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Do personalities co-vary with metabolic expenditure and glucocorticoid stress response in adult lizards?

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Running headline: Covariation between physiology and personality in lizards

ABSTRACT

Stable differences in physiology among individuals may facilitate the evolution of consistent individual differences in behavior. In particular, according to the pace-of-life syndrome (POLS) hypothesis, individual variation in metabolic expenditure and stress physiology should be linked with exploration, aggression, or risk taking behaviors. Previous studies have uncovered stable individual differences in metabolic expenditure and circulating glucorticoids in common lizards (*Zootoca vivipara*). We tested for correlations between standard metabolic rates (SMR), glucorticoid stress response and behavioral traits (activity, aggressiveness, risk taking and sociability) in males. In ectotherms, the thermal dependence of SMR should be included in the POLS hypothesis; we therefore measured SMR at three temperatures from rest to preferred body temperature. Activity, aggressiveness and risk taking, but not sociability, exhibited significant, short term repeatability, and little correlation was found between behavioral traits. The SMR of lizards with a low metabolism at rest increased faster with body temperature. The SMR at rest was negatively correlated with behavioral variation in sociability and activity but not with risk taking behavior. In addition, the plasma corticosterone level after an acute, handling stress increased slightly but not significantly with aggressiveness. We discuss alternative interpretations for these relationships and conclude that the link between inter-individual variation in physiology and behavior is trait-dependent in the common lizard.

Keywords: locomotion, metabolism, corticosterone, temperament, personality, reptiles.

SIGNIFICANCE STATEMENT

Selection better promotes the evolution of consistent differences in behavior, or personalities, when they are coupled with differences in physiology. In adult common lizards, inter-individual differences in metabolic expenditure and glucocorticoid stress response are consistent and could play a crucial role in the maintenance of personalities. This study supported this hypothesis. We found that more sociable and active personality types had a lower metabolic expenditure, while more aggressive personality types tended to have a higher physiological stress response. At the same time, physiology was not correlated with individual differences in risk taking behavior and drove little part of behavioral variation. The coupling between personalities and physiology appears to be trait-dependent, suggesting that behaviors may be relatively free to evolve independently from physiology.

INTRODUCTION

The concept of "animal personality" refers to consistent inter-individual differences (CIDs) in behavior across time and/or contexts (Réale et al. 2007). Empirical evidence of CIDs in behavior are widespread in the animal kingdom (reviewed in Bell et al. 2009), and personality traits may play a crucial role in some ecological and evolutionary processes (Sih et al. 2004a; Réale et al. 2007; Dingemanse and Wolf 2010). Animal personalities are generally organized along a few major behavioral dimensions, including activity and exploration, risk taking, aggressiveness and sociability (Réale et al. 2007). Two or more of these dimensions may be associated with suites of correlated traits called behavioral syndromes (reviewed in Sih et al. 2004b), particularly the syndrome linking activity, exploration, risk taking and aggressiveness (Sih and Bell 2008). This syndrome, found in several species, is referred to as the shy-bold axis (Wilson et al. 1994) or the reactive-proactive continuum (Koolhaas et al. 1999).

A potential explanation for the occurrence of repeatable, consistent and correlated differences in behavior is that suites of behavioral traits may co-vary with stable differences in physiology (Biro and Stamps 2010; Coppens et al. 2010; Dingemanse and Wolf 2010). In particular, CIDs in behavior along the reactive-proactive continuum should be linked to the physiological stress response (i.e., stress-coping style hypothesis, Koolhaas et al. 1999, 2010; Øverli et al. 2007; Coppens et al. 2010). The reactive and proactive behavioral types are considered adaptations for life in unstable and stable environments, respectively; thus, shy and reactive individuals are characterized by higher levels of physiological stress responses than bold and proactive individuals (Cockrem 2007). In vertebrates, the physiological stress response involves activation of the hypothalamo-pituitary-adrenal (HPA) axis, where exposure to stress stimulated secretion of glucocorticoids (e.g., Cockrem 2007). In turn, glucocorticoid secretion elicits a cascade of physiological and behavioral processes that are essential to cope with stressful events (Wingfield and Ramenofsky 1999; Landys et al. 2006). The stress-coping style hypothesis makes the specific predictions that proactive and bold individuals should have lower baseline concentrations of glucocorticoids and a less reactive HPA axis. These predictions are well-supported by research with domestic and laboratory-bred animals (Koolhaas et al. 1999; Groothuis and Carere 2005), especially lines selected for coping styles in mice (Veenema et al. 2003) and great tits (Carere et al. 2003; Baugh et al. 2012), but less by more recent field studies (Lendvai et al. 2011; Baugh et al. 2013). They have not yet been tested in squamate reptiles (lizards and snakes).

In addition, a link could exist between energy expenditure and behavior (Careau et al. 2008; Biro and Stamps 2010; Careau and Garland 2012) because energy acquisition and allocation constraints should influence behavioral traits involved in net energy gain (e.g., foraging) and/or those that are energetically costly (e.g., aggressiveness, see Mathot and Dingemanse 2015). In particular, the basal metabolic rate (BMR, a measure of the minimal energy expenditure in post-absorptive individuals at rest) is both repeatable and consistent through time (Nespolo and Franco 2007) and should be correlated with activity, risk taking, exploration and aggressiveness (Wolf and McNamara 2012). Two opposite scenarios have been proposed to explain the partition between BMR and the total energy expenditure (Careau et al. 2008; Mathot and Dingemanse 2015). The first states that higher total energy expenditure might imply investment in physiological processes and anatomical features that support higher productivity. In this case, we expect a higher BMR to correlate with bolder and/or more proactive behaviors (i.e., production model of bioenergetics, Careau et al. 2008; Careau and Garland 2012). Examples include numerous studies of aggression, risk taking and exploration in fishes, mammals and a few bird species (e.g., Cutts et al. 2001; Mathot and Dingemanse 2015). In contrast, a negative relationship between BMR and proactivity is expected when the amount of energy spent in maintenance is unavailable to sustain net energy gain and energy is limited (i.e., allocation model of bioenergetics, Careau et al. 2008; Careau and Garland 2012). This prediction has received less support (Mathot and Dingemanse 2015), despite evidence that BMR may represent a cost to growth and survival (e.g., Steyermark 2002; Artacho and Nespolo 2009).

