Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*

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Summary

1. Considerable within-population variability of locomotor performance traits has been shown to exist in several species of squamate reptiles. In general, high values for speed and endurance are thought to have positive effects on the ability to capture prey, escape from predators, compete with conspecifics and acquire mates. On the other hand, variation in performance might trade-off with other components of fitness such that the net effect on Darwinian fitness is unpredictable.

2. Gravid females of the common lizard (*Lacerta vivipara*) were captured and several phenotypic traits of their offspring measured immediately following birth. These were endurance, body length and body mass. Offspring were marked for individual identification, released into the field, and correlations between the phenotypic traits and their subsequent growth, activity and survival rate over the next months were then tested for. Parasitism by hematozoa was monitored and predation risk by tail losses estimated.

3. It was found that individuals with a low endurance at birth tended to have reduced activity and growth rate, and higher parasite load; on the positive side, however, they experienced lower predation risk as assessed by tail losses. Conversely, individuals with a high endurance at birth had high activity and growth rates, low parasite load, but higher incidence of broken tails. Finally, endurance at birth was not correlated with survivorship up to the age of sexual maturity. Thus, individuals with varying locomotor endurance seem to exhibit behaviours that may result in the same level of Darwinian fitness.

4. The possibility that our results reveal a trade-off between the risk of becoming infected with parasites when lizards are less active (which is related to having lower endurance) *vs* the risk of being predated when the lizards are more active (higher endurance) is discussed.

Key-words: Activity, growth rate

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Introduction

Natural populations typically show substantial individual variation at the levels of both genotype and phenotype. How this individual variation is maintained has long been of interest to evolutionary biologists (e.g. see Mitton 1997). It was suggested, among other possibilities, that variation in organismal performance abilities (*sensu* Arnold 1983; Garland & Losos 1994) might be maintained as a consequence of negative frequency-dependent selection (Alexander 1996) or as a consequence of genetic or phenotypic trade-offs with other components of life history (Pounds 1988; Schluter, Price & Rowe 1991). For example, individuals

with high-performance abilities may be better able to capture prey, escape from predators or establish social dominance (e.g. see Garland, Hankins & Huey 1990; Robson & Miles 2000). Those same individuals, however, might have to pay the cost of sustaining a high activity rate in terms of greater energy expenditure, more social interactions (leading to higher production of corticosteroid hormones, Holst 1998), a greater exposure to predation (Montgomerie & Weatherhead 1988), and/or a higher risk of parasitism (Oppliger, Christie & Richner 1997). In such cases, individual difference in locomotor performance abilities may not lead to net differences in Darwinian fitness.

For historical reasons, the relationships between

morphology, organismal performance abilities, behaviour and fitness have been particularly often studied in squamate reptiles, especially lizards (Huey, Pianka & Schoener 1983; Bennett & Huey 1990; Garland & Losos 1994; Vitt & Pianka 1994). Locomotor capacities, such as endurance (stamina) or maximal sprint running speed, as measured under laboratory conditions, result from the integration of behavioural, morphological and physiological traits and are considered to be good indicators of organismal performance abilities (e.g. on lizards see Garland 1984, 1993; Garland & Else 1987; Gleeson & Harrison 1988; Losos 1990; Miles 1994; John-Alder *et al*. 1996; Macrini & Irschick 1998; Bonine & Garland 1999). Although measures of locomotor performance are not life-history traits or fitness components *per se* (*sensu* Schluter *et al*. 1991), they are generally thought to be closer to fitness than are such lower-level metric traits as body proportions, heart rate or enzyme activities (see Arnold 1983; Garland & Losos 1994). Nonetheless, only a few studies of lizards have attempted to relate locomotor performance to fitness components measured under field conditions, and their results are contradictory (Miles 1989; Bennett & Huey 1990; Jayne & Bennett 1990; D. Miles, personal communication; R. B. Huey, personal communication).

We investigated the relationship between locomotor performance and components of Darwinian fitness, using the Common Lizard (*Lacerta vivipara* Jacquin) as a model system. This species has been the subject of a long-term project in which several populations have been monitored for many years, thus allowing the gathering of longitudinal data (Clobert *et al*. 1994). Longitudinal data are particularly suited to investigation of the interactions between individual variation in performance and fitness.

