

# Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances

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## Summary

1. Consistent individual differences in behaviour are seen in numerous animals and could be maintained by life-history trade-offs and integrated within a pace-of-life syndrome involving physiological and locomotor traits.
2. Lizard species are characterized by inter-specific variation in activity and foraging behaviours associated with differences in locomotor performances and metabolic rates. Similar syndromes could exist within species, but have not been investigated so far.
3. We scored the exploratory behaviour of newborn common lizards (*Zootoca vivipara*) using a neutral arena test and measured concomitantly resting metabolic rate (RMR), maximal sprint speed (MSS) and endurance capacity. Animals were released in outdoor enclosures exposed to avian predation and measured again for the same traits 1 year later.
4. Common lizards displayed consistent individual differences over a week for an exploration score associated with high activity in the neutral arena. Individual differences in three activity scores were also consistent over the first year of life.
5. Correlations among behavioural, metabolic and locomotor traits were weak, except for a marginally significant, positive correlation between exploration score and MSS and endurance at the age of 1 year.
6. Correlational survival selection was found for RMR and exploration score such that newborns with low exploration score and high RMR and newborns with high exploration score and low RMR survived better. Correlational growth selection was also found with faster growth in newborns with low exploration score and high RMR.
7. The results are discussed against recent hypotheses to explain the maintenance of animal temperaments.

**Key-words:** locomotion, metabolism, personality, reptile, temperament

## Introduction

Consistent individual differences (CID) in behaviour have been reported in numerous animal species and are called temperaments or personalities (Sih, Bell & Johnson 2004; Réale *et al.* 2007). These CIDs are observed in a wide range of contexts (Réale *et al.* 2007), may imply limits on behavioural plasticity (Sih, Bell & Johnson 2004; Bell, Hankison & Laskowski 2009) and can have important

fitness consequences (Smith & Blumstein 2008). A major behavioural dimension includes activity (defined as the general level of activity of an individual in a familiar situation) and exploration (defined as the response of an individual to novel situations and varying from thorough to superficial exploration). These behaviours are thought to be associated with foraging, patrolling for territorial defence and mate finding, and dispersal as well as habitat choice (Réale *et al.* 2007; Biro & Stamps 2008; Cote *et al.* 2010). Activity and exploratory behaviours often display CIDs (Bell, Hankison & Laskowski 2009) and are also

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heritable in great tits (Drent, van Oers & van Noordwijk 2003), sticklebacks (Bell 2005), squids (Sinn, Apiolaza & Moltschaniwskyj 2006) and deer mice (Careau *et al.* 2011).

Recently, it has been proposed that consistent individual differences in exploration and activity could evolve by frequency-dependent selection (i.e. the fitness of a behavioural type depends on the relative frequency of this and other behavioural types in the population) when behavioural variation shapes a life-history trade-off between production (growth and reproduction) and survival (Stamps 2007; Wolf *et al.* 2007; Biro & Stamps 2008). For example, high activity increases both growth and the risk of mortality from predation, thus resulting in a similar lifetime reproductive success than low activity (Stamps 2007). This idea is well supported by some studies of the production-mortality trade-off in fish (Biro & Post 2008 and references therein), hexapod (Brodin & Johansson 2004) and mammal species (Boon, Réale & Boutin 2008). However, a recent meta-analysis reported that high activity and superficial exploration increase on average survival across studies but have no significant average effect on reproductive success (Smith & Blumstein 2008). Further investigations are therefore needed to test the generality of the trade-off hypothesis for the maintenance of CIDs in exploration behaviour.

In addition, the life-history trade-off hypothesis predicts that CIDs in activity or exploratory behaviour should correlate with traits associated with a higher productivity (Stamps 2007; Biro & Stamps 2008; Careau *et al.* 2008). One such well-supported correlation is the behavioural syndrome between activity, superficial exploration, boldness and aggressiveness (Sih, Bell & Johnson 2004). Réale *et al.* (2010) recently generalized the concept to include also covariation with physiology (immunity, metabolism and oxidative stress). This so-called 'pace-of-life' syndrome emphasizes integration of behavioural variation within a slow-fast demographic and metabolic continuum. It stresses out that correlational selection plays an important role in the co-adaptation of behaviour with physiology. In particular, a positive correlation should exist between activity, superficial exploration and resting metabolic rates (RMR), when high RMRs are associated with higher food intake, digestion capacity and a more productive lifestyle (reviewed in Careau *et al.* 2008; Biro & Stamps 2010). For example, high rates of body growth, mortality and energy expenditure are linked with variation in activity, boldness and aggression across breeds of domestic dogs (Careau *et al.* 2010). The pace-of-life syndrome hypothesis further predicts a positive correlation between high activity, superficial exploration and maximal locomotor performances, that is the ability of an animal to conduct an ecologically relevant locomotor task at its maximal capacities such as sprinting, running at slow speed or jumping (Careau & Garland 2012). This prediction is based on the idea that more pro-active individuals must perform better during foraging and territorial defence to support the energetic demands of their behavioural strategy (Garland 1999; Farwell & McLaughlin 2009).

