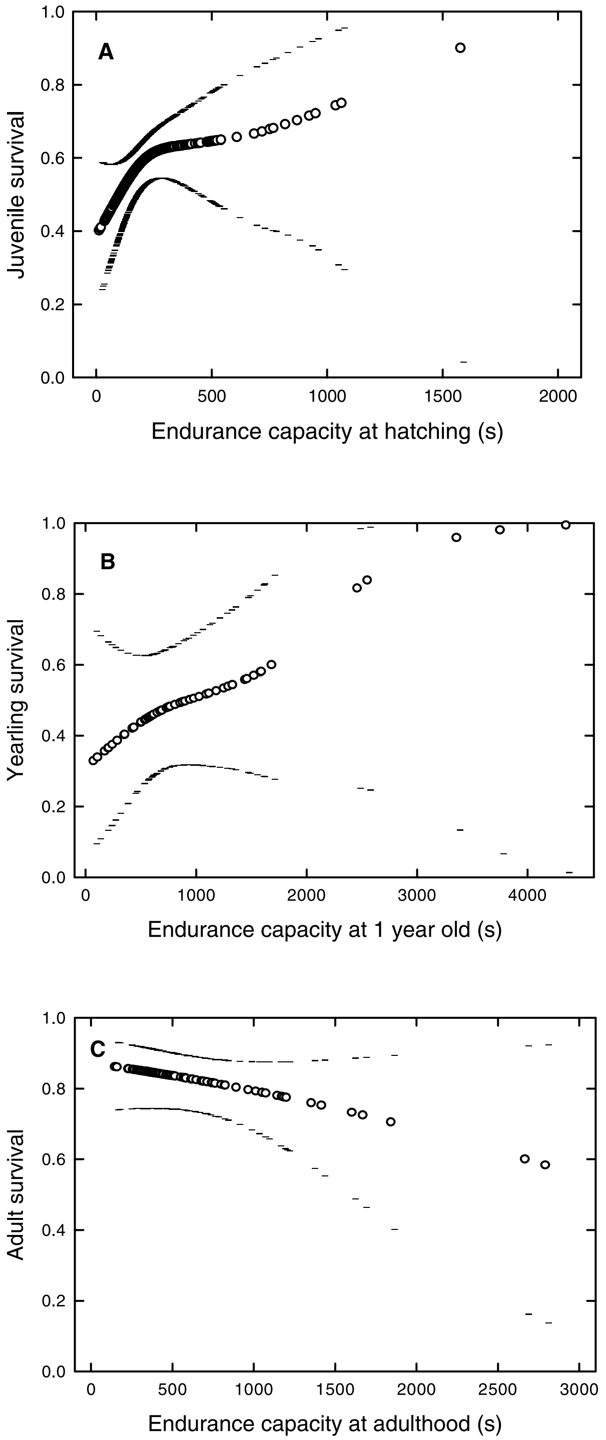
Natural selection in yearlings

Endurance capacity was measured for 59 yearlings in spring 2000 (mean ± standard deviation = 993 ± 836 s, range 73–4351 s). Study animals were captured in outdoor enclosures maintained at low or high population density since 1999. Mean (± standard error) population densities in spring 2000 were 22.2 ± 5.6 individuals in low-density enclosures and 55.2 ± 14.2 individuals in high-density enclosures. Two days after capture, yearlings were measured for their maximal endurance capacity. The repeatability of endurance measurements was strong and highly significant (45 yearlings measured twice, $F_{44,45} = 14.03$, $P < 0.0001$, $r = 0.78$). We first used a multivariate regression to test for the effects of sex, morphology (body size, body condition, and relative hindlimb length), and population density (high vs. low density) on endurance capacity. The only significant variable after backward selection was body condition ($F_{1,43} = 4.45$, $P = 0.04$), and endurance capacity increased with body condition.