As a measure of locomotor performance, we recorded endurance. This measure was chosen for several reasons. First, as compared with other potential measures of locomotor performance, such as speed or acceleration, endurance seems more likely to correlate with activity levels in nature, which was also investigated. Indeed, interspecific variation in endurance measured on a motorized treadmill (Garland 1994) correlates positively with measures of locomotor activity in the field (Garland 1999), suggesting that endurance and behaviour are coadapted. Second, measurements of individual differences in endurance are repeatable both across days in the laboratory (see Sorci *et al*. 1995 regarding this population of *Lacerta vivipara*) and across longer time periods in the field for other species of lizards (Van Berkum *et al*. 1989; Huey *et al*. 1990). Third, several previous studies of lizards have shown that individual differences in endurance are related to underlying variation in morphological, physiological and biochemical traits (e.g. Garland 1984; Garland & Else 1987; review in Garland & Losos 1994). Fourth, in *Lacerta vivipara* (Sorci *et al*. 1995) and in other lizards (Tsuji *et al*. 1989), endurance shows within-family resemblance and hence may be heritable. Thus, natural

or sexual selection acting on endurance could result in evolutionary change.

To explore the consequences of interindividual variability in locomotor performance, endurance at birth is first correlated to the level of activity displayed by these individuals later in life. Activity levels may have important effects on the frequency with which an individual encounters conspecifics, predators, parasites or prey; hence, activity levels may themselves be subject to selection. We then investigate whether individual differences in endurance correlate with differences in such fitness components as growth and juvenile survival. Studies of variation in reptile life-history traits and sensitivity analyses (Caswell 1989) have shown that juvenile survival and age at maturity (which is determined by body size and growth rate) are the most important life-history traits determining fitness in species with life-cycles similar to the Common Lizard (Sorci, Clobert & Bélichon 1996a; Clobert, Garland & Barbault 1998; Boudjemadi, Lecomte & Clobert 1999). Finally, high endurance or activity rate may trade-off with a low investment in predator avoidance (such as vigilance or remaining near a refuge) or resistance towards parasites, or may cause an individual to be more prone to predation or to become infected with parasites. Therefore, we also correlate endurance at birth to risks of parasitism later in life and to risks of predation, as assessed by tail loss. Taken together, these analyses should help explain the maintenance of individual variation in endurance at birth.

Materials and methods

SPECIES AND STUDY SITE

The Common Lizard (*Lacerta vivipara*) is a small (60 mm adult snout–vent length) lacertid species inhabiting peatbogs and heathlands (Castanet & Guyetant 1989). Adult males emerge from hibernation in April, followed by yearlings and adult females in early May. Mating takes place as soon as females are active. Gestation lasts 2 months and, in late July or early August, females lay on average five soft-shelled eggs (little or no calcium is present in the shells): juveniles (20 mm of snout–vent length) usually hatch within 1 h (Massot *et al*. 1992). The studied population (see Massot & Clobert 1995; Sorci, Massot & Clobert 1994; for more details) is situated on the Mont Lozère (1500 m elevation, Cévennes National Park).

MEASUREMENT OF ENDURANCE AT BIRTH AND PROBABILITY OF BEING PARASITIZED AT 1 YEAR OF AGE

In July 1993 and 1994, 109 gravid females were captured over 2 years from a natural population and kept in the laboratory until parturition. Two days after parturition, endurance of juveniles was measured by running them on a motorized treadmill until apparent exhaustion

(see Sorci *et al*. 1995 for details) following standard techniques (Garland 1984, 1993, 1994; Garland & Else 1987; Garland *et al*. 1990). Lizards were motivated to walk by light tapping on the tail with a small paint-brush until the individuals stopped to move after 10 consecutive taps given within 5 s. A speed of 0·15 km h^{-1} was chosen based on a comparison with other ecologically and morphologically similar species. Each juvenile was tested once on each of two consecutive days. We measured 275 juveniles in 1993 (Sorci *et al*. 1995) and 325 juveniles in 1994 (mean endurance 7·78 min, SD 7·753; see Sorci *et al*. 1995 for more details). The repeatability of the trait was high ($r = 0.842$, $P < 0.05$, for double-log transformed data from 1993, $N = 251$), thus demonstrating that it describes real individual differences in performance ability (Sorci *et al*. 1995). The higher value of the two trials was used as an estimate of the maximum endurance capacity of each individual. Offspring were then released on the study site at the mother's last capture point.