Yet, evidences against the pace-of-life syndrome hypothesis exist, which should caution against its excessive generalization. First, high RMR and locomotor capacities are not necessarily associated with a higher production (Irschick *et al.* 2008; Burton *et al.* 2011). Second, correlations between CIDs in activity or exploration, metabolism and locomotor performances are still rarely reported and the few results published so far are contradictory (reviewed in Réale *et al.* 2010). For example, correlation between RMR and activity can be positive, negative or non-significant depending on the species in mammals and fishes (Careau *et al.* 2011 and references therein), while no data are available for reptiles. Third, to the best of our knowledge, no study has yet examined correlational selection on exploration behaviour, metabolism and locomotor performances, and therefore tested for co-adaptation among these traits (Réale *et al.* 2010; Careau & Garland 2012). To this aim, we investigated variation and natural selection in a cohort of common lizards (*Zootoca vivipara* Jacquin 1787) measured at birth and at the age of 1 year for their exploratory behaviour in a neutral arena, as well as for RMR and locomotor performances (maximal sprint speed and endurance). Lizards are characterized by extensive variation in activity and foraging behaviours along a gradient ranging from 'sit-and-wait' to 'actively foraging' species, which is associated with differences in morphology, locomotor performances and metabolism (Garland 1999; Reilly, McBrayer & Miles 2007). Similar syndromes could exist within species, but no studies of lizards had examined before CIDs in exploration and their relationship with locomotor performances and metabolic rates.

We measured both short-term (over a week) and long-term (over a year) consistency of exploratory behaviour, assessed phenotypic correlation with RMR and locomotion, and quantified growth and survival selection on behavioural, metabolic and performance traits during the first year of life. Common lizards are active foragers characterized by overlapping home ranges, high endurance and slow sprint speed capacities relative to other species of the same family, and a strong mortality and fast body growth early in life (Le Galliard, Clobert & Ferrière 2004; Le Galliard & Ferrière 2008). The previous analyses of body growth and juvenile survival within and between populations of the common lizard pointed out to the existence of a growth-survival trade-off (Sorci, Clobert & Bêlichon 1996; Clobert *et al.* 2000; Mugabo *et al.* 2010). Our previous studies also uncovered substantial and repeatable inter-individual differences in locomotor capacities and RMR (Le Galliard, Clobert & Ferrière 2004; Le Galliard & Ferrière 2008; Massot *et al.* 2011). Directional growth and survival selection on endurance capacity at birth has already been demonstrated (Clobert *et al.* 2000; Le Galliard, Clobert & Ferrière 2004), but selection on sprint speed and metabolism remains untested and none of our previous studies examined correlational selection on these traits. According to the life-history trade-off and pace-of-life syndrome hypotheses, we predicted that high activity

or superficial exploration should be positively correlated with RMR and locomotor performances. We further predicted positive directional growth selection on activity and superficial exploration balanced by negative directional survival selection. If positive correlations between traits are adaptive, we also expect correlational selection on behaviour and metabolism, and correlational selection on behaviour and locomotor performances.

## Materials and methods

### GENERAL PROTOCOL

Animals used in this experiment ( $n = 174$ ) were obtained from gravid females ( $n = 37$ ) captured from late June to early July 2007 around the Mont Finiels, South-Central France (Lozère, 44°27' N, 3°45'E). Gravid females were maintained until their parturition under *ad libitum* feeding in a laboratory located close to the field sites (see Le Galliard, Le Bris & Clobert 2003b for details on maintenance conditions). Terraria were checked daily for newborns. Parturitions occurred from July 16th to July 30th. Upon the day of birth (day 0), live hatchlings were marked by clipping one to three toes, measured for snout-vent length (SVL) to the nearest mm and for body mass to the nearest mg and sexed by counting their ventral scales (Lecomte, Clobert & Massot 1992). On day 1, hatchlings were also measured for their resting metabolic rate (RMR, see details below). Hatchlings were then maintained in family groups (one to two families per terrarium) under *ad libitum* feeding. All hatchlings were measured for sprint speed on day 3, and half of the hatchlings from each family were also measured for endurance capacity on day 4 ( $n = 88$ ). We could not measure more than half of the hatchlings for logistic reasons, but the sample size remained large enough for our statistical analyses. Locomotor performances were measured using standard protocols at a body temperature of 32 °C, which corresponds to the preferred body temperatures in the common lizard (Le Galliard, Le Bris & Clobert 2003b). Maximal sprint speed (MSS) was calculated as the fastest 0.1 m race attained after we ran each lizard during three consecutive trials a 1-m-long racetrack equipped with photoreceptors (Sorci *et al.* 1995). Endurance capacity was calculated as the time elapsed until exhaustion when a lizard was motivated to run at a slow speed on a non-motorized, circular treadmill (running speed = 0.03 m s<sup>-1</sup>). These protocols yield repeatable measurements of locomotor performances (Sorci *et al.* 1995; Le Galliard, Clobert & Ferrière 2004).

