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

3 Hugo Mell<sup>1</sup>, Rémy Josserand<sup>1</sup>, Beatriz Decencièrè<sup>2</sup>, Paulina Artacho<sup>3</sup>, Sandrine Meylan<sup>1,4</sup> and  
4 Jean-François Le Galliard\*<sup>1,2</sup>

5  
6 <sup>1</sup> CNRS/UPMC, UMR 7618, iEES Paris, Université Pierre et Marie Curie, 7 Quai St. Bernard,  
7 75005, Paris, France

8 <sup>2</sup> CNRS/ENS UMS 3194, CEREEP – Ecotron IleDeFrance, École Normale Supérieure, 78 rue  
9 du Château, 77140 St-Pierre-lès-Nemours

10 <sup>3</sup> Instituto de Ciencias Ambientales y Evolutivas, Campus Isla Teja, Universidad Austral de  
11 Chile, Valdivia, Chile

12 <sup>4</sup> ESPE de Paris, Université Sorbonne Paris IV, 10 rue Molitor, 75016 Paris, France

13

14 \* Author for correspondence

15 Jean-François Le Galliard

16 CNRS, UMR 7618, iEES Paris, Université Pierre et Marie Curie

17 7 Quai St Bernard, 75005 Paris, France

18 Tel: +33(0)1.44.27.26.68

19 Fax.: +33(0)1.44.27.35.16

20 E-mail: galliard@biologie.ens.fr

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22 **Running headline:** Covariation between physiology and personality in lizards

23

24 **ABSTRACT**

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

43

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

45

46 *SIGNIFICANCE STATEMENT*

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

57 *INTRODUCTION*

58 The concept of "animal personality" refers to consistent inter-individual differences (CIDs) in  
59 behavior across time and/or contexts (Réale et al. 2007). Empirical evidence of CIDs in  
60 behavior are widespread in the animal kingdom (reviewed in Bell et al. 2009), and personality  
61 traits may play a crucial role in some ecological and evolutionary processes (Sih et al. 2004a;  
62 Réale et al. 2007; Dingemanse and Wolf 2010). Animal personalities are generally organized  
63 along a few major behavioral dimensions, including activity and exploration, risk taking,  
64 aggressiveness and sociability (Réale et al. 2007). Two or more of these dimensions may be  
65 associated with suites of correlated traits called behavioral syndromes (reviewed in Sih et al.  
66 2004b), particularly the syndrome linking activity, exploration, risk taking and aggressiveness  
67 (Sih and Bell 2008). This syndrome, found in several species, is referred to as the shy-bold  
68 axis (Wilson et al. 1994) or the reactive-proactive continuum (Koolhaas et al. 1999).

69 A potential explanation for the occurrence of repeatable, consistent and correlated  
70 differences in behavior is that suites of behavioral traits may co-vary with stable differences  
71 in physiology (Biro and Stamps 2010; Coppens et al. 2010; Dingemanse and Wolf 2010). In

72 particular, CIDs in behavior along the reactive-proactive continuum should be linked to the  
73 physiological stress response (i.e., stress-coping style hypothesis, Koolhaas et al. 1999, 2010;  
74 Øverli et al. 2007; Coppens et al. 2010). The reactive and proactive behavioral types are  
75 considered adaptations for life in unstable and stable environments, respectively; thus, shy  
76 and reactive individuals are characterized by higher levels of physiological stress responses  
77 than bold and proactive individuals (Cockrem 2007). In vertebrates, the physiological stress  
78 response involves activation of the hypothalamo-pituitary-adrenal (HPA) axis, where  
79 exposure to stress stimulated secretion of glucocorticoids (e.g., Cockrem 2007). In turn,  
80 glucocorticoid secretion elicits a cascade of physiological and behavioral processes that are  
81 essential to cope with stressful events (Wingfield and Ramenofsky 1999; Landys et al. 2006).  
82 The stress-coping style hypothesis makes the specific predictions that proactive and bold  
83 individuals should have lower baseline concentrations of glucocorticoids and a less reactive  
84 HPA axis. These predictions are well-supported by research with domestic and laboratory-  
85 bred animals (Koolhaas et al. 1999; Groothuis and Carere 2005), especially lines selected for  
86 coping styles in mice (Veenema et al. 2003) and great tits (Carere et al. 2003; Baugh et al.  
87 2012), but less by more recent field studies (Lendvai et al. 2011; Baugh et al. 2013). They  
88 have not yet been tested in squamate reptiles (lizards and snakes).