The 59 yearlings were released back into their original enclosures at low or high population density. Their survival and body growth until the age of 2 years was then assessed by recapturing all surviving animals in spring 2001. The survival probability was modelled as a function of maximal endurance capacity, population density, sex, body size, and body condition. The only significant predictor of survival probability was maximal endurance capacity, although the test statistic was only marginally significant (logistic regression, $\chi^2 = 3.9$, d.f. = 1, $P = 0.049$) (Fig. 1B). Survivors had greater endurance capacity (mean ± standard error: 1217 ± 191 s, $n = 30$) than yearlings that died during the study year (761 ± 85 s, $n = 29$; $\beta = 0.280$). Annual body growth was greater in males than in females ($F_{1,28} = 14.8$, $P = 0.0006$), but endurance capacity did not explain variation in body growth ($F_{1,28} = 0.08$, $P = 0.78$). A significant correlation between endurance capacity and annual change in body condition from yearlings to adults was observed ($F_{1,30} = 6.76$, $P = 0.01$). Animals with large endurance capacity gained more condition (mass per unit body size) from yearlings to adults than animals with poor endurance capacity.

Natural and sexual selection in adult males

We recorded endurance capacity in 90 adult males during spring 2001 (mean ± standard deviation: 638 ± 441 s, range 84–2794 s). Adult males used in this study were obtained from a single natural population ($n = 36$) and from outdoor enclosures maintained at low and high population densities since 1999 ($n = 54$). A first multivariate analysis tested for the influence of morphology (body size and condition) and geographic origin on endurance capacity and found no significant effects. We then tested for the effects of age (2 years, 3 years, and ≥4 years old) and population density (high vs. low) in the subset of animals obtained from the outdoor enclosures for which we had both precise age data and density


A
Juvenile survival
1.0
0.8
0.6
0.4
0.2
0.0
0
500
1000
1500
2000
Endurance capacity at hatching (s)
B
Yearling survival
1.0
0.8
0.6
0.4
0.2
0.0
0
1000
2000
3000
4000
Endurance capacity at 1 year old (s)
C
Adult survival
1.0
0.8
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Endurance capacity at adulthood (s)

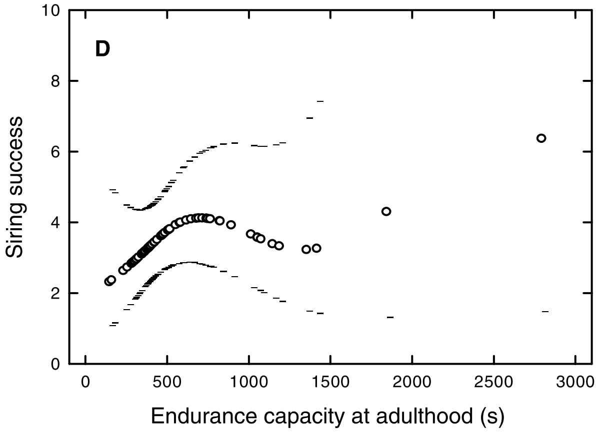

Fig. 1. Fitness surfaces for viability selection on maximal endurance capacity in juveniles (A), yearlings (B), and adult males (C), and for sexual selection on maximal endurance capacity in adult male (D) common lizards. Viability selection is measured by annual survival probabilities. Sexual selection is measured by siring success, the number of eggs sired by each male. Data are predicted values (circles) and confidence intervals (horizontal marks) of a generalized additive model (GAM). The mean and confidence intervals reported in each panel were obtained by adding the linear and partial predictions of the GAM. See text for more detail on the statistical procedures.

treatments. Endurance capacity was affected by a significant interaction between age and population density ($F_{2,48} = 4.91$, $P = 0.01$). Adult males in low-density populations displayed a trend towards larger endurance capacity later in life (Fig. 2), while adult males in high-density populations tended to lose endurance capacity as they aged.

Staged encounters were conducted in the laboratory to assess the relationship between social dominance and locomotor capacity in adult males. None of the aggressive or submissive behaviours recorded was correlated with maximal endurance capacity (ranked based Spearman correlations, all $P > 0.57$, $n = 90$ males). Between two competing males, the difference in endurance capacity did not explain the difference in time spent basking on the heating spot ($F_{1,97} = 1.56$, $P = 0.21$). Furthermore, in 38 staged encounters for which a winner could be identified subjectively (see Methods), the endurance of the winner did not differ significantly from the endurance of the loser (paired t-tests, $t = 1.33$, d.f. = 37, $P = 0.19$; winners: 634 ± 60 s; losers: 543 ± 35 s [standard error]). Thus, endurance capacity was not related to aggressiveness or social dominance in adult males.