Energy metabolism, glucorticoid stress response and personality should thus be integrated into a general syndrome called the Pace Of Life Syndrome, or POLS (Ricklefs and Wikelski 2002; Careau et al. 2009; Réale et al. 2010; Le Galliard et al. 2013). However, intra-individual variation induced by thermal conditions (neglected thus far) might complicate the relationship between metabolic expenditure and behavior in ectothermic species (Artacho et al. 2013). For example, in previous studies, metabolic rates were obtained by repeated measurements at a single temperature. In ectotherms, the standard metabolic rate (SMR, a measure of BMR at a given temperature) significantly increases with body temperature, and the thermal dependence of SMR might differ markedly among individuals (Nespolo et al. 2003; Careau et al. 2014). Hence, energetic data in ectotherms should preferably be calculated from SMR obtained along a thermal gradient. For example, a recent study of the slimy salamander (*Plethodon albagula*) by Careau *et al.* (2014) found significant inter-individual variation in the thermal dependence of metabolism, in that the metabolic ranking of individuals changed with body temperature. Thus, additional data on ectotherms is needed in order to rigorously assess the relationship between personality traits and metabolism after taking into account intra-individual differences in metabolic thermal sensitivity.

To explore the links between personality traits, standard metabolic rates and the glucocorticoid stress response, we conducted two independent observational studies with male common lizards, *Zootoca vivipara*. In a first study, we measured covariation between personality traits and resting metabolic rates measured at three relevant body temperatures. In a second study, we tested for covariation between personality traits and individual plasmatic levels of corticosterone, quantified both in the field and in the laboratory after exposure to an acute stress. Rather than examining the correlation between physiology and a single personality trait (reviewed in Mathot and Dingemanse 2015), we measured several behavioral dimensions simultaneously, including activity, risk taking, sociability and aggressiveness. CIDs in behavior have been documented previously for activity, exploration, sociability and risk taking in juvenile common lizards (Cote and Clobert 2007; Le Galliard et al. 2013, 2015), and there is independent variation in activity, risk taking and sociability (Le Galliard et al. 2015). In adults, measurements of SMR are repeatable and consistent over short time periods (e.g., Artacho et al. 2013). The link between SMR and behavioral activity has been explored in juvenile lizards but no significant correlation was found (Le Galliard et al. 2013). However, by taking into account intra-individual variation in metabolism and several behavioral traits, we expect to gain greater insight into the relationship between behavioral syndromes and metabolism. In addition, plasma corticosterone levels of common lizards are repeatable over several days in the laboratory (SM & J-FLG unpubl. data) and increased corticosterone secretion in response to a stressor modifies activity and foraging behaviors (de Fraipont et al. 2000; Cote et al. 2006). Whether this intra-individual variation parallels inter-individual variation along a general proactive-reactive continuum remains to be tested.

MATERIALS AND METHODS

Study species

The common lizard (*Zootoca vivipara*) is a small viviparous lacertid (50-70mm adult snout-vent length) widely distributed in Eurasia. In our study populations at the Centre de Recherche en Ecologie Expérimentale et Prédictive, France (48°17'N, 2°41'E), hibernation takes place from October to February-March for males, while females emerge a few weeks later in March-April. Mating season begins upon the emergence of females and lasts 2-4 weeks. The size of our semi-natural enclosures (each 100 m^2) is similar to the area occupied by overlapping ranges of several lizards. Dispersal was prevented, lizards were protected from terrestrial and avian predators, and no food or water supplements were provided. Only male individuals were considered in this study so as to avoid interferences of gravidity on metabolic measurements and general sex differences in physiology and behavior. To minimize observer bias, blinded methods were used: the persons in charge of recording and analyzing behavioral data were not aware of the physiological scores of lizards, and different persons collected and processed behavioral and physiological data.

Study 1: covariation between behavior and metabolism

Thirty-nine adult males (n = 7 two-years old and n = 32 more than two-years old) were captured in 2011 between May 16 and 19 from ten enclosures and measured for snout-vent length (SVL, range=53-63 cm, mean = 57.7) and body mass. Right after their capture, all lizards were placed in individual terraria (25 x 16 x 15 cm) and kept under standardized day-night (16h night: 8h day) and temperature conditions (16°C night: 23°C day) with food and water *ad libitum* (see Le Galliard et al. 2003 for detailed protocols). Individuals were measured once for three behavioral traits, activity (N=29), boldness (N=30) and sociability(N=30) within eight days of capture. Then, from July 1 to July 10, the SMR was measured for each lizard at 15°C, 25°C and 35°C (see details below). These temperatures were chosen because they cover the range of variation of body temperatures experienced during different activities, including temperature at rest, preferred body temperature and an intermediate value (Le Galliard et al. 2003). We did not take repeated measurements of activity, boldness and sociability. However, short-term repeatability estimates were calculated at the same time from another sample of adult lizards maintained in the same conditions and tested twice for the same behaviors the same year. In the data set involving measurement of repeatability, behaviors were also recorded within eight days of recapture of individuals, and repeated measures were taken the same day a few hours apart.