As part of a long-term study of the population dynamics of this species, ongoing since 1986, every year individuals are captured or recaptured by hand during the lizard activity season. In 1994 and 1995, blood samples were collected of individuals for which endurance had been measured in previous years (4 individuals belonging to the 1993 cohort and 26 to the 1994 cohort). The survival and recapture probability of juveniles are small so that we could not obtain blood samples of many individuals of which endurance was known at birth. Smears were fixed in methanol and stained with May-Grünwald Giemsa (Colorap de Bioréac, Lausanne). Stained slides were examined under oil immersion microscopy (500×) to enumerate blood parasites (see Oppliger, Célérier & Clobert 1996; Oppliger & Clobert 1997 for further details). Haemogregarine parasites are naturally widespread in *Lacerta vivipara*. This protozoan (phylum Sporozoa) has a complex life cycle, which involves a blood-feeding (arthropod) vector (Manxell 1977; Sorci 1996). Parasitaemia was estimated in a qualitative way (i.e. parasitized or not parasitized). This method was chosen because there were only nine parasitized individuals, and they had on average the same parasite load (about one cell parasitized per 200–400 red cells). A logistic regression (GENMOD, SAS Institute 1992) was used to examine the effect of endurance at birth on the probability of being parasitized at 1 year of age.

MEASUREMENT OF ENDURANCE AT 1 YEAR OF AGE AND OF PARASITE LOAD

During summer 1996, a total of 135 yearlings was collected in a population close to our study site. At capture, body mass, tail length and snout–vent length (SVL) were measured and each individual was examined for blood parasites (see above). The day after capture, endurance was measured by running each individual in a circular racetrack (the motorized treadmill used

the previous year was no longer available). The circular racetrack is the other commonly used technique to measure endurance (Garland 1984, 1993; Bennett 1989; Jayne & Bennett 1990; Mautz, Daniels & Bennett 1992; Garland & Losos 1994). Our racetrack had 60-cm exterior and 50-cm interior diameters. The track had PVC walls 15 cm high and its floor was cork, which provided good traction. Lizards were placed in the racetrack and motivated to run by light tapping on the tail with a small paint brush, as with the treadmill measurements (Sorci *et al*. 1995). Endurance was measured as the time until the individual stopped running in spite of the taps given. In a previous year, this measure was shown to be repeatable ($r = 0.78$, $P < 0.001$, $n = 256$) as in the case for the treadmill (Sorci *et al*. 1995). All trials were performed at 30 °C, which is near the mean body temperature of animals from this population when active in the field (Van Damme, Bauwens & Verheyen 1990). After the experiment, all the individuals were released at their capture site.

Parasitemia of new yearlings collected in the field was estimated in a semiquantitative way. Each individual was assigned to one of the following categories: (0) free of parasite; (1) very low level of parasitized cells (one every 10 000–120 000 cells); (2) low level (one every 400–10 000 cells); (3) moderate (one every 200–400 cells); (4) high (one every 80–200 cells); (5) very high (one every 10–80 cells). The relationship between endurance and parasite load was estimated using Pearson's correlation coefficient. The relationship between prevalence (presence or absence of parasites) and endurance at one year of age was also examined.

ESTIMATES OF SURVIVAL AND RECAPTURE (ACTIVITY) RATE

After being released in the field, offspring belonging to the 1993 and 1994 cohorts were recaptured in September of the year of release (recapture session 1) and in June and August (recapture session 2, 3, etc.) of the following years. Recaptures were done from 0900 h in the morning until 1900 h in the evening, largely covering all the daily activity period of the species. Each recapture session consisted of several days of capture (>5); however, the recaptures within a session were not enough to perform the analysis at the day level. The data within a session were therefore amalgamated. Because not all individuals are recaptured in a given session, methods that allow estimation of survival probabilities separate from recapture probabilities had to be used (Nichols 1992; Lebreton, Pradel & Clobert 1993). By estimating, among individuals marked at occasion t and recaptured at occasion $t + 2$, the proportion of individuals that were recaptured at occasion $t + 1$ (recapture probability at occasion $t + 1$), the survival from occasion t to $t + 1$ could be estimated by comparing those individuals captured at occasion $t + 1$ to those marked at occasion t, corrected for the recapture probability at occasion $t + 1$ (see Lebreton

et al. 1992 for more details). In this species, capture probability largely depends on activity rate because no lizard temporarily emigrated from the study area (Massot *et al.* 1992) and all times of activity within a day are equally sampled. In agreement with this view, we found in a previous analysis that capture probability was much less dependent on capture effort (i.e. number of hours searching, number of persons involved in the capture session) than on the number of lizards that were active on a given day (Lebreton *et al.* 1992; Massot *et al.* 1992). Capture probability can therefore be safely taken as a descriptor of the activity rate. By 'activity rate' we mean individuals that are not in or close to a refuge, those individuals being, by definition, neither detectable by human observers nor capturable. As in many other cases (Clobert 1995; McCleery *et al.* 1996), capture probability turns out to be a parameter of considerable biological interest; here, it provides an objective index of lizard activity (Sorci, Clobert & Michalakis 1996b).

