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An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability

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Abstract

Temperament traits are seen in many animal species, and recent evolutionary models predict that they could be maintained by heterogeneous selection. We tested this prediction by examining density-dependent selection in juvenile common lizards *Zootoca vivipara* scored for activity, boldness and sociability at birth and at the age of 1 year. We measured three key life-history traits (juvenile survival, body growth rate and reproduction) and quantified selection in experimental populations at five density levels ranging from low to high values. We observed consistent individual differences for all behaviours on the short term, but only for activity and one boldness measure across the first year of life. At low density, growth selection favoured more sociable lizards, whereas viability selection favoured less active individuals. A significant negative correlational selection on activity and boldness existed for body growth rate irrespective of density. Thus, behavioural traits were characterized by limited ontogenic consistency, and natural selection was heterogeneous between density treatments and fitness traits. This confirms that density-dependent selection plays an important role in the maintenance of individual differences in exploration-activity and sociability.

Introduction

Density-dependent feedbacks describe how changes in population size influence components of population growth, and are essential to understand population dynamics (Herrando-Pérez *et al.*, 2012). Density dependence is also involved in evolutionary dynamics as density-dependent feedbacks can alter the strength of selection on life-history traits and promote the maintenance of alternative, genetically based, life-history strategies (Reznick *et al.*, 2002; Sinervo *et al.*, 2007). In empirical studies, density-dependent selection has been observed for foraging behaviour, dispersal propensity, aggressiveness or territorial behaviour (Sokolowski *et al.*, 1997; Duckworth & Badyaev, 2007). Thus, density-dependent selection is likely to play an important role in the maintenance of behavioural types.

Consistent individual differences (CIDs) in single behaviours, also called temperament traits or personalities, and correlations among suites of distinct behaviours, also called behavioural syndromes, have been observed in numerous animal species (Sih *et al.*, 2004b; Réale *et al.*, 2007). Some evolutionary models suggest that CIDs in a single behaviour could evolve by frequency-dependent and/or fluctuating selection, which maintains stable differences in behaviours linked with stable differences in state, such as body growth or energy metabolism (Dall *et al.*, 2004; Wolf *et al.*, 2007; Dingemanse & Wolf, 2010). Density dependence could be one of the main processes involved in the maintenance of CIDs in behaviours. Indeed, most natural populations are subjected to density-dependent feedbacks and, to some extent, to temporal and spatial fluctuations in density (Herrando-Pérez *et al.*, 2012). Density-dependent regulation can lead to the

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frequency-dependent selection needed to evolve behavioural polymorphism (Heino *et al.*, 1998; Reznick *et al.*, 2002; Sinervo *et al.*, 2007). Population density influences resource availability and competitive interactions, and therefore the relative fitness of sociability (Cote *et al.*, 2008), activity and exploration (Quinn *et al.*, 2009), habitat use behaviour (Kobler *et al.*, 2009) or infanticide behaviour (Korpela *et al.*, 2011). For instance, low nutrient availability for fruit fly larvae *Drosophila melanogaster* at high population density can change selection on a polymorphic gene involved in foraging strategy (Fitzpatrick *et al.*, 2007). Yet, only two natural selection studies investigated density-dependent selection on temperament traits to our knowledge, and none of these have examined the potential for selection to act on several, distinct behavioural traits (Cote *et al.*, 2008; Quinn *et al.*, 2009).

It is generally predicted that densities well below the carrying capacity of the habitat at a given time and location should favour fast life histories, whereas slow life histories may be advantageous in a more competitive environment (Chitty, 1970; Reznick *et al.*, 2002). Initially, ecologists considered that this should lead to individual plasticity in behaviour, such that individuals become more active, less shy and bolder towards natural predators at low population density (e.g. Anholt & Werner, 1995; Biro *et al.*, 2003). Recently, it has been proposed that temperament traits are integrated within a pace-of-life syndrome according to which more active, superficially exploring, bold and less sociable behavioural types follow a fast life history (Réale *et al.*, 2010). This scenario predicts selection against behavioural syndromes associated with fast life histories at high population density. There is indeed evidence for selection at high population density against temperaments of high aggressiveness in birds (Duckworth & Badyaev, 2007) and low sociability in lizards (Cote *et al.*, 2008). Yet, the cost of a fast behavioural strategy at high population density could depend on the type of intraspecific competition (contest vs. scramble), the association between temperament, energy expenditure and life-history productivity, and the degree of intra-individual flexibility in behaviour (Quinn *et al.*, 2009; Réale *et al.*, 2010). More studies of multivariate selection in heterogeneous environments are therefore needed to draw general conclusions on natural selection acting on temperament traits.

Here, we combine laboratory assessments of individual behaviour in juvenile common lizards *Zootoca (Lacerta) vivipara* with a field enclosure experiment to investigate density-dependent selection on a behavioural syndrome involving exploration, boldness and sociability. The aggressiveness-boldness-exploration syndrome has already been evidenced in several species; however, we know less about other axes of behavioural variation such as sociability. In a birth cohort of newborns, we scored locomotor activity, boldness and sociability at birth and at the age of 1 year, and investigated CIDs across time for the same behaviour as well as the presence of behavioural syndromes. To allow precise measurements of natural selection in a realistic environmental setting (Le Galliard *et al.*, 2004), all newborns were maintained in populations kept inside field enclosures and ranging from low to high density levels below and above the carrying capacity (Mugabo *et al.*, 2013). We measured three life-history traits (juvenile survival, body growth rate and reproduction) and quantified density-dependent selection on behavioural traits for each life-history trait. Natural populations of common lizards are subject to significant temporal and spatial variation in density, and there is a reduced body growth and reproduction of lizards at high population densities (Massot *et al.*, 1992; Cote *et al.*, 2008; Mugabo *et al.*, 2013). CIDs in exploration, locomotor activity and sociability have been found in juveniles (Cote & Clobert, 2007; Le Galliard *et al.*, 2013). Yet, multivariate selection on behavioural traits had not been examined so far. According to the pace-of-life syndrome hypothesis, we expected selection against low sociability, high boldness and high activity at high population densities.