Study 2: covariation between behavior and stress response

For this study, fifty adult males (n = 13 two-year-olds and n = 37 older than two years) were captured on March 31, 2014 from 10 different enclosures and measured for SVL (range=48-62 cm, mean =57.5 cm) and body mass. Blood samples were taken immediately following capture. In order to avoid biases due to capture and handling stress, we performed short visits to each enclosure (in general, less than 5 min) and collected all blood samples within less than 3 min of capture. To account for potential stress due to our visits to the enclosures, we measured the time between each capture and the first visit for each lizard (hereafter called time spent in the enclosure). Lizards were then transferred into individual terraria and held under the same conditions as lizards experienced in study 1. Activity, boldness and aggressiveness were measured during a first series of behavioral tests starting on day 7. On day 7, half of the lizards were tested for activity and aggressiveness, while the other half were measured for boldness and aggressiveness. On day 8, each group was tested for the behavior not measured during day 7, and then fed with a standard quantity of live crickets to ensure similar digestive state before the next measurements. The second session started on day 9 and followed the same procedure as the first one to obtain repeated measures. At day 11, another blood sample was collected in order to assess the corticosterone stress response under laboratory conditions. To ensure that peak corticosterone levels were reached, lizards were exposed to handling and simulated predation stress by scaring them with a paint brush for 10 minutes before blood sampling (Dauphin-Villemant and Xavier 1987). Plasma corticosterone levels were assessed using an immuno-enzymatic reaction following protocols previously used in (Meylan et al. 2003).

Collection of behavioral data

We used a neutral arena test to investigate exploratory behavior and locomotor activity (Le Galliard et al. 2013). All tests were done during the daily activity period between 10 am and 5 pm. Each lizard was placed in a plastic box (44.5 cm x 24 cm x 26 cm) maintained in a room at a standard temperature of 23-25°C with one heat source (40 W bulb) at the centre and two white light sources (Iguana Light 10.0 UV-B, ZooMed, 40 W). The soil was covered with clean sand before each trial to avoid interference with odors from conspecifics. Each lizard was placed in the plastic box for a 10 min acclimation period, and then filmed from above for 30 min with a webcam (Hercules Deluxe). The film was downloaded using Virtual Dub 1.7.8 and image sequence from each video was obtained (one frame per second). From these videos, we recorded lizard position (x-y coordinates) in ImageJ v1.40 (http://rsbweb.nih.gov/ij/) using a particle analysis procedure (Mallard et al. 2013). We calculated the percentage of time spent walking and the travel distance during each trial. For study 2, we also calculated the total time spent basking and the total time spent scratching the wall with real-time recordings of behaviors.

We measured risk-taking (or boldness) behavior based on the behavior of a lizard after a simulated attack by a human (e.g., López et al. 2005; Le Galliard et al. 2015). 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 acclimation 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 behavior 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 (body and head outside the refuge), and the time spent before basking under the heat source on the opposite side of the box. Recordings stopped after 60 min. This procedure allowed for "censoring" of boldness scores for one lizard in each study (i.e., less than 3% of recordings). We replaced boldness scores by the maximum value (3,600 secs) for these animals.

We quantified sociability by scoring the preference of lizards for odors of adult males during a simultaneous choice test of 20 min (Le Galliard et al. 2015). Two identical plastic shelters were placed on each side of the terrarium. We put a piece of absorbent paper impregnated with the odor of adult males under one shelter and a piece of odorless paper under the other shelter. Lizards were filmed from above and two indices of sociability were measured: an absolute index calculated as the difference between time spent in the shelter with the odor and time under the shelter without the odor scaled to the total duration of the test, and a relative index, where time difference was divided by the total time spent hidden (Cote and Clobert 2007; Cote et al. 2008; Le Galliard et al. 2015). In each study, odors were obtained from four groups of 3 randomly chosen adult males after a minimum period of six days. Odorless papers were collected from a cage without lizards located in the same room.

We measured aggressiveness in response to capture and handling when we removed the lizards from the exploration and risk taking tests. One experimenter grabbed the lizard in his hand and held it in front of himself until it was relatively immobile. The experimenter then touched the tip of the nose with the side of his finger four times in order to elicit aggressive reactions and counted the total number of biting attempts. The score thus ranged from 0 (no bite) to 4, and scores are reported as “aggressiveness after exploration” and “aggressiveness after risk taking” depending upon the behavioral test preceding the measurement.

Measurement of metabolic rate

The standard metabolic rate (SMR) is defined as the minimum rate of energy expenditure under post-absorptive conditions in a resting phase at dark and at a given temperature within the animal's range of activity (Andrews and Pough 1985). Metabolic rates were estimated with a multiple-channel flow-through respirometry system (Qubit Systems, Canada) coupled with a differential O_2 analyzer (DOX; S104 Differential Oxygen Analyzer) and a CO_2 analyzer (S157) connected to respirometry software (QS Research). Metabolic records were processed by a macro program recorded in ExpeData software (Sable Systems) to transform the measurements from parts per million to milliliters per hour, taking into account the flow rate (140 mL/min). SMR was measured once at each of three body temperatures (15°C: minimum temperature, 25°C: intermediate body temperature during activity and 35°C: inside the range of preferred body temperature) after a fasting period of 72 hours to ensure post-absorption conditions. Individuals were placed in a room at a constant temperature of 15°C the night before recording, and were kept in the dark until being weighted and placed in the measurement chamber for an hour of acclimation at the test temperature. Excurrent O_2 and CO_2 concentrations were then measured continuously for 45 minutes at the same temperature. The average respiratory quotient of the population, calculated from the production of CO_2 and consumption of O_2 obtained from all individuals, was then used to convert the values of CO_2 production (mL/h), averaged over the recording, into energy expenditure (J/h).