Once these measurements were completed (August 2nd), offspring and their mothers were transferred to another laboratory located nearby Paris (Seine-et-Marne, 48°17'N, 2°41'E). Adult females and juveniles were then maintained in separate terraria and were fed *ad libitum*. Recordings of exploratory behaviour (see details below) were done after a minimum period of 5 days of rest following transport and after 1 day of fast. After each behavioural test, from August 7th to August 13th, alive juveniles from the same family were released together with their mother and other unrelated adult females in one of four randomly chosen outdoor enclosures ( $n = 173$  juveniles). Juveniles were released in family groups to mimic the situation encountered in nature and avoid disturbing movement behaviours of juveniles in the field (Le Galliard, Ferrière & Clobert 2003a). Enclosures were all located in the same natural meadow, each outdoor enclosure measured 12 by 8 m, and each enclosure was equipped with wood piles, rocks and two artificial ponds to provide lizards with a permanent access to basking site, refuges and water (see Lecomte & Clobert 1996 for a detailed description of outdoor enclosures). Initially, each population had the same number of juveniles and adult females, and populations did not differ in juvenile sex ratio as well as mean

SVL and body mass of juveniles (ANOVA, all  $P > 0.15$ ). Enclosures were protected from terrestrial predators with plastic fences, but potential avian predators could prey on lizards freely. Wild avian predators observed during this study included crows, magpies and kestrels (Le Galliard, pers. obs.).

In late April and early May 2008, all surviving lizards ( $n = 53$ ) were captured, identified and measured for SVL and body mass. Animals were then maintained under *ad libitum* conditions in the same laboratory room. For each animal, we measured again RMR (after 3 days of fast), MSS and exploratory behaviour following our standard procedures. We also measured endurance capacity on a motorized treadmill at the running speed of 0.07 m s<sup>-1</sup> following the protocol in Mugabo *et al.* (2010). A random sample ( $n = 28$ ) was tested twice for exploratory behaviour after a week to calculate the short-term consistency of behavioural differences.

### COLLECTION OF BEHAVIOURAL DATA

We used a neutral arena test to investigate exploratory behaviour like in the previous studies of temperaments (Réale *et al.* 2007). All tests were carried out during the daily activity period between 10 AM and 5 PM. After a period of fasting of 1 day, each lizard was placed in a wood arena (50 cm × 18 cm) divided into two equal compartments separated by a removable opaque plastic wall. Neutral arenas were maintained in a room at a standard temperature of 23–25 °C. Two heat sources (25 W bulb) at each corner and a light source (Iguana Light 10.0 UV-B, ZooMed, 40 W) enabled locomotor activities at optimal body temperatures and lighting conditions. The soil was covered with clean sand before each trial to avoid interference with odours from conspecifics. At the beginning of each trial, animals were placed in one compartment (hereafter called the familiar compartment) for a 40-min adaptation period. We used a long adaptation period because we wanted to avoid the effects of stress and to familiarize the lizard with one compartment. Familiarization involved behaviours such as walking, basking and scent marking (Le Galliard, pers. obs.).

After the familiarization period, the removable wall was lifted and locomotion behaviour in the familiar and non-familiar compartments was filmed during 30 min from above with a CCD camera. The film was downloaded using Pinnacle Studio 11, and image sequence from each video was obtained using VirtualDub (one frame per second). From this, we recorded the lizard position ( $x$ - $y$  coordinates) into IMAGEJ v1.40 (<http://rsbweb.nih.gov/ij/>) using a particle analysis procedure. For each trial, we calculated the percentage of the time spent in the non-familiar compartment, the time spent until the first visit of the non-familiar compartment, the percentage of time spent walking, the travel distance during each trial, the total number of visits of compartments and the time until the first move.

### MEASUREMENT OF METABOLIC RATE

The resting metabolic rate (RMR), also called standard metabolic rate for ectothermic species, is defined as the minimum rate of energy expenditure under post-absorptive conditions in a resting phase at day and at a given temperature within the animal's range of activity (Andrews & Pough 1985). Our estimation of RMR relies on the measurement of the volume of oxygen consumed per unit of time, which assumes that energy production related to the consumption of a given volume of oxygen is roughly constant (Schmidt-Nielsen 1997). Oxygen consumption was measured using an open air flow respirometer from Sable Systems (Las Vegas, NV, USA) comprising a two-channel pump PP-2, two mass flow controllers, electronics units MFC-2, an eight-channel multiplexer TR-RM8, an FC-10a Oxygen analyser and the sub-sampler/