In early June 2001, we released 88 of the 90 adult males measured for their endurance capacity in outdoor enclosures maintained at a similar, high population density (16 yearlings, 16 adults, and about 55–60 hatchlings) for one year (Le Galliard *et al.*, 2005). Of the 88 animals released, 67 adult males survived and survivorship of adult males to the next year was not influenced by endurance capacity (multivariate logistic regression, $\chi^2 = 1.17$, d.f. = 1, $P = 0.28$, $\beta = -0.073$), body size, body condition, geographic origin or age (all $P > 0.08$). However, given the sample size and low mortality of adult males, the statistical power of a logistic regression between survival and standardized endurance capacity to detect a meaningful strength of selection ($|\beta| = 0.120$) (see Irschick *et al.*, 2008) was not entirely satisfactory [power = 0.55 computed from equation (1) in Hsieh *et al.* (1998)]. Similarly,

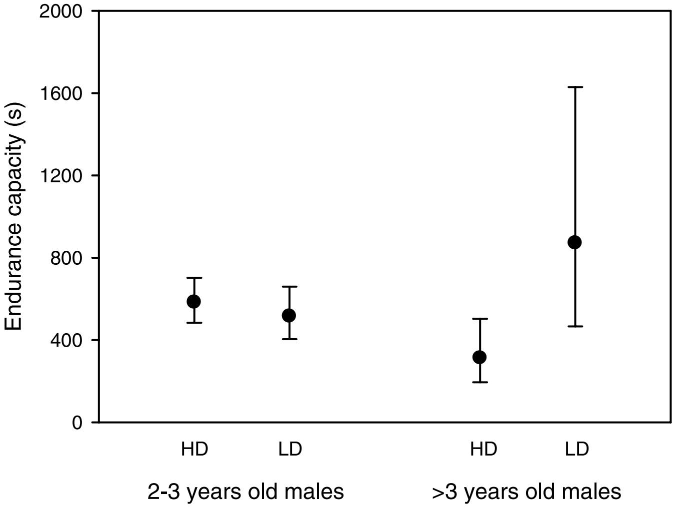

Fig. 2. Variation in endurance capacity in adult male common lizards according to age and population density. Data are means with 95% CI per age class and density treatment. Age (2 years old, 3 years old, and ≥4 years old) was best modelled by separating young males (2 and 3 years old) from older males.

endurance capacity did not predict annual growth in body size or annual change in body condition (size: $F_{1,52} = 0.58$, $P = 0.54$; condition: $F_{1,52} = 0.27$, $P = 0.60$). Growth was only affected by translocation (size: $F_{1,52} = 21.82$, $P < 0.0001$; condition: $F_{1,52} = 5.09$, $P = 0.03$). Animals imported from the natural population just before the study grew larger and heavier than animals obtained from the outdoor enclosures.

All surviving males were recaptured in spring 2002 and measured for body size and mass. The siring success (number of sired eggs) of surviving adult males varied from 0 to 19 sires (mean ± standard deviation: 3.51 ± 3.69, $n = 67$) and their mating success (number of genetic mate partners) varied from 0 to 5 mating partners (1.45 ± 1.27). A non-linear model of sexual selection suggested stabilizing selection on endurance capacity (Fig. 1D). However, in the log-linear regressions, none of the quadratic selection coefficients was significant (all $P > 0.05$). Sexual selection on adult males was significant and positive for body size in the case of siring success (log-linear regressions, siring success: $\chi^2 = 4.28$, d.f. = 1, $P = 0.04$; mating success: $\chi^2 = 2.38$, d.f. = 1, $P = 0.12$), but not for endurance capacity (siring success: $\chi^2 = 3.11$, d.f. = 1, $P = 0.08$; mating success: $\chi^2 = 0.40$, d.f. = 1, $P = 0.53$) or body condition (all $P > 0.90$). The weak positive correlation between endurance capacity and siring success remained unchanged when body size was removed from the model ($\chi^2 = 2.97$, d.f. = 1, $P = 0.08$; $\beta = 0.113$). However, removing the lizards performing above the mean from this analysis (endurance capacity > 1000 s; see Fig. 1D) resulted in the detection of strong positive directional selection on endurance capacity through siring success ($\chi^2 = 11.42$, d.f. = 1, $P = 0.0007$, $n = 57$; $\beta = 0.196$) but not through mating success (number of genetic mate partners: $\chi^2 = 0.53$, d.f. = 1, $P = 0.47$). Thus, there were indications of sexual selection against poor performances relative to intermediate phenotypes, but the strength of sexual selection in the entire sample was not significantly different from zero.