Statistical analyses

All statistical analyses were carried out in R 3.0.3 (https://www.r-project.org/). Repeated measurements of the three focal behaviors, activity, risk taking and aggressiveness, were analyzed with linear mixed-effects models (LMM) using the *lme* function (Pinheiro and Bates 2000). The LMM fitted to each behavioral variable included a fixed time effect to control for changes in behavior across repeated measures and a random individual effect. From this, we assessed the significance of random effects with likelihood ratio tests (LRT) and calculated a repeatability coefficient as the intra-class correlation coefficient (Wolak et al. 2012), which equals to the ratio of between-individual variance to total (between-individual and residual) variance. Since the between-individual variance can take only positive values, the χ^2 statistics of the LRT is distributed as an equally weighted mixture of χ^2 distributions with one and zero degrees of freedom (Careau et al. 2014 and references therein). Thus, we halved the P-values obtained from the standard χ^2 distribution with one degree of freedom (equivalent to $\chi^2_{0:1}$ in results below). In addition, behavioral syndromes were explored using principal component analyses (PCAs) of the mean, individual values of each behavioral trait. PCAs were implemented with the function *dudi.pca* in the R package *ade4* using a correlation matrix implicitly rescaling all variables (Chessel et al. 2004). The number of principal components retained for the analysis was determined on the basis of the broken-stick method (Legendre and Legendre 1998). We identified statistically significant contributions to the different PCs by calculating the inertia attributed to each variable. The contribution of the variable was considered significant when its inertia was greater than the mean inertia.

We analyzed the thermal sensitivity of SMR using individual linear regressions computed to calculate an intercept score (SMR value predicted at 15°C) and an intercept slope score (SMR thermal sensitivity) for each individual. We also calculated the thermal repeatability of SMR (Nespolo et al. 2003; Careau et al. 2014) by running a linear mixed-effects model. This model included a fixed effect of body temperature and random variation among individuals for the mean SMR across the thermal gradient. To obtain the thermal repeatability (R_T), we used the variance components (residual and between-individual variation) and calculated the ratio of between-individual to total variation. We tested the significance of the random inter-individual based on a LRT (see above). The SMR data were log-transformed prior to the analyses, which resulted in a better statistical distribution of the residuals and improved linearity of effects.

We used the PC scores obtained from the PCAs described above to explore the covariation between behavioral traits and physiology (SMR and plasma corticosterone levels). For SMR, we fitted a linear model with the SMR as a dependent variable and the individual scores for each PC, age class, and body mass as fixed-effect independent variables. For plasma corticosterone, field levels were analyzed with a linear model including fixed effects of age, SVL, and individual scores for each PC as well as time spent in the enclosure before capture. Laboratory stress-induced corticosterone levels were analyzed with the same model including the basal plasma corticosterone levels as a covariate to control for differences in basal secretion of corticosterone prior to handling stress. In all cases, model assumptions (normality and homogeneity of variance of the residuals) were fulfilled and the best model was chosen by a stepwise selection procedure based on AIC (Burnham and Anderson 1998). Several individuals came from the same enclosures in both studies but addition of a random effect of enclosure identity did not change the conclusions of our statistical analyses since there was very little variation among enclosures (all $p > 0.08$, results not shown). We report the mean and standard error of mean of estimates unless otherwise stated.

RESULTS

Consistent individual differences in behavior

We found consistent individual differences for most behavioral variables, except for time with head hidden during study 2 and for sociability scores and time spent walking in study 1 (Table 1). The PCAs suggested different patterns of behavioral covariation in the two studies (Table 2). In study 1, we retained three major axis explaining 85% of the total variance. The first principal component (PC1) loaded significantly with two variables measuring risk taking, while variables related to sociability (and to some extent activity) showed a strong positive correlation with PC2. PC3 was positively correlated with variables measuring activity and one boldness score. Thus, PC1 measured variation in risk taking and PC2 score indicated variation in sociability, while PC3 scored activity and exploration. In study 2, we retained three major axes explaining 81% of the variance. PC1 was positively correlated to variables related to activity and negatively correlated to risk taking. PC2 was negatively correlated to mobility and risk taking but positively correlated to basking time. PC3 loaded only significantly with the variables related to aggressiveness.

The removal of one outlier for boldness scores in study 1 influenced the correlation pattern represented by PC2 and PC3 (Table S1 provided as supplementary information). Without the outlier, the second principal component (PC2) was positively related to activity and sociability, while PC3 had a strong negative correlation with variables measuring activity but was positively correlated with sociability. Thus, PC2 score indicated variation in both activity and sociability (and not only sociability like in Table 2), while PC3 made the contrast between more sociable but less active lizards from less sociable and more active lizards.

Covariation between metabolism and personality

The SMR increased significantly and almost linearly with body temperature on the log scale (mixed-effects model, body temperature effect: slope= 0.10 ± 0.0048, $F_{1,79} = 437.1$, $p < 0.001$; Fig. 1A). According to individual regressions, slopes (log SMR, mean = 0.10 ± 0.009 SD) and intercepts at 15°C (log SMR, mean = 1.65 ± 0.47 SD) were strongly negatively correlated (Pearson moment-correlation : $r = -0.85$, $p < 0.0001$). Given this pattern of crossing thermal sensitivity curves (Fig. 1A), the thermal repeatability of SMR was small ($R_T = 0.052$) and not significant ($\chi^2_{0:1}$=0.30, $p = 0.27$). The best model (adjusted $R^2 = 0.126$) describing metabolic variation (intercept at 15°C) included the PC2 score measuring variation in sociability (slope =-0.103 ± 0.05, $F_{1,36} = 4.21$, $p = 0.047$, Fig. 1B) and a marginal negative effect of PC1 score (slope = -0.08 ± 0.04, $F_{1,36} = 3.30$, $p = 0.077$). This effect of PC1 did not hold when we removed one outlier for boldness score (Table S2).