pump/mass flow metre unit TR-SS3. After a period of fasting of 3 days, lizards were placed individually in 50-mL darkened chambers for the measurements, which occurred between 9 AM and 6 PM with airflow of 20 mL min<sup>-1</sup> and temperature set at 25 ± 0.5 °C. To limit stress, lizards were maintained for one night in a dark and cold room and were allowed to accustom with the chambers for at least 30 min before measurements. Oxygen concentration was measured every 5 s over 30-min period, and animals were weighed after each measurement. Oxygen consumption was calculated as the difference between the oxygen consumption in the ambient air and that at the exit of the chamber and we used the minimum consumption value to calculate the RMR (mL O<sub>2</sub> h<sup>-1</sup>). Mass-specific RMR values averaged 0.157 mL O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (±0.009 SE) at the juvenile stage and 0.127 mL O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (±0.005 SE) at the yearling stage in accordance with previous data (Massot *et al.* 2011). RMR increased with body mass when all data measured in this study and data obtained on the same animals in fall 2007 were pooled (log–log regression,  $r^2 = 0.30$ ,  $P < 0.001$ ), but the relationship was weak and non-significant at the juvenile stage (juvenile stage:  $r^2 = 0.06$ ,  $P = 0.40$ ; yearling stage:  $r^2 = 0.38$ ,  $P = 0.005$ ).

#### STATISTICAL ANALYSES

Mean values of all traits are reported in Table S1. All statistical analyses were carried out in R 2.14.1 software (<http://cran.r-project.org/>). We analysed separately the pairwise correlations among all six behavioural traits measured independently at the juvenile and at the yearling stage. Because we found some significant correlations, we further carried out a principal component analysis (PCA) on all behavioural data collected at each life stage. Our PCA was implemented using a correlation matrix implicitly rescaling all the variables (Venables & Ripley 2002). On the basis of the broken-stick method (Legendre & Legendre 1998), we retained two principal components (PCs) accounting for more than 60% of the variance for further analyses (see Table 1). We also rotated principal components using the *varimax* method to ease the understanding of loading patterns (Venables & Ripley 2002). We identified statistically significant contributions of behavioural traits to these two PCs by a bootstrapped eigenvector method with 1000 samples. For each individual and each trial, we calculated a score for each PC, which was used to compare individuals. In addition, we measured the repeatability of behaviour on the short term between the two independent measures taken a week apart at the yearling stage and on the long term between the measures taken independently at the juvenile stage and at the yearling stage. To do this, we fitted a linear mixed-effect model (LMM) on each

behavioural variable including a fixed time effect to control for changes in behaviour across repeated measures and a random individual effect. From this, we calculated a repeatability coefficient as the ratio of between-individual variance to total (between-individual and residual) variance and assessed the significance of random effects with likelihood ratio tests.

Behavioural scores for each PC at the juvenile stage were normally distributed and were analysed with a LMM including age (days), sex, body mass at birth, body mass at release and time of the day, and with maternal identity as a random effect to control for sibship. Behavioural scores for each PC at the yearling stage were also analysed with a LMM including age (days), sex, body mass at recapture, time of the day and enclosure identity (categorical variable). The best model was chosen by a stepwise selection procedure based on AIC (Burnham & Anderson 1998). From this best model, we calculated broad-sense heritability as twice the percentage of variation among families (Falconer 1989). Once a best model was selected, we further tested for the fixed effects of RMR, MSS, endurance capacity and motivation to run. One sprint speed data collected in a yearling was discarded from the analysis because the animal was not willing to run but all other data were included (Losos, Creer & Schulte 2002). Motivation to run was assessed by the number of taps during a race for sprint speed and by the number of taps per unit distance for endurance capacity (Le Galliard, Clobert & Ferrière 2004). The best model was chosen again by a stepwise selection procedure based on AIC.

We examined survival and growth selection following on the methodology of multivariate selection analysis by Lande & Arnold (1983). Survival probability was measured by assuming that animals that were not recaptured were dead, an assumption that is valid given the high recapture rates in our enclosures (Le Galliard, Clobert & Ferrière 2004). Survival probability was analysed with logistic regression models like recommended by Janzen & Stern (1998). Body growth of survivors was measured by the increase in body mass from release to recapture and was analysed with linear regression models like recommended by Mitchell-Olds & Shaw (1987). Body growth and annual survival probability were regressed against the fixed effects of sex, birth date (days), enclosure identity (categorical variable) and individual covariates (body mass at birth, MSS, RMR and PCs of behavioural data). All individual covariates were standardized to obtain standardized estimates of natural selection (Arnold & Wade 1984). Endurance capacity was not tested in the full model because it was only measured in half of the individuals. For the survival analysis, we first checked the linearity of fitness curves with a generalized additive model assuming a binomial distribution (Schluter 1988). We found no graphical evidence of nonlinearity. We then tested the

**Table 1.** Principal component (PC) analysis of behavioural data based on a correlation matrix at the juvenile stage ( $n = 176$ ) and at the yearling stage ( $n = 53$ )