To assess the effect of body mass, SVL and endurance at birth on subsequent survival and capture probability, a capture–recapture method had to be selected that allows the modelling of survival and capture probability at the individual level. The computer program SURPH (Skalski, Hoffman & Smith 1993; Smith *et al.* 1994; Kingsolver & Smith 1995; the computer program is available on request to the authors) allows the use of individual covariates. This statistical package allows fitting of an array of models, either with or without covariates, and comparison of the models by either log-likelihood ratio tests or the Akaike information criteria (AIC; Lebreton *et al.* 1992). The model with the smallest AIC value (Anderson, Burnham & White 1994) is the one that most parsimoniously describes variation in the data. This computer program also provides a goodness-of-fit of the final model.

ESTIMATES OF MOVEMENT, GROWTH RATE, AND TAIL AUTOTOMY

For the Common Lizard, it is well known that a reduction in activity rate is associated with a decrease in home range size and/or in the 'amplitude' of movements within the home range (Bauwens & Thoen 1981; Clobert *et al.* 1994; Lecomte *et al.* 1994). This is likely to result in a decrease of the distance moved between two consecutive recapture locations. The amplitude of movements was therefore estimated by computing the sequential distances between all the recapture points for a given individual within a year and then computing the mean of these distances, and that the variance of mean distances across groups of individuals was not significantly different was verified. However, individual differences in the amplitude of movement may also reflect individuals inhabiting habitat of different structure. We know this is influencing movements (Clobert *et al.* 1994), and so is not corresponding to a different level of activity *per se*.

Importantly therefore it was verified that parasitized and non-parasitized individuals were randomly distributed within the area, and that home ranges of individuals were largely overlapping (Lecomte *et al.* 1994). The comparison of the parasitized and non-parasitized individuals must then reflect difference in activity (large meaning), rather than a difference in their habitat structure.

Growth rate was estimated as the difference in SVL between two captures separated by more than 3 weeks, divided by the number of days separating the two captures. One-year-old individuals were used because most of the growth in SVL occurs at this age.

Tail loss is a component of the antipredator strategy in many species of lizards (Arnold 1988; Greene 1988), mostly against non-efficient predators (Jaksic & Greene 1984; Medel *et al.* 1988). In the Common Lizard, social interactions rarely, if ever, lead to the loss of the tail (Arnold 1988; J. Clobert, personal observation), and no 'efficient' predators (*sensu* Arnold 1988 and Medel *et al.* 1988; i.e. predators that almost always caught the lizard entirely such as birds of prey) were present on the study area (Massot *et al.* 1992). The proportion of broken tails, when accounting for age (Arnold 1988), is likely, then, to reflect the number of predation attempts attributable to 'inefficient' predators (however, inefficient predators are those which nevertheless kill a lizard in more than half of their attempts, Medel *et al.* 1988). 'Inefficient' predators (snakes, shrews, frogs, crows) were the only ones present in our study area.

STATISTICAL ANALYSES

Each individual was considered as an independent observation because the probability of reobserving sibs was very low (less than 10%). Moreover, we corrected for the variance inflation in the analysis of survival and recapture probability (variance inflation factor, see McCullagh & Nelder 1989; Lebreton *et al.* 1992), which also reduces bias caused by the non-independence of juveniles belonging to the same family. Most of the analyses have been done using GLM for continuous dependent variables and GENMOD for categorical ones (SAS Institute 1992). We first fit a model with all the interactions and drop those which were not significant from the model (backward selection). Fisher or likelihood ratio (χ^2) tests have been used to test for significance.

Results

RELATIONSHIP BETWEEN ENDURANCE AT BIRTH AND PROBABILITY OF BEING PARASITIZED AT 1 YEAR OF AGE

For the 1993 and 1994 animals, the probability of being parasitized at 1 year of age was negatively correlated with treadmill endurance at birth (logistic regression with year of birth as cofactor: endurance $\chi^2_1 = 8\cdot8$,

Table 1. Comparisons of the Akaike information criteria (AIC) of a selection of models: T effect of the session, ECS endurance corrected for size (at birth), p capture probability, s survival probability. Models differing by more than two units in their AIC are considered as significantly different (Anderson *et al.* 1994). + means an additive effect of the two variables, * means that the interaction between the two variables is also considered into the model. p(T),s(T) is a model where both survival and capture probability depend on the session of capture (time or T). AIC equals the maximum likelihood function value for the model plus twice the number of estimated parameters by this model