Covariation between glucorticoid stress response and personality

Mean plasma corticosterone levels were higher in the field than after exposure to a handling stress in the laboratory (mean level in the field: 56.3 ng/mL ± 2.33, range: 21.4-92.8; mean stress-induced level: 35.0 ± 2.66, range: 6.98-117.6, paired t-test: $t_{49} = 7.35$, $p < 0.001$; Fig. 2A). We found no significant effects of behavioral score, SVL, time spent in the enclosure and age class on plasma corticosterone concentration in the field (all $p > 0.21$). The best model (adjusted $R^2 = 0.16$) selected to describe variation in stress-induced corticosterone levels in the laboratory included two variables, a positive effect of field corticosterone (slope = 0.41 ± 0.15 SE, $F_{1,47} = 6.32$, p = 0.015) and a marginal, negative effect of PC3 score, which is positively correlated to aggressiveness (slope = 3.60 ± 1.92 SE, $F_{1,47}= 3.49$, $p = 0.068$, Fig. 2B). The removal of one "outlier" for corticosterone titer (Fig. 2A) weakened the effect of PC3 (slope = 2.69 ± 1.60 SE, $F_{1,46} = 2.85$, $p = 0.099$, Fig. 2B), as well as the correlation between field corticosterone and the stress response (slope = 0.21 ± 0.13 SE, $F_{1,46} = 1.94$, $p = 0.17$, Fig. 2A).

DISCUSSION

In male common lizards, behavioral traits describing variation in activity, aggressiveness and risk-taking exhibited significant, short-term repeatability, while behavioral traits describing sociability did not. These results agree with previous findings of consistent individual differences in behavior in juveniles (Cote and Clobert 2007; Le Galliard et al. 2013, 2015). However, they are contradictory to those of earlier studies, where sociability was consistent on the short-term in juveniles (Le Galliard et al. 2015). Differences in short-term consistency of sociability between adults and juveniles are not just a consequence of a small and relatively homogeneous data set of adult males in this study, because it was confirmed in a longitudinal study including both sexes and more age classes (HM & J-FLG, unpubl. data). The higher consistency of sociability in juveniles than in older individuals may be due to a more pronounced sensitivity to odors of adult males in juveniles than in adults, and/or changes in the ecological relevance of the test with age (Bell et al. 2009). For example, sociability is involved in dispersal behavior and consistently associated with the natal dispersal type in juveniles but may be of limited relevance in adults, since this age class disperses less (Le Galliard et al. 2005). The use of a shelter choice experiment in adults may also be problematic since adult males tend to prioritize direct social interactions and are bolder and less attracted to the shelter than juveniles (J-FLG pers. obs.).

The principal component analyses highlighted relatively weak and non-significant associations between most personality traits. Yet, there was evidence of a positive association between activity and risk taking in study 2 for PC1. In study 1, the association between activity and risk taking for PC1 was in the same direction but was not significant based on the inertia criterion. Activity was also associated positively with sociability in study 1. Behavioral syndromes have been little investigated so far in squamate reptiles relative to other taxa. Similar to our results, a behavioral syndrome linking independent measures of activity, boldness, sociability and/or aggression was not found in juvenile common lizards (Le Galliard et al. 2015) and in adult White's skinks (McEvoy et al. 2015). Rodriguez-Prieto et al. (2011) also suggested that exploration, sociability and boldness represent three independent facets of the personality of adult Iberian wall lizards (but see Stapley and Keogh 2004). Considering these results with our own could indicate that behavioral syndromes are not organized in squamate reptiles as they are in other vertebrate taxa. However, it could be that we lacked statistical power to detect small but meaningful correlations among traits. Larger sample sizes (here, $N < 50$) and more repeated measurements (here, 1 to 2) may be needed to score personality when traits are poorly repeatable (here, $0.14 < r < 0.70$) and to obtain unbiased estimates of correlations (reviewed in Garamszegi et al. 2012).

Regarding the individual variation in the standard metabolic rate (SMR), we found variation among individuals at the lowest body temperature (intercept), in addition to showing that lizards with a low intercept had a greater increase of their SMR with body temperature. Although these results must be considered with some caution, as we only tested animals once at each temperature, they suggest crossing thermal sensitivity curves for SMR (Careau et al. 2014). This could indicate that lizards that minimize basal energy expenditure at rest (low body temperatures) have higher basal expenditures at activity (high body temperatures). The robustness and generality of this pattern remains to be tested in larger samples of common lizards and in other species, and with several repeated measures at each temperature. In addition, we found that individuals with high values of sociability, and to some extent activity, were characterized by a lower SMR at 15°C.