Materials and methods

Model species

The common lizard is a small (adult snout-vent-length, SVL: 50–75 mm) ovoviviparous species inhabiting humid habitats across northern Eurasia. It is characterized by a short life expectancy (3–4 years), a continuous growth, and a 20–40% mean juvenile survival, whose variation determines importantly lifetime reproductive success (Le Galliard *et al.*, 2004). Natural populations can be divided into three age classes: juveniles, yearlings and adults ($\geq$ 2 years old). Age at first reproduction is plastic and varies from 1 to 2 years old in our study site; thus, breeding at the age of 1 year indicates a faster sexual maturation and life history (see Mugabo *et al.*, 2010). In natural populations, mean density ranges from 200 to 2000 adults and yearlings per ha (Massot *et al.*, 1992). In our outdoor enclosures, the prebreeding equilibrium population size averages 2000 yearlings and adults per ha.

General protocol

During the summer 2008, we manipulated the post-breeding density of 24 experimental populations maintained in outdoor enclosures at the CEREEP-Ecotron IleDeFrance (48°17′N, 2°41′E). Enclosures measuring 10 × 10 m each were located in a natural meadow and provided lizards with access to shelters and basking sites (four artificial piles of wood and stones), water (two artificial ponds) and natural food (see Lecomte *et al.*, 2004 for a full description). Enclosure size corresponds to the average home range of an adult in natural populations. All enclosures were protected from terrestrial predators with plastic fences, but avian predators could prey on lizards freely. Wild avian predators observed during this study included crows, rooks, magpies, and kestrels (Le Galliard, pers. obs.). Enclosures did not allow for dispersal movements. Populations were established post-breeding following five density levels. Level 1 had one adult male, two adult females, two yearling males, two yearling females, as well as 5–6 and 4–5 juvenile males and females, respectively, equivalent to 700 adults and yearlings per ha. Density levels 2–5 differed from density level 1 by a multiplicative factor of 2–5, respectively, but had similar age and sex structures (for more details on experimental procedures, see Mugabo *et al.*, 2013). The number of enclosures per treatment was adjusted to reach a similar sample size per treatment (level 1: $N = 10$, level 2: $N = 5$, level 3: $N = 4$, level 4: $N = 3$, level 5: $N = 2$). All animals were individually marked by toe-clipping.

In May 2008, adults and yearlings were captured at our study site from enclosed populations at variable densities around the mean, equilibrium population size (i.e. level 3 in our experiment). They were maintained in the laboratory under standard conditions and released on the 12th and 13th of June inside experimental enclosures, except for gravid females which were released 1 day after parturition (from the 11th of June to the 23rd of July). Adults ($n = 162$) and yearlings ($n = 216$) were randomly assigned to populations. Newborns are autonomous and active right after birth. On their birth day, newborns were sexed according to their ventral scales and measured for SVL to the nearest mm and for body mass to the nearest mg. Newborns from the same litter were then stored in separate boxes equipped with a shelter and damp soil and provided with food and water *ad libitum*. All newborns ($n = 609$) were measured for three behaviours (see details below), and 549 randomly chosen juveniles were subsequently released according to a split-clutch design. Offspring from the same clutch were released the same day inside distinct enclosures chosen from all density treatments. We did not account for density experienced by the mother in our study as we controlled for random variation among families in all analyses, and the split-clutch design made it impossible that density-dependent selection on offspring traits could be due to maternal effects. Moreover, in a field experiment, Meylan *et al.* (2007) found that maternal effects did not influence juvenile life-history traits in a different way according to density.

Animals were recaptured in late spring 2009 (May–June) on average 167 ± 8.55 (SD, range = 150–204 days) activity days after their birth date (excluding 5 months where lizards hibernate and do not grow, pers. obs.). After several days of hand capture in each enclosure, all surviving juveniles ($n = 213$) were recaptured and measured for SVL and body mass. Lizards were then kept in the laboratory, where we measured again their behaviour following our standard procedures except for 10 individuals captured late in June. Gravid females were kept in individual boxes under *ad libitum* food, water and thermal conditions until they gave birth (mean duration of 52 days, range = 40–70 days). Their fecundity (total litter size) was measured knowing that it is little influenced by conditions encountered during gestation (Bleu *et al.*, 2013). Density levels at the end of the experiment were still highly different among treatment groups and were also positively correlated with those at the beginning of the experiment (Mugabo *et al.*, 2013). Thus, density-dependent effects on life history could not vanish due to a very strong and fast density regulation.

Collection of behavioural data

Behavioural data were gathered between 10 am and 5 pm in plastic boxes maintained in the same room at a standard temperature of 23–25 °C and filled with a layer of clean sand before each trial to avoid interference with odours from congeners. During recordings, optimal light and basking conditions were provided by a combination of heat (25 W bulb) and UV-enhanced white light sources (Iguana Light 10.0 UV-B, ZooMed, 40 W) located above the plastic boxes. We scored lizards after an acclimatization period of 5 min and recorded all behaviours from above with webcams. During trials, plastic boxes were placed behind opaque walls to minimize disturbance. For each behavioural trait and life stage, a random sample of 45–70 lizards was measured again the next day to score short-term repeatability.