DISCUSSION

Traditionally, most studies in evolutionary physiology have involved morphological or physiological traits at levels below the whole animal, such as limb proportions, bill dimensions, or immune performances (Endler, 1986; Kingsolver *et al.*, 2001). Bartholomew (1966), Bennett (1980), Huey and Stevenson (1979), Arnold (1983), and Pough (1989) all emphasized that one weakness of evolutionary studies is that they neglect crucial intermediate phenotypes corresponding to whole-animal performance abilities, such as maximal locomotor capacities. Whole-animal locomotor performances should be a more direct target of selection than lower-level traits (e.g. van Damme and van Dooren, 1999). However, the shape of natural and sexual selection on whole-animal locomotor performances remains poorly understood. Squamate reptiles have long been a choice material for the evolutionary ecology and physiology of animal locomotion (for a review, see Irschick *et al.*, 2008). Our study uses the common lizard to provide the first integrative assessment of the relative strength and shape of natural and sexual selection on locomotor performance and morphological traits across age classes in a single species.

Inter-individual variation in endurance capacity

Large individual variation in endurance capacities was observed in all age classes – a result in line with most studies conducted in other wild animal populations (Bennett and Huey, 1990). The interfamilial variation in endurance capacity at hatching was also significant and substantial ($h^2 = 0.40$), as found in other squamates (reviewed in Garland and Losos, 1994) and in a previous study with the same species (Sorci *et al.*, 1995). Interfamilial variation in endurance capacity at hatching may be caused by additive genetic effects, non-additive genetic effects, as well potential effects of maternal or external environments. Variation caused by maternal and external environments was reduced by our rearing protocol (standardized enclosure and laboratory conditions). Furthermore, we controlled for the effects of maternal traits like body size, age, and putative maternal effect of population density in the analysis of interfamilial variation in hatchlings' endurance. Important maternal traits like maternal age, maternal population density, and maternal stress do not influence endurance capacity at hatching in this species (Le Galliard *et al.*, 2004; Meylan and Clobert, 2004). Altogether, these results lend weight to the view that differences among families were largely due to genetic effects. The significant and large heritability in maximal endurance capacity at hatching observed in the common lizard supports the hypothesis that this locomotor trait should respond strongly to selection on neonates' performances.

In addition, we found that longer and heavier hatchlings had higher endurance capacities at birth and that heavier yearlings performed better, as expected from the *Bigger is better* hypothesis (Garland, 1994). Several mechanical and physiological factors may explain why longer hatchlings had larger endurance capacities: body size increases the strength of the lateral trunk bending used for forward propulsion by lizards, a higher body size is linked to faster limb cycling frequencies, and body size correlates with limb dimensions and muscle development (Farley and Ko, 1997). The positive relationship between body condition and endurance in hatchlings and yearlings also suggests an effect of general health or stockiness. For example, body condition may indicate the relative muscle mass that reflects the capacity to utilize oxygen and the relative mass of the heart and lungs that reflects the maximal oxygen consumption capacity (Garland, 1984). Although endurance capacity did not correlate significantly with body size or condition in adult males, we found age-dependent variation according to population density within this age class. The pattern was one of decreased performances in older adult males in the high-density populations relative to the low-density populations. Thus, senescence in locomotor performances was detected in the environment where competition for food and mates, social stress, and exposure to parasites were presumably higher. Relatively few studies have investigated ageing in maximal performances in wild animal populations and our analysis indicates that interactive developmental effects are involved in the expression of locomotor performances (Gibert *et al.*, 2001; Reznick *et al.*, 2004). The underlying physiological mechanisms are unknown, but senescence in locomotor traits could be attributed to declines in neuromuscular functions and reductions in aerobic scope with age (Delbono, 2003).