Loadings	Juvenile stage				Yearling stage			
	PC1		PC2		PC1		PC2	
Percentage of time spent walking	<b>0.486</b>	0.483	<b>-0.163</b>	0.172	<b>0.486</b>	0.479	<b>-0.150</b>	0.171
Total distance travelled	<b>0.439</b>	0.537	<b>-0.310</b>	-	<b>0.466</b>	0.577	<b>-0.340</b>	-
Number of visits of compartments	<b>0.424</b>	0.585	<b>-0.407</b>	-	<b>0.426</b>	0.615	<b>-0.458</b>	-0.112
Time spent before first move	<b>-0.454</b>	-0.111	<b>-0.329</b>	-0.506	<b>-0.366</b>	-	<b>-0.385</b>	-0.528
Time before first visit to non-familiar compartment	<b>-0.401</b>	-0.161	<b>-0.315</b>	-0.529	<b>-0.429</b>	-0.134	<b>-0.351</b>	-0.538
Percentage time spent in non-familiar compartment	0.159	-0.314	<b>0.710</b>	0.656	0.218	-0.195	<b>0.618</b>	0.625
Eigenvalue	3.58		1.33		3.74		1.31	
Variance explained	59.7%		22.2%		62.4%		21.8%	
Broken-stick percentage	40.8%		24.2%		40.8%		24.2%	

Factor loadings before (left column) and after (right column) a *varimax* rotation of the two-first principal components are indicated. Bold typeface indicates the statistically significant loadings before *varimax* rotation.

significance of the sibship effect by fitting a mixed-effect model with fixed effects of body mass and enclosure identity and a random effect of family identity using the *lmer* procedure with a Laplace approximation and a binomial distribution (Bolker *et al.* 2009). This model found very little variation in survival among families within enclosures. We thus proceeded to the analysis of survival probability with a standard logistic regression including all main effects (directional selection) and interactions between behavioural traits and the three other individual covariates (correlational selection). The best model was then chosen by a stepwise selection procedure. For body growth, data conformed to a normal distribution and were analysed with a LMM including the same factors as above.

## Results

### BEHAVIOURAL VARIATION AND REPEATABILITY

Pairwise correlations among the behavioural traits revealed strong and positive associations between three traits linked with locomotor activity (percentage of time spent walking, movement distance and number of visits to compartments), and intermediate and significant correlations between these three traits and the time spent before the first move and before the first visit to the non-familiar compartment (Table S2). Correlations between these five traits and the percentage of time spent exploring the non-familiar compartment were not significant. In line with this, the PCA revealed a shared pattern of behavioural variation at the juvenile and the yearling stages (Table 1). A first major axis (PC1) explained most of the variation and was positively correlated with total distance travelled, number of visits to compartments and percentage of time spent walking, and negatively correlated with time spent before first move and time spent before the first visit to the non-familiar compartment. A second major axis (PC2) was nearly significant according to the broken-stick method and loaded significantly with all behavioural traits, including a strong positive loading with percentage of time spent in the non-familiar compartment. The interpretation of the loading patterns remained essentially the same after the *varimax* rotation (Table 1).

The short-term and long-term repeatability of PC1 score was, respectively, 0.65 (significant,  $\chi^2 = 15.1$ , d.f. = 1,  $P < 0.001$ ) and 0.15 (non-significant,  $\chi^2 = 1.13$ , d.f. = 1,  $P = 0.29$ ). Repeatability was not significant for PC2 (short term: 12%,  $\chi^2 = 0.39$ , d.f. = 1,  $P = 0.53$ ; long term: 20%,  $\chi^2 = 2.16$ , d.f. = 1,  $P = 0.14$ ). For the original behavioural traits, we found significant repeatability on the short term varying between 0.59 and 0.65 for percentage of time spent walking, movement distance and number of visits to compartments, and between 0.28 and 0.36 on the long term (Table S3). The short-term repeatability was significant for time spent before the first move and the time spent before the first visit to non-familiar compartment, but long-term repeatabilities were not significant. Short-term and long-term repeatability for percentage time spent in the non-familiar compartment were all non-significant (Table S3).

### DETERMINANTS OF BEHAVIOURAL VARIATION

The best selected model describing variation for PC1 at the juvenile stage had a positive effect of body mass at birth ( $F_{1,133} = 6.84$ ,  $P = 0.01$ ), a positive effect of age ( $F_{1,133} = 6.15$ ,  $P = 0.02$ ) and no significant effect of sex, body mass at release, or time of the day (all  $P > 0.16$ ). PC1 varied also significantly between families ( $\chi^2 = 8.49$ , d.f. = 1,  $P = 0.004$ ) totalling 16% of the trait variation unexplained by fixed effects. This implies a broad-sense heritability  $h^2 = 0.32$ . The best model for PC2 at the juvenile stage was the constant intercept model and PC2 varied weakly and non-significantly among families (7%,  $\chi^2 = 2.06$ , d.f. = 1,  $P = 0.15$ ). Including RMR, MSS, endurance capacity and motivation to run did not improve the model fit (see also Table 2 for pairwise correlations).