We used a neutral arena test to investigate locomotor activity 1 day after birth in 2008 and 4 days after capture in 2009. Plastic boxes were equipped with two heat sources (one at each corner) to enable locomotion at optimal body temperature. After the acclimatization period, the locomotion behaviour was filmed during 20 min and an image sequence was obtained using VirtualDub. From this, we recorded the lizard position into IMAGEJ v1.40 (http://imagej.nih.gov/ij/) using a particle analysis procedure. We calculated the movement distance, which allows to measure consistent individual difference in activity (i.e. general activity of a lizard in his familiar environment) and/or exploratory behaviour (i.e. behaviour in an unfamiliar environment, sensu Réale *et al.*, 2007). We did not obtain independent measurements of activity and exploration because the two may be functionally related and our previous tests found no difference in locomotor activity between familiar and unfamiliar environments (Le Galliard *et al.*, 2013).

We measured boldness (or risk taking) behaviour the day after measuring the activity behaviour. We assessed the refuge use by a lizard facing a simulated attack by a human (e.g. López *et al.*, 2005). Plastic boxes were equipped with a cardboard shelter on one corner to provide a refuge and with a heat source on the opposite corner to provide a stimulus for basking. After the acclimatization period, we simulated several consecutive predator attacks with a paintbrush, softly touching the tail to force the lizard into the shelter. If the lizard was already inside the shelter, we simulated attacks around the shelter to force the head of the lizard into the shelter. We then filmed the behaviour from above and calculated the time spent hiding (body and head inside the refuge) before leaning out of the refuge (body inside the refuge but tip of the nose emerging from the shelter), the time spent before emerging from the refuge (head and body outside the refuge), and the time spent before basking under the heat source on the opposite side of the box. Recordings were stopped after a predetermined duration of 50 min. This procedure caused 'censoring' of data for 44 lizards in 2008 (7% of recordings) and three lizards in 2009 (1% of recordings). We expected a strong correlation between the three boldness scores because they are nonindependent by construct.

We measured sociability the day after the boldness test with a protocol modified from Cote & Clobert (2007). We quantified the simultaneous choice between a control shelter and a shelter with odours of adult males. Prior to the test, trios of adult males ($n = 4$ groups) were maintained in the same terrarium and provided with water *ad libitum*. Odours were collected during a minimum period of 1 week on blotting paper placed on the floor of the terrarium. To avoid collection of odours from preys, one male from each trio was removed every 3 days and fed with live crickets in a separate terrarium. We also collected control odours by placing a blotting paper on the floor of an empty terrarium maintained under the same conditions in the same room. During the behavioural trials, each plastic box was equipped with one heat source at the centre and with two identical plastic shelters located on each corner. Under each shelter, we positioned a piece of blotting paper with or without odours of adult males. The lizard could choose between staying under the shelter with or without a conspecifics' odour, or being exposed out of the shelters. Location in or out of the shelters was recorded during 20 min after the acclimatization period. We scored the total time spent hidden under a shelter during the test, the time spent under the shelter with odour minus the time under the control shelter (hereafter called absolute sociability score), and the absolute social score divided by the total time spent hidden (hereafter called relative sociability score). The absolute social score has already been used to measure consistent individual differences in social behaviour in common lizards (Cote & Clobert, 2007) and in wall lizards *Podarcis hispanica* (Rodriguez-Prieto *et al.*, 2011). We expected a strong correlation between the two sociability scores because they are nonindependent by construct. Summary statistics of all variables are provided in Table S1.

Statistical analyses

All statistical analyses were done in R 3.0.1 software (http://cran.r-project.org/). We analysed short-term as well as interannual consistency of the seven behavioural traits using Spearman rank correlation tests. We calculated pairwise correlations among the seven behavioural traits measured independently at the juvenile and at the yearling stage. We further carried out a principal component analysis (PCA) on all behavioural data collected at the newborn stage. Our PCA was implemented using a correlation matrix implicitly rescaling all the variables (Venables & Ripley, 2002), and boldness scores were log-transformed to achieve normality. Based on the Kaiser–Guttman criterion (Legendre & Legendre, 1998), we retained three principal components (PCs) accounting for more than 60% of the variance (see Table 1). We identified statistically significant contributions of behavioural traits by a bootstrapped eigenvector method with 1000 samples. For each individual, we calculated a behavioural score for each PC.

We then examined survival, growth and maturation selection using the framework of multivariate selection analysis (Lande & Arnold, 1983). Survival probability was measured by assuming that animals that were not recaptured were dead, and was analysed with logistic regression models. Body growth rate of survivors was measured by the increase in body size from release to recapture divided by the age (number of activity days) at recapture and was analysed with linear regression models. We controlled for ceiling effect by fitting size at birth in the model describing body growth rate.

Table 1 Retained principal component analysis of behavioural data based on a correlation matrix at the newborn stage ($n = 598$). Bold typeface indicates the statistically significant loadings for each variable. The correlation matrix is provided as Supplementary Information in Table S2.

	PC1	PC2	PC3
Loadings			
Movement distance	0.077	0.077	**0.840**
Time head hidden	**−0.556**	−0.024	**0.123**
Time body hidden	**−0.582**	−0.019	**0.108**
Time until basking	**−0.561**	−0.009	0.043
Absolute sociability score	−0.032	**0.704**	−0.066
Relative sociability score	−0.029	**0.704**	−0.050
Time spent hidden	**−0.170**	−0.044	**−0.508**
Eigenvalue	2.73	1.83	1.006
Variance explained	39.03	26.16	14.37

Breeding frequency was scored in females by recording breeding events in the laboratory and was analysed with a logistic regression. Our starting models were the best models describing density-dependent survival, growth rate and maturation in Mugabo *et al.* (2013). In our study, these models further included the linear effects of PC scores at the juvenile stage, as well as the two-way interactions between density (linear effect) and PC scores to test for density-dependent selection on behavioural traits. We also included multiplicative and quadratic effects of PC scores to test for potential stabilizing and correlational selection across all density treatments. To obtain standardized estimates of natural selection, all individual covariates were centred and scaled to unit variance, growth data were divided by the sample mean, and estimates of logistic regressions were transformed to an average gradient following Janzen & Stern (1998). Models were fitted using the *lmer* procedure with a Laplace approximation and additive random effects of family identity and enclosure identity. The random family effect was removed if not significant. The best model was chosen by a stepwise elimination procedure of nonsignificant fixed factors starting from interaction terms to main effects. Marginal (including fixed effects only) and conditional (including fixed and random effects) pseudo-R^2 and difference in AIC with the null model were calculated following Nakagawa & Schielzeth (2012). We verified that the shape of natural selection was well captured by our models by comparing best models with results of generalized additive models (GAM) assuming smooth, nonparametric functions. Because our three PC scores generally reflect different measures of the same temperament trait (see below), we also run our full models with one score from each test (movement distance, absolute sociability and mean boldness score). Our main results remained qualitatively unchanged (results not shown).