Endurance capacity and body growth

It is usually assumed that sustained foraging activities require relatively high levels of energy expenditure and stamina in actively foraging ectotherms like the common lizard; and that maximal stamina may constrain foraging success and basking activities in heterogeneous habitats (Bennett and Huey, 1990). A few studies have looked at field metabolic rates in actively foraging species and published data suggest that widely foraging lizard species have larger field metabolic rates than their sit-and-wait relatives that rely less on stamina for daily movements (Nagy *et al.*, 1984; Anderson and Karasov, 1988). Against the hypothesis that stamina can constrain food intake and growth, however, we found a poor correlation between maximal endurance capacity and body growth in outdoor enclosures. Endurance capacity did not predict annual growth in body size. The relationship between endurance capacity and annual change in body condition was only significant for yearlings. These results suggest that maximal endurance capacities did not constrain foraging and basking activities in any of the three age classes. Maximal endurance capacity might be well above the stamina required for most routine activities, and thus have little influence on natural abilities to forage and search suitable habitats for growth (e.g. Hertz *et al.*, 1988; Husak and Fox, 2006). Further interpretation of the relationship between growth and endurance capacity would require additional data on food intake, field metabolic rates, and activity patterns.

Natural selection on endurance capacity

Despite a non-significant relationship between body growth and maximal locomotor performances, endurance capacity may still be important for social selection, and ultimately for survival. In accordance with this hypothesis, significant directional selection for larger endurance capacities was detected at the juvenile and yearling stages. The strength of viability selection on endurance capacity in the common lizard was of the same order of magnitude as the average strength of selection on morphological traits in wild animal populations (Kingsolver *et al.*, 2001). In contrast, most earlier field studies of selection on endurance capacity failed to detect significant viability selection on this locomotor trait (Bennett and Huey, 1990; Jayne and Bennett, 1990; Clobert *et al.*, 2000). Unfortunately, the strength of selection on endurance capacity has not been reported systematically. In fact, selection may have been hard to detect or measure due to low statistical power or difficulties obtaining robust estimates of survival in wild animal populations (Irschick *et al.*, 2008). Only two of the previously published studies identified significant selection on endurance capacity:

endurance capacity was found to be under weak positive directional selection in yearling garter snakes and under strong positive directional selection in adult female side-blotched lizards (see Table 1 in Irschick *et al.*, 2008).

It is difficult to draw more general conclusions from field studies of natural selection on endurance capacity since only four species have been examined to date. The best candidates for relating maximal performances to fitness should be species that make substantial use of their maximal locomotor performances in the field (Irschick *et al.*, 2005), such as some Kalahari lacertids and some teids (R. Huey, personal communication). By analysing field locomotor behaviour and endurance capacity in lizards in the most comprehensive data set available to date, Garland (1999) was able to find a highly significant positive relationship across species between maximal endurance capacity measured in the laboratory and locomotor behaviour scored in the field. This suggests that maximal performances and field locomotor behaviours have co-evolved in lizard species and that endurance capacity may constrain the evolution of field locomotor behaviours in these taxa. Unfortunately, it is still unclear how much inter-individual variation in maximal endurance capacity reflects variation in standard field activities, and how often individuals make use of their maximal endurance capacity.

Sexual selection on endurance capacity

The analysis of siring success in adult males indicated weak and non-significant directional sexual selection on overall variation in maximal endurance capacity. The relationship between endurance capacity and mating success showed some signs of non-linearity: there was strong sexual selection against poor performances but the strength of sexual selection decreased for intermediate and large values of locomotor performances (Fig. 1D). Unfortunately, this non-linear pattern was not confirmed by the statistical analysis of sexual selection since none of the linear or quadratic selection gradients was significant. The absence of strong, directional sexual selection on endurance capacity is consistent with data from staged encounters showing that maximal endurance capacity did not predict agonistic behaviours or social dominance during competition for a basking site between adult males.