At the yearling stage, the best model for PC1 had no random family effect ( $\chi^2 = 0.03$ , d.f. = 1,  $P = 0.85$ ) and included only the marginally significant, fixed effects of MSS ( $F_{1,48} = 3.34$ ,  $P = 0.07$ ) and endurance capacity ( $F_{1,48} = 3.36$ ,  $P = 0.07$ ). The trend was for a positive correlation with MSS or endurance capacity (Table 2). The best model for PC2 at the yearling stage had no fixed effect, and PC2 did not vary significantly between families ( $\chi^2 = 1.24$ , d.f. = 1,  $P = 0.26$ ). Individual scores for PC1 decreased while those for PC2 increased significantly from the juvenile to the yearling stage (intra-individual change, PC1:  $t = 10.2$ ,  $P < 0.001$ ; PC2:  $t = 3.17$ ,  $P = 0.002$ , Table S1).

**Table 2.** Pearson's product-moment correlation between resting metabolic rate (RMR), locomotor performance traits and the behavioural variation for each of the principal components (PC) (see Table 1)

Physiological and performance trait	Juvenile stage		Yearling stage	
	PC1	PC2	PC1	PC2
RMR	0.03 (170)	0.05 (170)	-0.04 (52)	-0.03 (52)
Maximal sprint speed	0.00 (170)	0.03 (170)	<b>0.27 (52)</b>	0.08 (52)
Endurance capacity	0.13 (87)	-0.05 (87)	<b>0.25 (53)</b>	0.04 (53)
Motivation to sprint on the racetrack	0.05 (170)	-0.13 (170)	-0.15 (53)	0.11 (53)
Motivation to run on the treadmill	0.16 (87)	-0.01 (87)	-0.07 (53)	0.01 (53)

Sample sizes are indicated in brackets. Motivation to sprint on the racetrack was indexed by the number of taps during the race. Motivation to run on the endurance treadmill was indexed by the number of taps per unit distance during the run. All correlations were non-significant except for two that approached significance (bold numbers,  $P = 0.06$ ).

## NATURAL SELECTION ON ACTIVITY BEHAVIOUR

Among the 173 lizards released from the laboratory, 53 juveniles survived until the next summer season, a proportion similar to the average juvenile mortality in natural conditions (Le Galliard, Marquis & Massot 2010). The full logistic model fitted well the data (goodness-of-fit test,  $P = 0.12$ ). The best model describing survival included no effect of PC2 and no interaction term with body mass at birth (all  $P > 0.10$ ). The interaction between MSS and PC1 was marginally significant ( $\chi^2 = 3.22$ , d.f. = 1,  $P = 0.07$ ) indicating negative, correlational selection on the two traits (logit regression, estimate =  $-0.35 \pm 0.20$  SE). After the removal of this interaction, we obtained a model including no effect of MSS ( $P > 0.10$ ) and correlational selection on RMR and PC1 (see Table 3). The predicted fitness surface displayed two fitness peaks for lizards with low RMR and high PC1 prior to release and for lizards with high RMR and low PC1 prior to release (Fig. 1). In addition, survival increased with body mass at birth and decreased with the birth date like in natural populations (Le Galliard, Marquis & Massot 2010) and was higher in males (Table 3). In the subset of newborns measured for endurance ( $n = 87$ ), we found no directional or correlational selection on endurance capacity (all  $P > 0.10$ ).

Body mass increased from 0.39 g at release to 1.01 g at recapture, and body mass increase did not vary among families ( $\chi^2 = 0.11$ , d.f. = 1,  $P = 0.74$ ). Change in body mass (g) decreased with PC2 (estimate =  $-0.06 \pm 0.02$ ,  $F_{1,46} = 9.16$ ,  $P = 0.004$ ) and was also influenced by the interaction between RMR and PC1 ( $F_{1,46} = 9.94$ ,  $P = 0.002$ ) and by the interaction between MSS and PC1 ( $F_{1,46} = 4.25$ ,  $P = 0.04$ ). Body growth was maximal for lizards characterized by low PC1 and high RMR prior to release and minimal for lizards with high RMR and high PC1 or lizards with low PC1 and low RMR. Body growth decreased with PC1 in lizards with low MSS with a diminishing effect when MSS increased (Fig. 1).

**Table 3.** Selected model describing annual survival in juvenile common lizards measured for resting metabolic rate (RMR, mL O<sub>2</sub> h<sup>-1</sup>) and behaviour [principal component 1 (PC1) score, see Table 1]. Estimates are given on the logit scale