Results

Consistency and correlation among behavioural traits

Short-term consistent individual differences (CID) among newborns were found for all behavioural traits including movement distance (Spearman's rank correlation test, $n = 50$, $\rho = 0.73$, $P < 0.0001$), boldness ($n = 48$, time head hidden: $\rho = 0.33$, $P = 0.02$; time body hidden: $\rho = 0.32$, $P = 0.02$; time until basking: $\rho = 0.28$, $P < 0.05$), sociability ($n = 51$, absolute score: $\rho = 0.51$, $P < 0.001$; relative score: $\rho = 0.43$, $P < 0.001$) and time spent hidden ($n = 51$, $\rho = 0.69$, $P < 0.001$). At the yearling stage, CIDs in single behaviours were also found for all but one behavioural trait, namely sociability score (Spearman's rank correlation test, movement distance: $n = 45$, $\rho = 0.73$, $P < 0.0001$; boldness $n = 71$, time head hidden: $\rho = 0.46$, $P < 0.001$; time body hidden: $\rho = 0.50$, $P < 0.0001$; time until basking: $\rho = 0.41$, $P < 0.0001$; social behaviour, $n = 51$, absolute score: $\rho = 0.23$, $P = 0.10$; relative score: $\rho = 0.36$, $P = 0.009$; time spent hidden: $n = 51$, $\rho = 0.67$, $P < 0.001$). Calculations of short-term repeatability coefficients for all behavioural traits showed similar results (Table S1).

When comparing behavioural scores across the first year of life (see Table S1), we found that lizards were more active, bolder and less sociable at the yearling stage. Significant but weak CIDs in single behaviours across the first year of life were found for movement distance ($n = 202$, $\rho = 0.14$, $P = 0.04$) and for one boldness measure (time body hidden: $n = 202$, $\rho = 0.16$, $P = 0.02$), but not for sociability (absolute score: $\rho = -0.03$, $P = 0.60$; relative score: $\rho = -0.08$, $P = 0.23$) or for time spent hidden ($\rho = 0.07$, $P = 0.31$). Given the measurement error observed at each life stage, this low consistency could be due to a statistical bias (Dingemanse & Dochtermann, 2013). Yet, we checked that our sampling design had a good statistical power to detect meaningful long-term consistency values (see Appendix S1).

We found weak and mostly nonsignificant correlations among behavioural traits in newborns apart from the expected correlations between the three boldness scores and between the two sociability scores (see Table S2). There was also a positive correlation between total time spent hidden and the three boldness scores, indicating that refuge use in the sociability test was correlated with boldness in the risk taking test. The PCA (see Table 1) revealed three major axis of variation corresponding to boldness (PC1 score with positive values indicating bolder lizards in the risk taking and sociability tests), sociability (PC2 score with positive values indicating more sociable lizards) and locomotor activity (PC3 score with positive values indicating more active lizards in the activity and sociability tests). Very similar patterns of co-variation among traits were found for yearlings (data not shown).

Natural selection on behavioural traits

Of 549 released newborns, 213 individuals survived until the yearling stage, which is a proportion within the natural range of variation for annual juvenile survival in natural conditions (Le Galliard *et al.*, 2010). In line with a previous analysis (Mugabo *et al.*, 2013), juvenile survival increased linearly with body size at birth with a decelerating slope (i.e. significant, negative quadratic term of body size, see Table 2). Activity (PC3) marginally influenced survival through a two-way interaction with density level (Table 2, Fig. 1). Graphical analyses in each treatment with GAMs revealed a negative directional selection against PC3 at the lowest density, whereas selection was nearly neutral in intermediate and high density populations. Indeed, after

Table 2 Best selected model describing density-dependent survival probabilities during the first year of life as a function of behavioural scores at birth obtained from the principal component analysis described in Table 1 (PC3: activity score, effects of PC1 and PC2 were not significant). Confidence intervals were obtained by the profile likelihood method. A bootstrap test of the interaction between PC3 and density yielded $P = 0.07$ (1000 simulations). The model explained significant variation in the data (marginal $R^2 = 0.07$, conditional $R^2 = 0.19$, ΔAIC = 10.55 with d.f. = 5). Average gradients were calculated according to Janzen & Stern (1998). Confidence intervals for the variance components were calculated with a profile likelihood method.