Model	p(T), s(T)	p,s(T)	p(T),s	p(T + ECS),s(T)	p(T*ECS),s(T)	p(T + ECS),s(T + ECS)
AIC	736·15	746·31	737·03	733·87	734·69	735·64
Number of parameters	9	6	6	10	13	11

$P = 0.003$). Animals that were not infected with the haemogregarine had 40% higher locomotive endurance at birth than those that had become infected. Year of birth, SVL and interaction terms were not significant (year: $\chi^2_1 = 0.003$, $P = 0.949$; SVL $\chi^2_1 = 1.54$, $P = 0.210$; all interactions $P > 0.10$; this might however, be due to the small sample size). Juveniles with lower endurance were more likely to get a parasitic infection later in their life.

RELATIONSHIP BETWEEN ENDURANCE AT 1 YEAR OF AGE AND PARASITE LOAD AT THE SAME AGE

Yearling lizards harbouring blood parasites also had lower circular-track endurance than non-parasitized ones (parasitized: mean $\pm$ SE $= 49.5 \pm 1.2$ s, $n = 53$; non-parasitized: 56.2 ± 0.9, $n = 82$). The correlation between endurance at the age of one and parasite prevalence still holds after controlling for SVL (ANCOVA with endurance as dependent variable, sex as a factor, intensity of parasitism and SVL as covariates; SVL – $F_{1,124} = 0.09$, $P = 0.756$; sex – $F_{1,124} = 0.775$, $P = 0.380$; parasitism – $F_{1,124} = 15.241$, $P < 0.0001$; all interactions terms $P > 0.1$). Parasitemia, also, was significantly negatively correlated with endurance (Pearson's correlation coefficient: $r = -0.286$, $P = 0.001$, $n = 135$).

RELATIONSHIP BETWEEN ENDURANCE AT BIRTH, JUVENILE SURVIVAL AND CAPTURE PROBABILITY

A model was fitted in which capture and survival probabilities were functions of time since release (i.e. different for different recapture sessions) and size-corrected endurance at birth (residuals from log–log regression on body size, termed ECS). Models where the effects of time, size-corrected endurance at birth and/or their interaction terms were ignored were subsequently fitted. Based on the AIC, the best fitting model included a time effect on survival probability and a time plus a size-corrected endurance effect on capture probability (Table 1). This model was significantly different from a model in which the effect of size-corrected endurance on capture probability was excluded (log-likelihood ratio test, $\chi^2_1 = 4.18$, $P > 0.05$). Conversely, a model with an additive effect of ECS did not provide a better fit than the chosen model (log-likelihood ratio test $\chi^2_1 = 0.22$, $P > 0.5$). Size-corrected endurance at birth had no effect on subsequent survival probability, whereas capture probability (which, we believe, reflects activity) was positively correlated with endurance (Fig. 1).

RELATIONSHIP BETWEEN GROWTH RATE, MOVEMENTS (ACTIVITY) AND TAIL AUTOTOMY

Juvenile growth rate was significantly positively correlated to endurance at birth when corrected for date of capture and initial SVL (Pearson's correlation coefficient, $r = 0.39$, $P = 0.003$, $n = 59$).
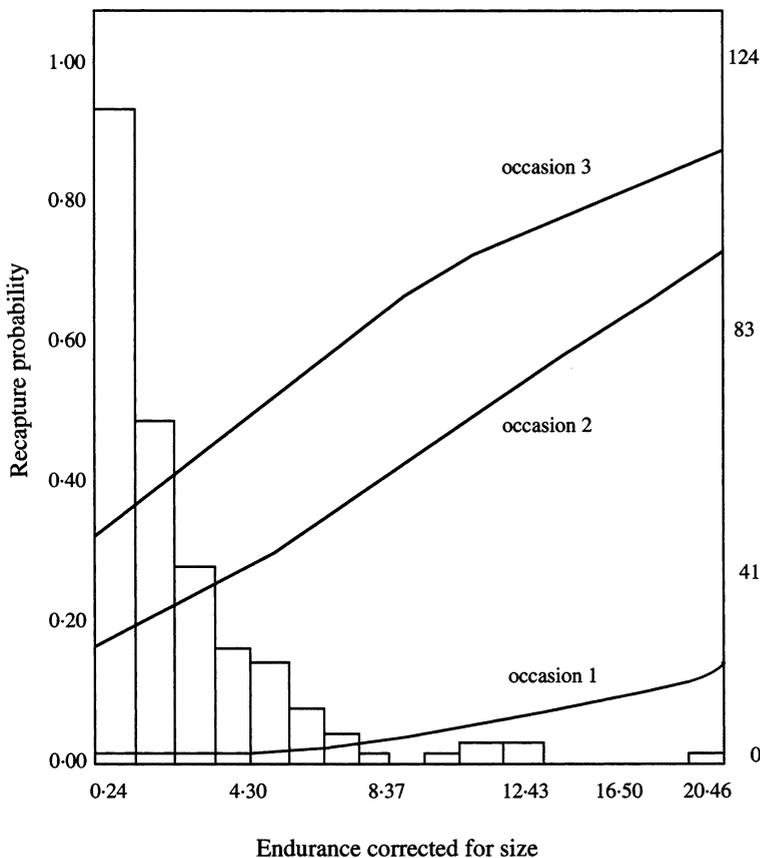