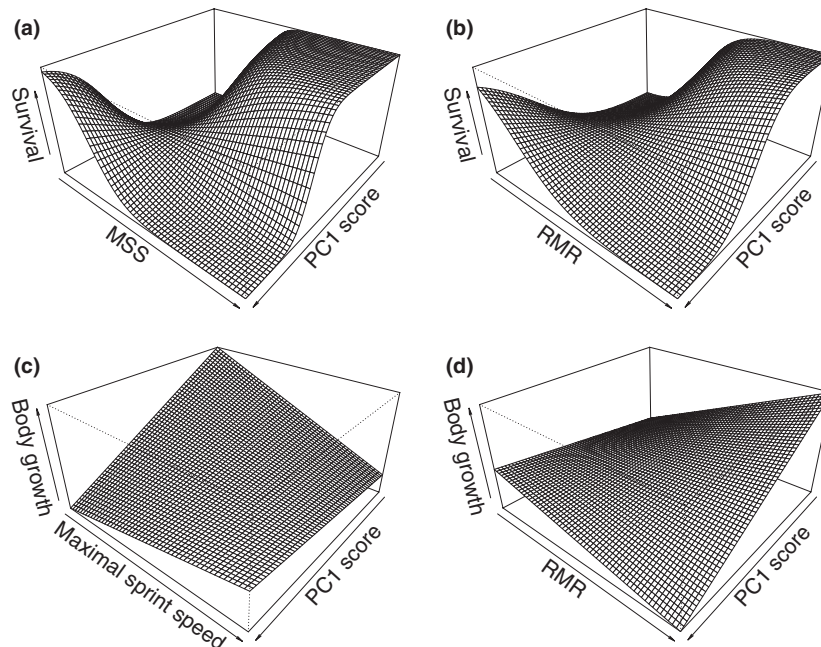
Factor	Estimate $\pm$ SE	Statistics (type III)
Intercept	$-7.69 \pm 2.74$	–
Sex	M: $1.20 \pm 0.38$	$\chi^2=10.3$ , d.f. = 1, $P = 0.001$
Birth date	$-0.31 \pm 0.38$	$\chi^2=5.02$ , d.f. = 1, $P = 0.02$
Mass at birth	$0.49 \pm 0.21$	$\chi^2=5.99$ , d.f. = 1, $P = 0.01$
PC1 score	$-0.05 \pm 0.20$	$\chi^2=0.07$ , d.f. = 1, $P = 0.78$
RMR	$-0.14 \pm 0.21$	$\chi^2=0.44$ , d.f. = 1, $P = 0.50$
PC1 score $\times$ RMR	$-0.56 \pm 0.24$	$\chi^2=6.45$ , d.f. = 1, $P = 0.01$
Enclosure	–	$\chi^2=8.59$ , d.f. = 3, $P = 0.03$

PC1, RMR and mass at birth were standardized prior to analysis. Mean relative birth date was 18 days after 1 July. M = males.

## Discussion

In the common lizard, behavioural traits describing variation in locomotor activity in a novel environment exhibited consistent individual differences (CIDs) over up to a year, and the exploration score from the principal component analysis displayed significant repeatability on the short term. These results add to a growing list of personality studies in reptiles and provide the first demonstration of long-term CIDs in exploratory behaviour in a lizard (Rodríguez-Prieto, Martín & Fernández-Juricic 2011). The exploration score quantified inter-individual variation in activity and varied significantly between families at the juvenile stage, indicative of high broad-sense heritability though this could be caused by maternal effects. A high exploration score could imply a more rapid exploration and more active locomotion, and therefore a more proactive behavioural type (Sih, Bell & Johnson 2004; Careau *et al.* 2011; Rodríguez-Prieto, Martín & Fernández-Juricic 2011). Alternatively, a high exploration score could be indicative of a more thorough exploration strategy, where thorough explorers spend more time walking to explore a novel environment (Careau *et al.* 2009). This is because exploration thoroughness is hard to quantify and distinguish from locomotor activity using a neutral arena test (Réale *et al.* 2007).

The pace-of-life syndrome predicts a positive correlation between activity, superficial exploration, energetic expenditure and locomotor performances (Careau *et al.* 2008; Biro & Stamps 2010; Réale *et al.* 2010; Careau & Garland 2012). Our study based on a population maintained in outdoor enclosures yields mixed support for this prediction despite a strong inter-individual variation in RMR, maximal sprint speed (MSS) and endurance capacity. Regarding metabolism, we found a 10-fold variation in mass-dependent RMR but no significant correlation with exploratory behaviour. Independence between RMR and behavioural activity was also documented in a fish (Farwell & McLaughlin 2009) and in a small rodent (Timonin *et al.* 2011). There is no clear consensus emerging from the literature about the causes of inter-individual variation in RMR and the relationship between RMR and activity (Careau *et al.* 2008, 2011; Réale *et al.* 2010; Burton *et al.* 2011). Biro & Stamps (2010) argued for the case of a general, positive relationship between RMR and activity, but a negative relationship is predicted if limited resources must be allocated to behavioural activity instead of RMR (Careau *et al.* 2008). Independence between RMR and activity is also expected because these traits could be supported by variation in the size and metabolic intensity of different organs (see Fig. 2 in Careau & Garland 2012). In addition, maintenance metabolism contributes very differently to the energy budget in ectotherms than in endotherms, for which RMR has a strong significance to the overall budget and supports the cost of endothermy (Speakman, Krol & Johnson 2004). Furthermore, the