Factor	Estimate ± SE	CI	Statistics	Average gradient
Fixed effects				
Intercept	−0.993 ± 0.381	[−1.81, −0.24]	$z = -2.61$, $P = 0.009$	–
Body size at birth*	0.306 ± 0.102	[0.10, 0.51]	$z = 2.98$, $P = 0.002$	0.187
Body size at birth$^{\wedge 2*}$	−0.152 ± 0.073	[−0.30, −0.014]	$z = -2.08$, $P = 0.04$	−0.093
Density treatment	0.201 ± 0.130	[−0.060,0.481]	$z = 1.55$, $P = 0.12$	0.123
PC3*	−0.447 ± 0.249	[−0.953,0.040]	$z = -1.80$, $P = 0.07$	−0.273
PC3* × Density treatment	0.129 ± 0.069	[−0.007,0.269]	$z = 1.85$, $P = 0.06$	0.079
Random effects (variance and 95% confidence intervals)†				
Enclosure	0.472 [0.430, 1.067]			

*These covariates were standardized prior to the statistical analysis.
†Nonsignificant family effect was removed from the best model.

reordering levels of the density treatment factor in the best model from Table 2, we found a significant difference in viability selection on PC3 between density level 1 and higher densities (density contrast: $z = 2.14$, $P = 0.03$; PC3: $z = -1.93$, $P = 0.05$; density contrast × PC3 score: $z = 2.03$, $P = 0.04$; increase in marginal $R^2 = 3.7\%$). Individual scores for boldness (PC1) and sociability (PC2) had no significant effects on survival (all $P > 0.10$).

Among survivors, body growth was influenced by density and sex (Mugabo *et al.*, 2013), and also by the three behavioural scores measured at birth (Table 3). First, sociability (PC2) was positively related to body growth rate in low density populations, but the strength of this relationship vanished to zero when population density increased (Figs. 2a,c; increase in marginal $R^2 = 37\%$). Graphical analyses with GAMs revealed that this was due to a smooth rather than a stepwise change across density levels. In addition, we found evidence of a correlational selection on boldness (PC1) and activity (PC3) such that body growth rate was lower in active and bold lizards and in inactive but shy lizards (Figs. 2b,c; increase in marginal $R^2 = 3\%$).

Of the 114 recaptured females, only 37 yearlings were sexually mature and bred, and this proportion depended importantly on body size in spring which was higher in low density populations (Mugabo *et al.*, 2013). There were no significant effects of PC scores on breeding frequencies, but a tendency for an interaction between density and sociability (PC2 × density, $P = 0.09$ according to Wald's z test). Breeding frequency tended to increase with PC2 at low densities, whereas the trend was reversed at higher densities. There were too few breeding females to examine satisfactorily the relationship between fecundity and behavioural scores, but exploratory, pairwise correlations with behaviours were all not significant.

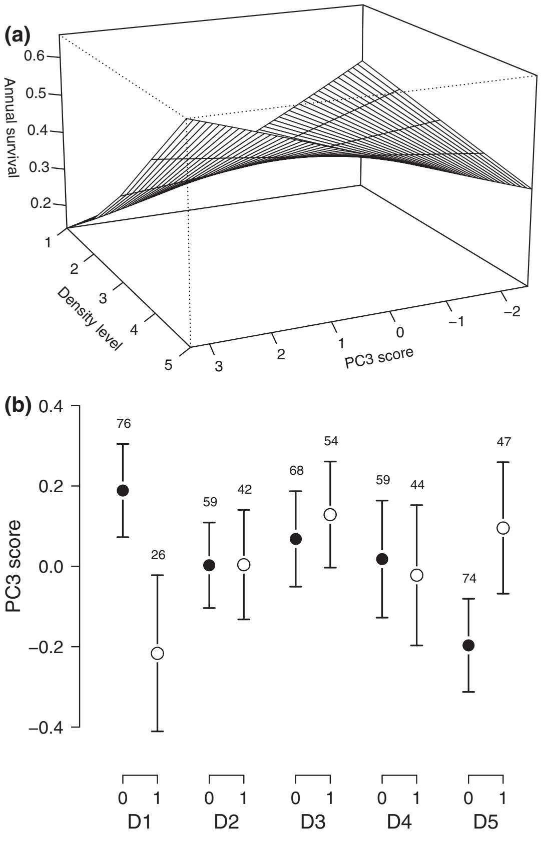

Fig. 1 Annual survival in relationship to PC3 score at birth (activity) and population density. (a) The plotted surface corresponds to predicted values of annual survival probability from the best statistical model described in Table 2 assuming a constant, mean value for covariates not included in the plot. (b) Raw data for PC3 score in dead (0) and surviving (1) lizards in each density treatment (D1 and D5). Sample sizes in each group are indicated.

Table 3 Best selected model describing density-dependent body growth rate (mm.day^{-1}) as a function of behavioural scores at birth obtained from the principal component analysis described in Table 1 (PC1: boldness score, PC2: sociability score, PC3: activity score). Growth rate was divided by the sample mean to calculate relative fitness. The fit of the model was very satisfactory (marginal $R^2 = 0.49$, conditional $R^2 = 0.66$, ΔAIC = 78.49 with d.f. = 9).

Factor	Estimate ± SE	Statistics (LR test, d.f. and *P* values)
Fixed effects		
Females	1.353 ± 0.04	–
Sex(males)	M: −0.172 ± 0.03	χ^2 = 29.8, d.f. = 1, *P* < 0.001
Density treatment	−0.164 ± 0.033	χ^2 = 33.2, d.f. = 1, *P* < 0.001
Density treatment$^{\wedge 2}$	0.017 ± 0.006	χ^2 = 7.93, d.f. = 1, *P* = 0.004
Sex × Density treatment	M: 0.031 ± 0.009	χ^2 = 12.43, d.f. = 1, *P* < 0.001
PC1*	0.003 ± 0.006	χ^2 = 0.34, d.f. = 1, *P* = 0.55
PC2*	0.037 ± 0.014	χ^2 = 6.1, d.f. = 1, *P* = 0.01
PC3*	0.008 ± 0.006	χ^2 = 1.5, d.f. = 1, *P* = 0.22
PC2* × Density treatment	−0.009 ± 0.004	χ^2 = 4.73, d.f. = 1, *P* = 0.03
PC1* × PC3*	−0.017 ± 0.006	χ^2 = 7.47, d.f. = 1, *P* = 0.006
Random effects (variance and 95% confidence intervals)		
Enclosure	0.031 [0.018, 0.050]	χ^2 = 15.67, d.f. = 1, *P* < 0.001
Family	0.037 [0.015,0.056]	χ^2 = 5.72, d.f. = 1, *P* = 0.02
Residual	0.071 [0.062, 0.082]	–

*Behavioural covariates were standardized prior to the statistical analysis.