Fig. 1. Relationship between recapture probability and size-corrected endurance at birth for the different occasions of capture. The open-bar histogram represents the total number of juveniles for which we measured endurance.

Parasitemia was significantly negatively correlated with the mean distance separating recapture locations (Pearson's correlation coefficient, $r = -0.262$, $P = 0.005$, $n = 114$). A similar relationship was found for prevalence ($F_{1,112} = 6.41$, $P = 0.013$, log mean distance: parasitized 1.06 m ± 0.07 SD, not parasitized 1.33 m ± 0.08 SD).

When corrected for age, the probability of having a broken tail was negatively correlated with parasitemia ($F_{1,155} = 7.03$, $P = 0.001$, log mean intensity: broken tail 0.23 ± 0.09, not broken 0.78 ± 0.075). The same relationship was found for prevalence ($\chi_1^2 = 14$, $P = 0.001$). A positive correlation between yearling growth rate and the probability of having a broken tail was also found (ANCOVA with year as a factor: year $F_{4,255} = 5.83$, $P = 0.002$, tail status $F_{1.255} = 4.98$, $P = 0.027$). Because of insufficient data (there were only 30 individuals where endurance was measured at birth and that were recaptured at 1 year of age), it was not possible to test for correlations between tail break frequency and either activity or endurance.

Discussion

For a population of the Common Lizard, *Lacerta vivipara*, we sought to determine if the observed variation in a measure of physiological performance, running endurance at birth, was associated with two measures of field activity, growth rate, susceptibility to attack by predators and a parasite, and finally survival. Lizards with higher endurance at birth were those with higher activity in the field (Fig. 1), higher growth rate and a higher probability of having been attacked by a predator (higher tail break frequency), but a lower probability of becoming infected with a parasite. Similarly, in a previous study, we have also shown that parasitized adult females had lower activity levels (lower capture probability) than non-parasitized ones (Sorci *et al.* 1996b). However, survival was not related to endurance. This suggests there are trade-offs between the ecological measures that we studied, such that the benefits of having a high endurance capacity (higher growth, lower probability of parasitism) may be offset by costs (increase predation). Understanding the nature of these trade-offs is confounded by lack of information about relationships between some of the measured traits; this is most acute for the relationship between parasitism and the physiological and life-history traits.

ENDURANCE AND ACTIVITY RATE

Endurance or its physiological correlates appear to be related to several important functions (Pough *et al.* 1992), including foraging (Garland 1993, 1994, 1999), reproduction (Wells & Taigen 1984; Taigen & Wells 1985) and predator avoidance (Bauwens & Thoen 1981; Cooper *et al.* 1990). Sustained activity requires relatively high levels of energy expenditure (Bennett &

Huey 1990; Autumn *et al.* 1997), and the capacity for sustained activity (stamina) depends on body temperature (Bennett 1990; Garland 1994). In ectotherms, energy expended in locomotor activity is a significant part of the total energy budget and, compared with mammals (Garland 1983), constitutes a disproportionately high part (in terms of energy) of all other activities (Christian, Baudinette & Pamula 1997).