To our knowledge, this is the first field test of sexual selection on endurance capacity and the second one for a locomotor trait (Irschick *et al.*, 2008). Equivocal results were obtained in behavioural studies that searched for associations between social dominance and locomotor performances in lizards (reviewed in Lailvaux and Irschick, 2006). Endurance capacity predicts social dominance in male tree lizards (Robson and Miles, 2000) but does not predict male competitive ability in *Anolis cristalletus* (Perry *et al.*, 2004) or in *Sceloporus occidentalis* (Garland *et al.*, 1990). Furthermore, endurance capacity does not influence male attractiveness for female green anoles (Lailvaux and Irschick, 2006) and therefore its role in mate choice is unclear. Several authors have pointed out that limited endurance capacity might constrain agonistic behaviours, territory size, and access to females in territorial lizards that require extensive use of aerobic performances during courtship and combats (Brandt, 2003; Sinervo *et al.*, 2000). Unfortunately, none of these studies examined mating or siring success in males, which is the correct metric of the intensity of sexual selection acting on a trait. Future studies of territorial and courtship behaviours should try to quantify the strength of sexual selection on performance traits, not only the relationship between performance traits and sexual behaviours.

Synthesis

We evaluated selection on inter-individual variation in endurance capacity. Fitness components included survival in three age classes (juveniles, yearlings, and adult males) and reproductive success in adult males. Studies that combine mark–recapture techniques with genetically based paternity analyses to assess both natural and sexual selection are rare for performance traits (Irschick *et al.*, 2008). These studies are needed to understand the mechanisms that shape current variation in performance traits. Natural selection may operate differently on performance traits across the life cycle, and this can only be revealed by examining survival at various life stages (Jayne and Bennett, 1990; Husak, 2006a, 2006b). Sexual selection may be a very strong selective force if high-performance males gain disproportionate mating advantages, but very few studies have used modern molecular techniques to quantify the strength of sexual selection on performance traits (Lailvaux and Irschick, 2006). More integrative field studies of natural and sexual selection are warranted to assess the 'pace of evolution' for performance traits in many more species (Irschick *et al.*, 2008).

We found evidence of positive viability selection on endurance capacity in juveniles and yearlings, as well as weak sexual selection in adult males. Yet, we consider that the patterns of selection evidenced here did not corroborate the classical hypothesis that exceptional locomotor capacities should be strongly promoted by natural and sexual selection (Arnold, 1983; Pough, 1989; Irschick and Garland, 2001). Against the classical performance–fitness hypothesis, selection on locomotor performances was non-linear for survival in juveniles and for mating success in adult males. In both cases, there were signs of strong counter-selection against poorly performing individuals, but intermediate locomotor performances and champion phenotypes were apparently selectively neutral. This unexpected form of selection may result from several non-exclusive behavioural and developmental processes, such as the sub-maximal use of performances in the field (Hertz *et al.*, 1988), behavioural compensation (Irschick *et al.*, 2005), trade-offs between performance traits (Vanhooydonck *et al.*, 2001), or low developmental consistency of endurance capacity (Le Galliard *et al.*, 2004). For example, a controlled experiment in the common lizard demonstrated that the expression of variation in physical performance strongly depended on dietary conditions experienced early in life. Under poor dietary conditions, 'champions' maintained their relative advantage early in life; but good dietary conditions prompted compensatory responses in poorly performing individuals (Le Galliard *et al.*, 2004). Thus, any putative advantage of intermediate or high performances was offset by rapid ontogenic changes under good dietary conditions. The relative importance of these potential explanations for the weak and inconsistent selection on performance traits should be addressed in future studies.

In addition to this non-classical shape of natural and sexual selection, we found a shift in natural selection throughout the life cycle since survival selection on endurance capacity was not significant in adult males. Potential reasons for the absence of natural selection on endurance capacity in adult males may be that natural selection is less stringent later in life since adult lizards dominate younger animals during competition for food and space. Another explanation is that adult males are less constrained by their maximal capacities since maximal performances are typically higher in adults. The age-dependent pattern of natural selection on endurance capacity in the common lizard is reminiscent of natural selection on sprint speed in collared lizards. In this species, sprint speed is under strong directional selection for hatchlings that are susceptible to predation and other mortality risks, while selection is weak for adults (Husak, 2006a, 2006b). This combination of non-linear and varying selection across the life cycle may account for the maintenance of both strong inter-individual variation and high heritability in locomotor performances. We urge field workers to undertake similar microevolutionary approaches in their model species to gather a more extensive database on natural and sexual selection for locomotor traits.

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