Discussion

We used a data set about behavioural and life-history variation in juvenile common lizards to ask three main questions: Do behavioural traits show significant consistency as well as interindividual covariation? Does selection on behavioural traits depend on population density? and Is there any evidence of linear and nonlinear selection on behavioural traits irrespective of population density? To test for heterogeneous selection across life-history traits, we compared natural selection acting on survival, body growth and reproduction. We found that behaviours differed consistently among individuals on the short term but rarely on the long term. At low density, growth selection favoured more sociable lizards and viability selection favoured less active individuals, whereas selection on boldness did not depend on density. There was limited evidence of correlational selection on behavioural traits and of a production-survival trade-off linked to behavioural variation. We discussed below these three main findings in the light of recent theories about the adaptive value of personality differences.

Consistent individual differences on different time scales

In line with previous studies in a wide range of species (Bell *et al.*, 2009) and in lizards (Rodriguez-Prieto *et al.*, 2011; Le Galliard *et al.*, 2013), we found consistent individual differences (CIDs) in all behavioural traits measured twice over a short period of time. Interestingly, the boldness and activity scores at birth varied also significantly between families suggestive of high broad sense heritability (random family component and intraclass correlation coefficient (ICC): PC1: $\chi^2 = 26.4$, d.f. = 1, $P < 0.001$, ICC = 0.15; PC2: $\chi^2 = 2.83$, d.f. = 1, $P = 0.09$; PC3: $\chi^2 = 38.33$, d.f. = 1, $P < 0.001$, ICC = 0.18). When we compared measurements spaced by several months of activity and the winter hibernation period, behavioural consistency was much weaker and was only significant for activity (see also Le Galliard *et al.*, 2013) and one boldness score. Although we cannot entirely exclude that we failed to detect weak temperament traits, our sampling design had a reasonable statistical power to detect meaningful long-term consistency levels. The absence of significant long-term CIDs in sociability contrasts with the previous finding of a positive correlation between sociability at birth and at the yearling stage (Cote & Clobert, 2007). We are confident that our estimates of behavioural consistency are more robust because they were obtained from a larger sample size (202 instead of 17 in Cote & Clobert, 2007). One explanation for the poor long-term consistency of behavioural traits could be density-dependent effects on repeatability. Yet, an examination of each treatment group did not reveal density-dependent changes in the consistency of behavioural traits (not shown).

Except for locomotor activity, these results suggest substantial ontogenic changes in the ranking of behavioural scores during the first year of life, which is associated with natal dispersal and sexual maturation as well as with a substantial body growth. This stands against the common assumption that temperament traits measured across a short time period reflect lifetime variation in behaviour (Bell *et al.*, 2009). At the same time, it is also well known that temperaments may be a consequence of short-term changes in hormonal balance and physiology linked with natal dispersal or sexual maturation (e.g. Hoset *et al.*, 2011). This result raises three important issues. First, the limited ontogenic consistency of behavioural differences could decrease the predictability of natural selection