**Fig. 1.** Survival and growth selection acting on principal components (PC1) score (exploration score, see Table 1), resting metabolic rate (RMR) and maximal sprint speed (MSS) in juvenile common lizards. Covariates were all standardized prior to analyses. (a, b) Correlational survival selection acting on maximal sprint speed (MSS) and PC1 (panel a) and on RMR and PC1 (panel b). The predicted fitness surface in panel (b) was calculated over the range of variation of each trait from the best model in Table 3 assuming a mean body mass at birth and birth date. Fitness surface in panel A was obtained from the same model including the interaction between MSS and PC1. (c, d). Correlational growth selection acting on MSS and PC1 (panel c) and on RMR and PC1 (panel d). Growth was calculated as the difference in body mass between recapture and release. The predicted fitness surface was calculated according to the best model described in the main text assuming a mean body mass at birth.

effect of activity metabolism on the energy budget can be very different in endotherms than in ectotherms, as the heat generated by activity metabolism can potentially substitute for thermoregulation in endotherms but not in ectotherms (Careau & Garland 2012). Hence, no universal link between activity and RMR is likely to hold across taxonomic groups including both endotherms and ectotherms with diverse life styles.

Regarding locomotor performances, there was a positive, though only marginally significant, correlation with exploration score at the yearling stage but no evidence of correlation at the juvenile stage. In lizards, interindividual variation in endurance relates to enzymatic, physiological and morphological attributes, such as body size, tight-muscle mass and aerobic metabolic capacity, while variation in MSS is more strongly correlated to limb length, body shape and muscle fibre diameter (e.g. Garland 1984; Garland & Else 1987; Bennett & Huey 1990). Hence, we do not expect correlations between exploratory behaviour and locomotor performances on biomechanical or physiological grounds. An alternative link is that temperament influences motivation to run, which contributes importantly to variation in maximal performances (Bennett & Huey 1990; Losos, Creer & Schulte 2002; Le Galliard, Clobert & Ferrière 2004). However, we found no correlation between exploratory behaviour and the motivation to run on the racetrack and the treadmill. Instead, our report of an age-dependent correlation between the exploration score and locomotor per-

formances suggests a combined effect of developmental history and natural selection. Ontogenic changes in locomotor performances have been reported in the common lizard and could be influenced by the temperament (Le Galliard, Clobert & Ferrière 2004). For example, lizards that are more active at birth may be better at allocating energy into locomotor performances. Natural selection could also shape the correlation between exploratory behaviour and locomotor performances if lizards with high exploration score, high MSS and high endurance survive better. Against this, we found a marginally significant negative correlational survival selection acting on exploration score and MSS, such that lizards with a negative correlation between MSS and exploration score tended to survive better. In addition, body growth decreased with the exploration score except for lizards with high MSS. These fitness landscapes are difficult to reconcile with the hypotheses of a pace-of-life syndrome and of a production-survival trade-off except if variation along the exploration score quantifies the thoroughness of exploration (Careau *et al.* 2009). The production-survival trade-off hypothesis would indeed predict that thorough exploration has a negative effect on growth but a positive effect on survival, which was true for the subset of newborns characterized by low MSS at birth. This suggests that the behavioural trade-off between growth and survival was influenced by sprinting abilities and only significant in lizards with poor performances at birth.

Another important finding was the significant correlational survival and growth selection involving exploration score and resting metabolic rates (RMR). Lizards characterized by high RMR and low exploration score and by low RMR and high exploration score survived the best during their first year of life. The relationship between RMR and body growth also changed from positive to negative as the exploration score at birth of lizards increased. Assuming that exploration score quantifies variation in activity, this correlational selection runs counter to the production scenario envisioned by Careau *et al.* (2008) and the pace-of-life scenario of Réale *et al.* (2010). These scenarios would predict (i) that lizards with a high activity should on average grow faster but survive less, (ii) that lizards with a high RMR should also on average grow faster but survive less and (iii) that lizards with both high activity and high RMR should grow and survive better than lizards that are active with a low RMR or than lizards that are inactive with a high RMR. A negative correlation between percentage time spent exploring and RMR was observed across species in murid rodents by Careau *et al.* (2009), who explained this as an adaptation along a trade-off between energy invested in maintenance (RMR) and energy invested in activity. These two energy expenditures represent significant components of the total budget in ectotherms (Reilly, McBrayer & Miles 2007), and our pattern of correlational selection could therefore also be interpreted according to this trade-off scenario. Alternatively, exploration score could quantify the thoroughness of exploration such that lizards with high exploration score are more thorough explorers that should follow a slower demographic and metabolic tactic (Careau *et al.* 2009). In this case, our analyses of natural selection in juvenile common lizards would support co-adaptation between exploration thoroughness and energetic along a slow-fast demographic continuum. Altogether, these results indicate that concurrent variation in personality traits and energetic can contribute to explain significant demographic variation within species.

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## Authors contributions

J.-F. Le Galliard and L. Montes designed the study. All authors contributed data collection and J.-F. Le Galliard and M. Paquet analysed the data. J.-F. Le Galliard wrote the article.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Univariate statistics for all measured traits.

**Table S2.** Correlation matrix of the six behavioural traits.

**Table S3.** Repeatability coefficients of the six behavioural traits.