For an ectotherm, therefore, an effective way to limit its overall energy expenditure is to reduce its locomotor activity and remain in a cool place. In the Common Lizard, we found that individuals with the lowest endurance (corrected for size) also had the lowest probability of being captured. This was not the result of lower-endurance individuals being temporarily absent from the study site, because no individual from this study site was recaptured in the closest nearby population (3 years and over 2000 recaptures; Massot & Clobert 1995). In addition, the probability of capture has been shown to depend mainly on activity level in reptiles generally (Dunham, Morin & Wilbur 1988) as well as in our species (Lebreton *et al.* 1992; Massot *et al.* 1992). In our study population, when an individual is seen or heard, fewer than 10% escape capture (J. Clobert, unpublished data). It is therefore most likely that endurance and activity are strongly positively correlated. That is, individuals with high endurance also tend to be more active. In support of this finding, studies of laboratory house mice have suggested a positive relationship between maximal aerobic capacity, measured on a motorized treadmill, and voluntary activity levels on running wheels (Friedman, Garland & Dohm 1992; Swallow *et al.* 1998).

Finally, we did not find a positive relationship between endurance and survival up to the age of maturity, which may indicate that low-endurance individuals tend to rely on foraging tactics that are less physically demanding and less energetically expensive (for example, a sit-and-wait strategy). However, endurance may have indirect effects on other fitness components, such as fecundity, given that low-endurance individuals had a lower growth rate and were also the most parasitized.

ENDURANCE AND PARASITISM

Blood parasites have not been shown to affect survival or fecundity of *Lacerta vivipara* (Sorci *et al.* 1996b), but they do have various physiological consequences, including a lower maximal sprint speed (Oppliger *et al.* 1996), a lower resting metabolic rate (Oppliger *et al.* 1996), an increased reproductive effort (Sorci *et al.* 1996b) and a decreased ability to regrow the tail (Oppliger & Clobert 1997). Similar physiological and behavioural costs of malaria infections have been reported in *Sceloporus* lizards (Schall, Bennet & Putnam 1982). The lack of a relationship between parasitism and survival suggests a behavioural compensation. As well, parasitized individuals exposed to high temperatures
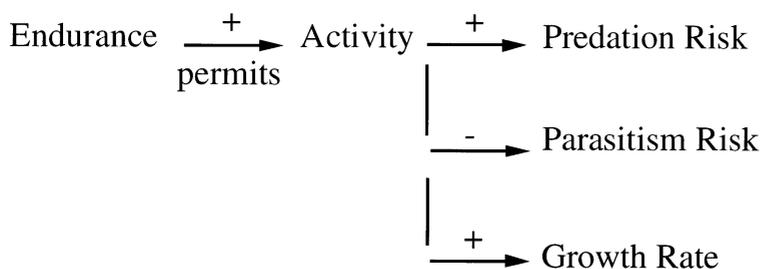
Endurance $\xrightarrow[\text{permits}]{+}$ Activity $\xrightarrow{+}$ Predation Risk

Activity $\xrightarrow{-}$ Parasitism Risk

Activity $\xrightarrow{+}$ Growth Rate

Fig. 2. Proposed model for the relationships between endurance, activity, parasitism, predation rate and growth rate. High endurance capacity at birth permits a high activity rate, which in turn entails a low parasite prevalence and a high growth rate, but also a high risk of predation. As discussed in the text, these conflicting effects of selection may have a net effect such that individuals with differing endurance nevertheless have similar Darwinian fitnesses.

developed higher parasite loads than individuals exposed to low temperatures (Oppliger *et al*. 1996). If temperature directly affects multiplication rate of the parasite, then we might expect parasitized individuals to be less active during the warmest weeks, in order to control the multiplication rate of the parasite. In agreement with this hypothesis, we found that parasitized adult females were less likely to be captured in summer than were non-parasitized females (Sorci *et al*. 1996b). However, endurance, as measured at birth, was also positively correlated with activity, and negatively with parasite load when 1 year old. Given that endurance and parasitism were measured at different ages, it is likely that individuals with low endurance are more prone to be parasitized through the reduction of activity associated with endurance. In fact, whereas parasite prevalence and intensity increase as exposure time increases, low endurance at birth was concomitant with a reduction of activity immediately after birth.

PARASITISM, ENDURANCE AND TAIL BREAKAGE

Low endurance at birth and high parasite loads could reflect generally poor phenotypic quality, e.g. poor health or vigour which might be translated in to a poor body condition (see also Schluter *et al*. 1991). However, although growth rate was reduced for lower-endurance individuals, we did not find any correlation on the one hand, between endurance and survival up to the age at maturity, and, on the other hand, between parasitism and fecundity or female adult survival (Sorci *et al*. 1996b). As we did not directly relate endurance to fecundity or adult survival (only through the negative relationship between endurance and parasitism), it might still be that fecundity and/or adult survival rate are lower for individuals with low endurance, when corrected for individual parasite load. If this is the case, then it will still mean that endurance does not have a major effect on fitness because it did not show up when its impact on parasitism was considered in the first place. Moreover, to produce a noticeable effect on fitness, differences in fecundity and adult survival

would have to be large because fitness (as measured by the population growth rate, Caswell 1989) does not have a high sensitivity with respect to these two traits (Clobert *et al*. 1994, 1998; Boudjemadi *et al*. 1999). It follows that differences in fitness components induced by a low endurance are not large, and might be mainly evident in old (senescing) individuals (Sorci 1996; but see Huey *et al*. 1990). It may also be that having low endurance and high parasite loads are only costly under particular environmental circumstances (see also Schluter *et al*. 1991). However, we did measure survival over several years without any indications of a significant interaction between endurance or parasitism and years.