At first glance, the negative relationship obtained between the SMR at 15°C and the sociability-activity axis seems to support the allocation model of energy management, where SMR constrains the expression of energetically costly behaviors (Careau et al. 2008; Careau and Garland 2012; Mathot and Dingemanse 2015). However, a more detailed examination of the results cautions against such a straightforward explanation. First, PC1 and PC3 scores directly related to risk taking and activity were not correlated with SMR even though these may reflect variation in energetically costly behaviors (Mathot and Dingemanse 2015). Second, even after accounting for the effect of PC2 score, much variation in SMR remained. Third, despite good evidence that SMR represents a significant part of total energy expenditure in lizards (e.g., Niewiarowski and Waldschmidt 1992), no empirical study has yet examined among-individual partitioning of energy into maintenance, activity and other energetic expenses. Given that an increased SMR does not seem to impair mean growth, survival or reproduction in this species (Le Galliard et al. 2013; Artacho et al. 2015), we cannot tell with certainty that differences in SMR represent a significant energetic constraint at the individual level. Fourth, our study indicates that conclusions from correlation patterns between behavior and physiology obtained with measures of SMR at one body temperature may be misleading. Since low SMR at 15°C was strongly, negatively associated with the thermal sensitivity of RMR, more sociable and active lizards did not necessarily have the lowest SMR at the highest body temperatures. Thus, when thermal repeatability of RMR is low, correlative studies linking animal personality and energetics may lead to results supporting the allocation model, the performance model or none of them, depending on temperature used during measurements. While estimates of SMR at one body temperature are generally repeatable over time (Nespolo and Franco 2007), the thermal repeatability of SMR can be low when individuals vary in the thermal sensitivity of their metabolism (Careau et al. 2014). This suggests that relevant aspects of thermal biology should be considered when examining behavioral and physiological syndromes in ectotherms. In particular, we advocate for future investigations of covariation patterns between behaviors and physiology by repeatedly measuring all traits at several body temperatures.

The plasmatic levels of corticosterone varied significantly among individuals, as was found in previous studies (Meylan et al. 2003; Fitze et al. 2009). Field plasmatic levels of corticosterone were positively correlated with, but also higher than, the stress-induced levels measured in the laboratory. This surprising difference could be due to elevated levels of corticosterone needed to sustain the locomotor activity and mating behavior of adult males in the field. In addition, the stress induced by confinement in the laboratory does not last more than a day in the common lizard (Dauphin-Villemant and Xavier 1987) and lizards might have returned to low basal levels before we started the handling stress measurements. Unfortunately, we did not measure basal levels in the laboratory prior to handling stress. The plasmatic level of corticosterone after exposure to a handling stress in the laboratory, corrected for basal variation in corticosterone levels from the field, was weakly and almost significantly positively correlated with aggressiveness. This link was tenuous and did not hold when we removed one extreme data point.

These results contradict the hypothesis that the glucocorticoid stress response constitutes a causal proximate mechanism behind the activity-aggressiveness-risk taking behavioral syndrome, since we found no correlation with activity and boldness. In addition, the weak correlation found for aggressiveness, if real, contrasts with findings in some bird and mammal species, where more aggressive individuals have a lower HPA axis activity and reactivity in response to a stressor (i.e., proactive coping style, Koolhaas et al. 1999; Groothuis and Carere 2005; Cockrem 2007). For example, house mice selected for low aggression have higher basal corticosterone levels during daytime and prolonged corticosterone secretion in response to a strong stressor (Veenema et al. 2003). Similarly, great tits (*Parus major)* selected for slow exploration speed are less aggressive and have more elevated corticosterone in response to a social stress than birds selected for fast exploration (Carere et al. 2003; Groothuis and Carere 2005; Baugh et al. 2012). The short-term increase of corticosterone concentration in response to a stressor also differs among individual birds, with stronger increase in slow than in fast explorers in *Parus major* and *Passer domesticus* (Lendvai et al. 2011; Baugh et al. 2013).

There is also some evidence of a positive correlation between measures of risk taking and/or exploration and reactivity of the HPA axis in zebra finches (Martins et al. 2007) and in domestic leghorns (reviewed in Groothuis and Carere 2005). Similar to the trend we found, this suggests that reactive coping at the physiological level may not be systematically coupled with a less aggressive, bold and exploratory behavioral type. In the only study to date on behavioral coping in lizards, Rodriguez-Prieto et al. (2011) found that more exploratory lizards habituated faster to a novel stress, and thus were more "reactive" because they acquired better and faster information about their environment. Additional data on behavioral coping styles are needed to confirm that this represents a general pattern in lizards.

Overall, our study uncovered some (albeit weaker than expected) relationships between behavior and physiology that we expected under the Pace Of Life Syndrome hypothesis, which states that behavioral syndromes are generally associated with physiological syndromes of the pace-of-life. The SMR at rest (measured at the lowest body temperature) was negatively correlated with behavioral variation in sociability and activity, and the plasma corticosterone level after an acute, handling stress increased slightly but not significantly with aggressiveness. Thus, correlations between physiology and behavior were trait-dependent and less consistent than predicted. In addition, even though we had reasonable sample size in this study, the observed correlations should be treated with some caution, because behavioral traits most likely to be correlated with physiology were not observed, correlations between behavior and physiology could be sensitive to a few extreme values, and the ranking of individual scores of metabolic expenditure was temperature-dependent. This suggests that stress physiology and metabolism drove only a small part of the inter-individual variation in behavior in the common lizard.

COMPLIANCE WITH ETHICAL STANDARDS

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Authors contributions: J-FLG, PA, SM and RJ designed the study. All authors contributed data collection and HM analyzed the data. HM and J-FLG wrote the first draft, and all authors contributed to the writing.

Conflict of Interest: Authors declare no conflict of interest.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Experiments were conducted under agreement A77-341-1 delivered by the Préfecture de Seine-et-Marne. Animals were captured and manipulated under authorization 2007-198-005 delivered by the Prefecture de Seine-et-Marne.