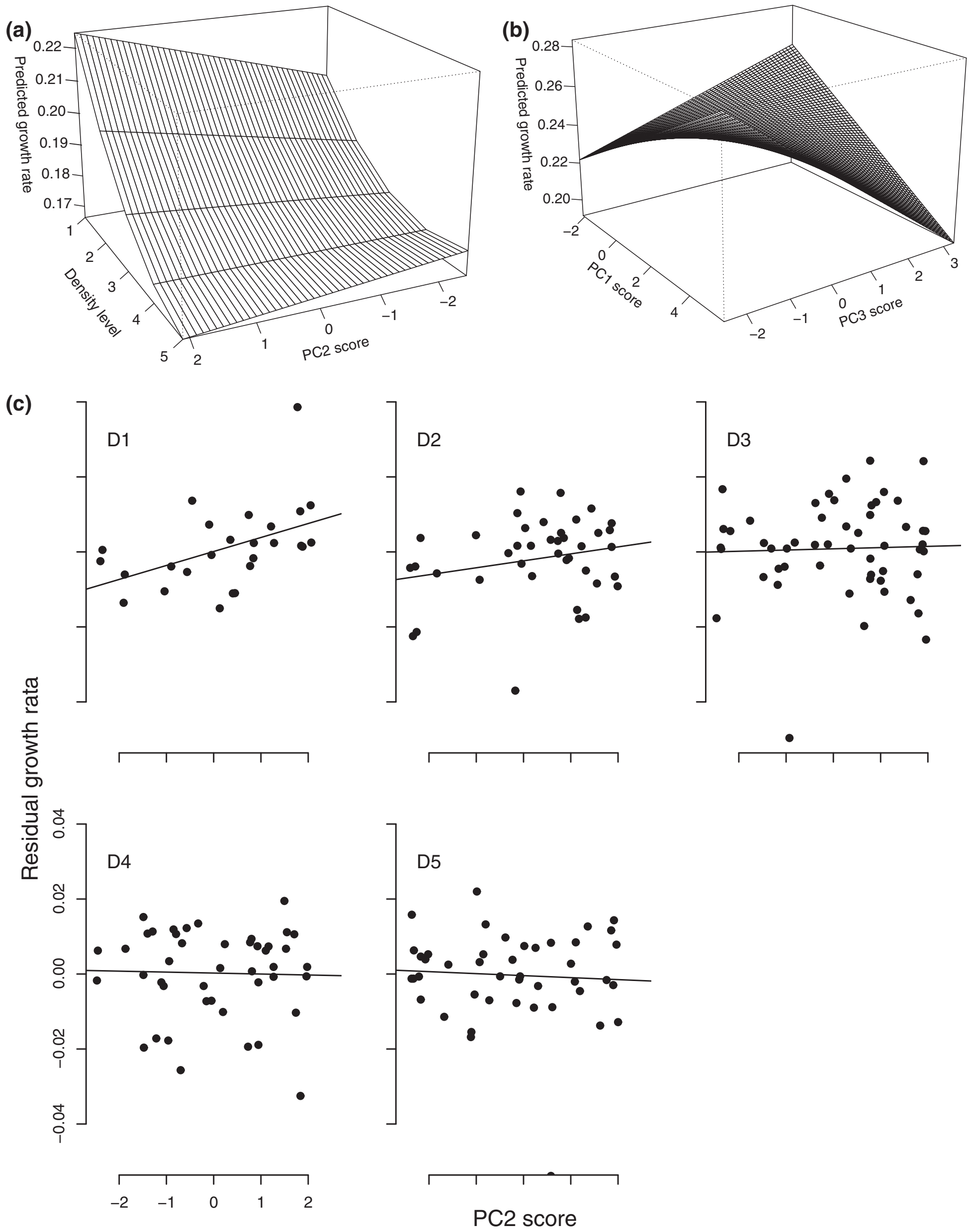

Fig. 2 Body growth selection in juvenile common lizards in relation to population density and individual traits. (a) Annual body growth rate (mm day^{-1}) in relationship to PC2 score at birth (sociability) and population density. (b) Annual body growth rate in relationship to PC1 score at birth (boldness) and PC3 score at birth (activity). The plotted surfaces correspond to predicted values from the best statistical model described in Table 3 for females assuming a constant, mean value for covariates not included in the plot. (c) Annual body growth rate in relationship to PC2 score in each density treatment. Data points correspond to residual body growth rate after controlling for the effects of all covariates except PC2 scores and lines correspond to regression fits in each density treatment.

because the ranking of individual scores in the population will change through time. Second, the weak correlation between a behaviour measured at birth and later in life may suggest that age-dependent behaviours are distinct traits and the presence of genotype-environment interactions. Future quantitative genetic studies will be needed to test these ideas. Third, such labile behaviours cause statistical difficulties when it comes to estimate true behavioural types because unbiased estimates of behavioural temperaments, behavioural syndromes and selection gradients would require several repeated measurements of the same behaviour for all individuals (Adolph & Hardin, 2007; Garamszegi *et al.*, 2012). Unfortunately and similar to previous studies of density-dependent selection (Cote *et al.*, 2008; Quinn *et al.*, 2009), it was logistically impossible to measure repeatedly all behavioural traits in all lizards included in our study.

Density-dependent selection of temperament traits

In our field experiment, density-dependent feedbacks generated a significant decline in the population growth with population growth below a density of 15–20 adults and yearlings, and population decline above that threshold (Mugabo *et al.*, 2013). This negative density-dependent feedback was mainly due a reduced body growth rate, breeding frequency of yearlings and fecundity of all age classes of females when population density increased, which was linked to food restriction instead of social stress (González-Suárez *et al.*, 2011; Mugabo *et al.*, 2013). Thus, density-dependent variation in growth and reproduction was dominated by indirect effects of food availability. In juveniles, annual survival was not importantly influenced by population density, maybe because lower food intake at high population density was compensated by a ‘parasite dilution effect’, hence a lower exposure to ectoparasites (see Mugabo *et al.*, 2015 for more details). We have no data on mortality causes, but it is likely that parasitism, starvation and predator exposure all contributed to explain differences in mortality among populations and behavioural types.

Here, density-dependent selection on sociability at birth was found for body growth rate and, to a lesser extent, maturation rates of females, whereas density-dependent selection on activity influenced juvenile survival. On the contrary, selection on boldness at birth was not heterogeneous across treatments. Thus, exploration behaviour and sociability, an often neglected dimension of behavioural variation (Cote & Clobert, 2007; Cote *et al.*, 2008; Dingemanse & Wolf, 2010), but not risk taking behaviours, were the main targets of density-dependent selection. Selection on risk taking behaviours may be more sensitive to variation in predation pressure and refuge availability, which influence risks of mortality from predators (Bell & Sih, 2007; Adriaenssens & Johnsson, 2013). This mortality risk was controlled for and was likely homogeneous among density treatments (see below).

The pace-of-life syndrome hypothesis (Réale *et al.*, 2010) would predict selection against high sociability, low boldness and low activity at low population densities. Instead, viability selection favoured less active lizards at the lowest population density, whereas selection was neutral at higher densities, similar to patterns of density-dependent selection on exploration in wild populations of male great tits (Quinn *et al.*, 2009). Assuming that high score for activity implies a more rapid exploration in the field, and therefore a bolder and more proactive behavioural type (Koolhaas *et al.*, 1999; Sih *et al.*, 2004a), we expected a higher mortality of this behavioural strategy especially at high population densities, which may diminish the daily resources needed to sustain a faster exploration strategy and may also attract predators. We found evidence of food restriction at high density (González-Suárez *et al.*, 2011) and have no comparative data on avian predation. However, juvenile mortality did not increase at high density (Mugabo *et al.*, 2013), which suggests that juvenile lizards did not suffer extra-mortality due to starvation or higher exposure to avian predators. In addition, activity-exploration was not correlated with boldness in our study, and it has recently been suggested that more active lizards could assess risk better and faster (Rodriguez-Prieto *et al.*, 2011). A potential explanation for density dependent on activity could be that less active lizards were less exposed to parasitism and ectoparasites may have been a leading mortality factor in low density populations, where exposure to ticks was much higher at the end of the experiment (Mugabo *et al.*, 2015).