A more likely explanation is that low endurance at birth could represent the trigger for a compensatory behavioural strategy. Individuals with low endurance may not be able effectively to adopt a high-activity lifestyle simply because they cannot sustain high levels of activity. The alternative is to adopt a low-activity lifestyle, which brings with it certain benefits and costs. On the positive side, reducing activity has the potential to decrease predation risks (Schwarzkopf & Shine 1992). On the possible negative side, reducing activity results in more time spent in a restricted part of the home range (near a burrow, as is observed for pregnant females) or hidden in a refuge (Bauwens & Thoen 1981; Cooper *et al*. 1990), which render them susceptible to parasites, and therefore may increase the risk of infection by certain parasites (Fig. 2). Specifically, haematozoa are transmitted by mites living in the substrate and having very limited dispersal ability; therefore, it is likely that immobile lizards are more exposed to these vectors. This is consistent with the observations that parasitized individuals are less active than non-parasitized ones, as measured both from capture probability and movements within the home range. Thus, our model suggests that low endurance is the ultimate cause of higher parasitism rates, not vice versa.

If parasitism is one potential cost of low activity rate in these lizards, then reduced predation risk can be one of the benefits. Activity rate is often positively associated with predation risk (e.g. Huey & Pianka 1981), at least at the within-population level (Henle 1992), and we found that parasitized individuals had their tail broken less often than did non-parasitized individuals. Tail loss has, however, been criticized as being a good indicator of predation (Medel *et al*. 1988), particularly the efficient one. Indeed, it might be that parasitized lizard are less efficient (a lizard is 'efficient' in escaping predation when only the tail is taken by the predator) in escaping non-efficient predators (non-efficient predators are those whose attack results often in obtaining only the tail of the lizard, such as some snakes or other lizard species), resulting in fewer tails broken for parasitized lizards. However, if this was true, then we should have observed a decreased survival for parasitized individuals, because these individuals would have to pay a cost caused by both parasites and predators.

According to our scenario, the costs and benefits associated with high *vs* low activity may balance each other, and turn out to be almost equivalent in terms of Darwinian fitness, as indicated by the absence of a correlation between survival and either parasitism or endurance, despite demonstrated physiological costs of parasitism, such as reduced rates of oxygen consumption and tail regeneration (this study; Sorci *et al.* 1996b; Oppliger *et al.* 1996; Oppliger & Clobert 1997). The complicated relationships between endurance, activity rate, parasitism and predation in turn may explain the high level of variation that we found for endurance (Sorci *et al.* 1995), although individual variation in endurance is often great in squamate reptiles (e.g. Garland 1984; Garland & Else 1987; Tsuji *et al.* 1989; Jayne & Bennett 1990). This variation in endurance might even be actively maintained if there is a trade-off (genetic or phenotypic) between susceptibility to parasite infection and endurance. However, only an experimental manipulation will allow demonstration of this possibility, and that the importance of endurance and parasitism for survival rate is not overridden by other factors.

Although low endurance at birth is associated with a low activity rate, a low growth rate and a high chance of being parasitized, no evidence has been found that it entails a significant reduction in juvenile or subadult survivorship. Hence, lower-endurance individuals seem at least partly able to compensate for the costs associated with low endurance. However, we were unable to test for associations with fitness components later in life, so it is still possible that difference in endurance may translate into differences in adult survival probability, mating success or fecundity. As noted above, however, these fitness components have less important consequences for overall fitness than do age at maturity and juvenile survival in this species, so that a greater difference according to endurance has to be found for the former than for the latter in order to have the same effect. At least with respect to parasitism, we did not find, in a previous study, any difference on the effect of parasitism on adult female survival and fecundity (Sorci *et al.* 1996b). In any case, determining whether our results reflect a trade-off, a manipulation of the host by the parasite, or the result of an individual optimization strategy by the host (Pettifor, Perrins & McCleery 1988) will require further studies.

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