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TABLES

Table 1 Repeatability estimates (REP), likelihood ratio test (LRT) statistics and associated p-values computed to assess the significance of the random, inter-individual variance for each behavioral trait in the first and second studies. Significant REP values are shown in bold

		Study 1 of personality		**Study 2 of personality**	
	Behavior	**LRT**	**REP**	**LRT**	**REP**
Activity	Movement distance	$\chi^2_{0:1}$=4.49,p=0.017	**0.48**	$\chi^2_{0:1}$=15.4,p<0.0001	**0.51**
	Time spent walking	$\chi^2_{0:1}$=0.29,p=0.29	0.27	$\chi^2_{0:1}$=20.9,p<0.0001	**0.58**
	Time spent scratching	/	/	$\chi^2_{0:1}$=25.2,p<0.0001	**0.71**
	Time spent basking	/	/	$\chi^2_{0:1}$=35.3,p<0.0001	**0.63**
Risk taking	Time head hidden	$\chi^2_{0:1}$=17.3,p<0.0001	**0.52**	$\chi^2_{0:1}$=0.97,p=0.32	0.14
	Time body hidden	$\chi^2_{0:1}$=3.69,p=0.027	**0.45**	$\chi^2_{0:1}$=19.0,p<0.0001	**0.56**
	Time until basking	$\chi^2_{0:1}$=2.95,p=0.043	**0.43**	$\chi^2_{0:1}$=20.9,p<0.0001	**0.58**
Sociability	Absolute sociability score	$\chi^2_{0:1}$=0.94,p=0.17	0.34	/	/
	Relative sociability score	$\chi^2_{0:1}$=0.20,p=0.32	0.25	/	/
Aggressiveness	Aggressiveness after exploration	/	/	$\chi^2_{0:1}$=17.5,p<0.0001	**0.54**
	Aggressiveness after risk taking	/	/	$\chi^2_{0:1}$=18.4,p<0.0001	**0.56**

Table 2 Principal component analysis (PCA) of mean individual behavioral data in each study was done on the correlation matrix, thus implicitly rescaling all variables, and the table shows the loading scores for each of the three retained principal components. Bold typeface indicates the statistically significant loadings (based on the mean inertia criterion, see main text) for each variable

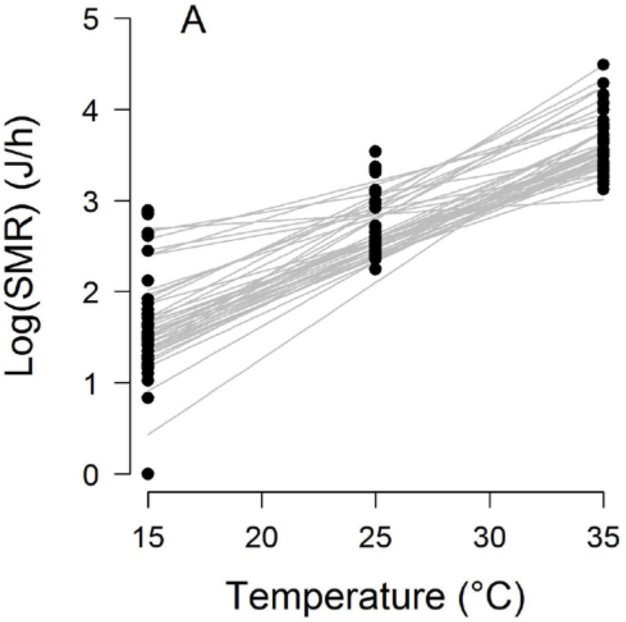
	Study 1 (n= 39)			**Study 2 (n=50)**		
Behavioral traits	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Movement distance	-0.460	0.486	**0.659**	**0.714**	-0.450	0.386
Mobility	-0.525	0.420	**0.652**	**0.695**	**-0.478**	0.406
Time spent scratching	/	/	**-0.570**	**0.726**	-0.089	0.010
Time spent basking	/	/	0.335	-0.465	**0.671**	-0.122
Time head hidden	0.457	-0.029	0.325	**-0.668**	**-0.548**	0.052
Time body hidden	**0.906**	-0.034	-0.369	**-0.816**	**-0.544**	0.045
Time until basking	**0.903**	-0.041	-0.303	**-0.787**	**-0.541**	0.080
Absolute sociability score	0.299	**0.812**	/	/	/	/
Relative sociability score	0.337	**0.834**	/	/	/	/
Aggressiveness after exploration	/	/	/	-0.321	0.303	**0.824**
Aggressiveness after risk taking	/	/	/	-0.284	0.380	**0.784**
Statistics of PC scores						
Eigenvalue	2.54	1.77	1.63	3.65	2.01	1.63
Variance explained	36.26	25.33	23.31	40.46	22.37	18.14

***F*IGURE LEGENDS**

Fig. 1 Relationship between behavioral variation and standard metabolic rate (SMR) in male common lizards (*n = 39*). A. The SMR increases significantly with body temperature. Black circles represent the observed SMR values and the grey lines the predicted thermal reaction norms obtained from the individual linear regressions. B. The SMR at 15°C is negatively correlated with the PC2 score measuring correlated behavioral variation in activity and sociability

Fig. 2 Relationship between behavioral variation and plasma corticosterone levels in male common lizards. A. The basal corticosterone level measured in the field was positively correlated with the stress response measured in the laboratory after a handling stress. B. The residuals of the stress response regressed on the basal level of corticosterone in the field decreased marginally with PC3 score measuring behavioral variation in aggressiveness. There was one outlier for corticosterone titer (stress response > 100 ng/mL)

FIGURE 1


A
Log(SMR) (J/h)
0
1
2
3
4
5
15
20
25
30
35
Temperature (°C)