At the same time, growth selection, and to a lesser extent maturation, favoured more sociable lizards at low population densities, a pattern also contrary to the predictions of the pace-of-life syndrome hypothesis. In the common lizard, attraction towards the odours of adult males is considered as a risk-prone social behaviour because adult males are socially dominant and more aggressive than lizards from other age and sex classes (Cote & Clobert, 2007). In addition, sociability influences space use and dispersal strategies in the field, such that more sociable lizards disperse more at lower population densities (Cote & Clobert, 2007). Thus, our experiment suggests that attraction towards socially dominant adult lizards may be beneficial for growth in a competition-free environment, but more costly and more constrained by food availability in dense populations. This result contradicts those of Cote *et al.* (2008) in the same species, where density-dependent viability selection favoured less sociable lizards at low density. In their original study, they focused on two density treatments equivalent to levels 3 and 5 in our experiment and measured sociability with a sequential choice test, whereas we used a simultaneous test here. Density-dependent feedbacks were weaker when we compared these two treatment levels than across the whole range of densities (Mugabo *et al.*, 2013). In addition, we repeated with our data their statistical analyses and found nonsignificant selection on absolute sociability score (Table S3).

It is difficult to understand why our results are so different from those of Cote *et al.* (2008). One explanation is that the sociability score in Cote *et al.* (2008) was positively correlated with the time spent basking out of the shelters by lizards during their tests and was therefore not independent of boldness or activity behaviours in contrast with our study. Thus, we were more likely to quantify direct selection on sociability, whereas estimates of selection gradients in Cote *et al.* (2008) may include both direct and indirect selection mediated by boldness and activity (Lande & Arnold, 1983). Another possibility is that density-dependent selection on sociability can fluctuate through time due to changes in environmental conditions. Our enclosure study allowed for exposure to avian predators but not for dispersal, whereas predation was absent in the previous study. Predator exposure is a major agent of selection on boldness and exploration (e.g. Bell & Sih, 2007; Biro & Post, 2008) and may also influence density-dependent selection on sociability. These shifting patterns of selection highlight the need of repeated estimates of selection on behavioural traits across multiple years.

Correlational selection and life-history syndromes

Independently from density-dependent selection, it is predicted that stable state-dependent differences in behaviours and behavioural syndromes are more likely when behaviours are involved in the same life-history trade-off (Biro & Stamps, 2008; Boon *et al.*, 2008; Smith & Blumstein, 2008). For example, high activity and boldness should increase both body growth and the risk of mortality from predation, thus resulting in a similar lifetime reproductive success than low activity and shyness (Stamps, 2007). This idea is supported in some studies of the production-mortality trade-off linked with differences in activity and boldness in fishes (Biro & Post, 2008 and references therein) and in some mammals (Boon *et al.*, 2008). Quantitative genetic models of multivariate selection on life-history traits further indicate that correlational selection, that is nonlinear selection on pairs of traits, can explain the maintenance of genetic and phenotypic correlations among traits and thus the evolution of functional co-adaptation (Lande & Arnold, 1983; Sinervo & Svensson, 2002; Réale *et al.*, 2010). For example, the pace-of-life syndrome hypothesis states that correlational selection plays an important role in the emergence of behavioural syndromes associated with a slow–fast demographic continuum (Réale *et al.*, 2010). Yet, it is generally the case that evolutionary studies do not test for nonlinear selection (Kingsolver *et al.*, 2012). Our analysis of directional and correlational selection for three distinct fitness components offered us the opportunity to test these additional hypotheses.

In newborns, pairwise correlations among distinct behavioural traits were nonsignificant and the PCA found three independent axes of variation for activity, boldness (including boldness in the risk taking and sociability tests) and sociability. In addition, we found no evidence of correlational selection for annual survival and female maturation rates, but some for body growth. Specifically, body growth rate was maximized for the subset of juveniles characterized by a negative correlation between activity and boldness at birth, irrespective of density. Thus, there was some evidence for an 'adaptive' behavioural syndrome linking shyness and activity, but this 'adaptation' runs counter to the standard prediction that boldness and activity should be positively associated with growth. One explanation of this counter-intuitive result is that the growth advantages of faster activity and higher boldness were counter-balanced by the maintenance and activity metabolic costs of these strategies. Finally, we note that none of the behavioural traits were involved in a life-history trade-off between growth and survival, even though such a life-history trade-off occurs in the common lizard (Mugabo *et al.*, 2010). However, we cannot rule out that trade-offs later in life are involved in the maintenance of behavioural variation in natural populations.

Conclusion

Our study demonstrates the existence of temperament traits of activity, boldness and sociability, but the consistency of behavioural differences through development over the first year of life was weak. We found density-dependent selection on sociability at birth for body growth rate and female maturation and on activity at birth for juvenile survival. This suggests that heterogeneous selection plays a role in the maintenance of individual differences in exploration activity and sociability because the fitness outcomes of a behavioural strategy should depend on spatio-temporal variation in density (Cote *et al.*, 2008; Quinn *et al.*, 2009). Across all treatments, correlational selection on boldness and activity was detected for body growth rate, but none of the behaviours were involved in a life-history trade-off between growth and survival. Future models for adaptive personality differences should include density-dependent selection to gain a better understanding of the ecological conditions most likely to favour the evolution of animal personality variation.

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Supporting information

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

Table S1 Univariate statistics for the seven behavioural traits

Table S2 Correlation matrix of the seven behavioural traits in newborns (above the diagonal, $n = 598$)

Table S3 Effects of population density and absolute social score at birth on fitness outcomes (survival probability, size growth calculated like size at the end of the experiment minus size at birth, and maturation probability)

Appendix S1 Analysis of statistical power to detect personalities

Data deposited at Dryad: doi: 10.5061/dryad.4vn13

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