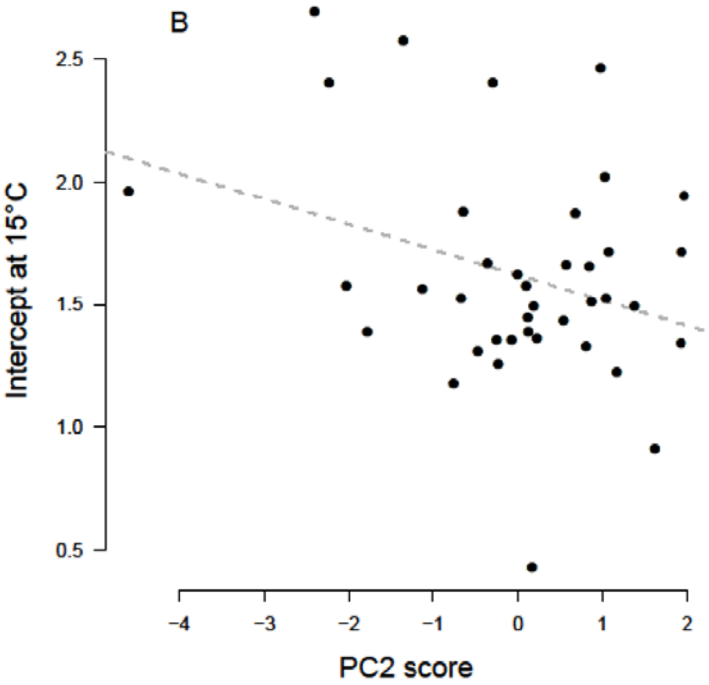
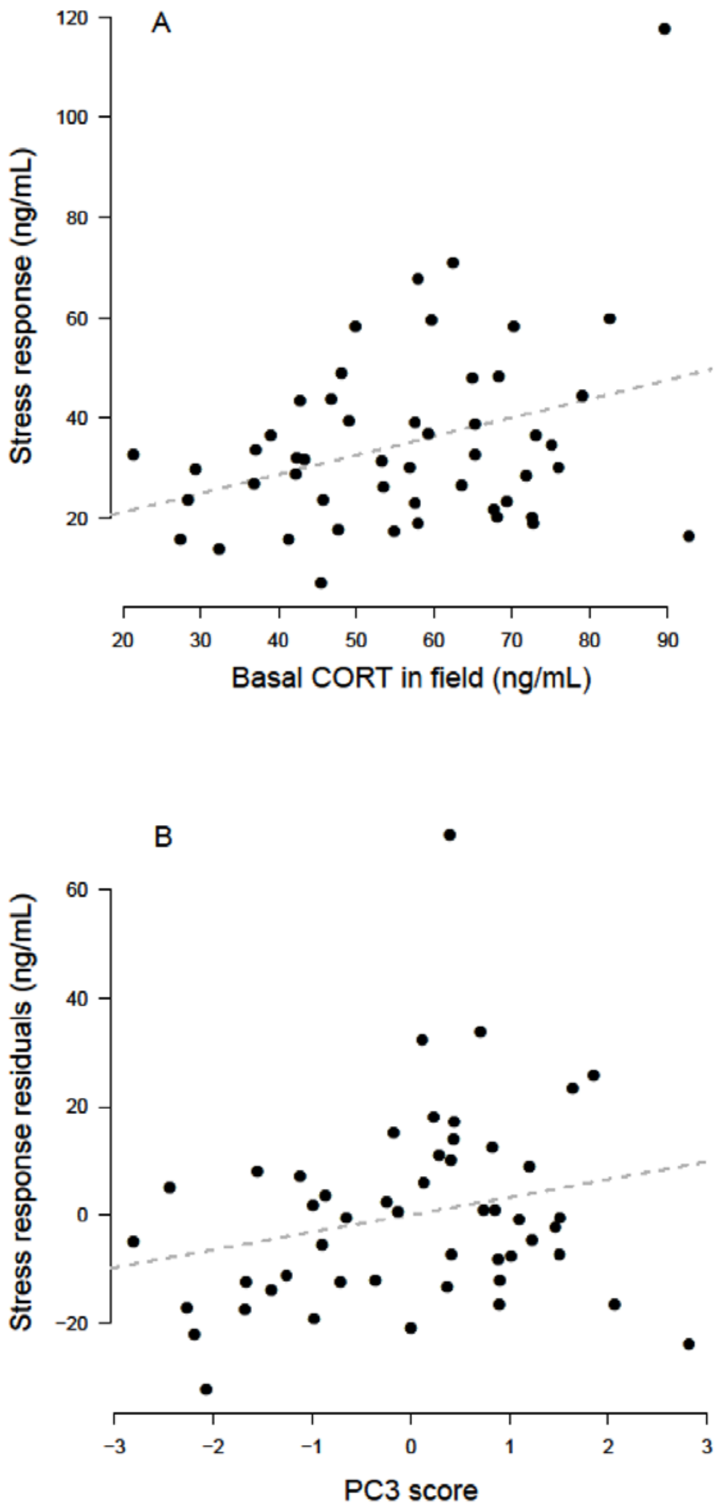

B
Intercept at 15°C
0.5
1.0
1.5
2.0
2.5
−4
−3
−2
−1
0
1
2
PC2 score

FIGURE 2


A
Stress response (ng/mL)
120
100
80
60
40
20
20
30
40
50
60
70
80
90
Basal CORT in field (ng/mL)
B
Stress response residuals (ng/mL)
60
40
20
0
−20
−3
−2
−1
0
1
2
3
PC3 score