89 In addition, a link could exist between energy expenditure and behavior (Careau et al.  
90 2008; Biro and Stamps 2010; Careau and Garland 2012) because energy acquisition and  
91 allocation constraints should influence behavioral traits involved in net energy gain (e.g.,  
92 foraging) and/or those that are energetically costly (e.g., aggressiveness, see Mathot and  
93 Dingemanse 2015). In particular, the basal metabolic rate (BMR, a measure of the minimal  
94 energy expenditure in post-absorptive individuals at rest) is both repeatable and consistent  
95 through time (Nespolo and Franco 2007) and should be correlated with activity, risk taking,  
96 exploration and aggressiveness (Wolf and McNamara 2012). Two opposite scenarios have  
97 been proposed to explain the partition between BMR and the total energy expenditure (Careau

98 et al. 2008; Mathot and Dingemans 2015). The first states that higher total energy  
99 expenditure might imply investment in physiological processes and anatomical features that  
100 support higher productivity. In this case, we expect a higher BMR to correlate with bolder  
101 and/or more proactive behaviors (i.e., production model of bioenergetics, Careau et al. 2008;  
102 Careau and Garland 2012). Examples include numerous studies of aggression, risk taking and  
103 exploration in fishes, mammals and a few bird species (e.g., Cutts et al. 2001; Mathot and  
104 Dingemans 2015). In contrast, a negative relationship between BMR and proactivity is  
105 expected when the amount of energy spent in maintenance is unavailable to sustain net energy  
106 gain and energy is limited (i.e., allocation model of bioenergetics, Careau et al. 2008; Careau  
107 and Garland 2012). This prediction has received less support (Mathot and Dingemans 2015),  
108 despite evidence that BMR may represent a cost to growth and survival (e.g., Steyermark  
109 2002; Artacho and Nespolo 2009).

110 Energy metabolism, glucocorticoid stress response and personality should thus be  
111 integrated into a general syndrome called the Pace Of Life Syndrome, or POLS (Ricklefs and  
112 Wikelski 2002; Careau et al. 2009; Réale et al. 2010; Le Galliard et al. 2013). However, intra-  
113 individual variation induced by thermal conditions (neglected thus far) might complicate the  
114 relationship between metabolic expenditure and behavior in ectothermic species (Artacho et  
115 al. 2013). For example, in previous studies, metabolic rates were obtained by repeated  
116 measurements at a single temperature. In ectotherms, the standard metabolic rate (SMR, a  
117 measure of BMR at a given temperature) significantly increases with body temperature, and  
118 the thermal dependence of SMR might differ markedly among individuals (Nespolo et al.  
119 2003; Careau et al. 2014). Hence, energetic data in ectotherms should preferably be calculated  
120 from SMR obtained along a thermal gradient. For example, a recent study of the slimy  
121 salamander (*Plethodon albagula*) by Careau et al. (2014) found significant inter-individual  
122 variation in the thermal dependence of metabolism, in that the metabolic ranking of  
123 individuals changed with body temperature. Thus, additional data on ectotherms is needed in

## Covariation between physiology and personality in lizards

124 order to rigorously assess the relationship between personality traits and metabolism after  
125 taking into account intra-individual differences in metabolic thermal sensitivity.

126 To explore the links between personality traits, standard metabolic rates and the  
127 glucocorticoid stress response, we conducted two independent observational studies with  
128 male common lizards, *Zootoca vivipara*. In a first study, we measured covariation between  
129 personality traits and resting metabolic rates measured at three relevant body temperatures. In  
130 a second study, we tested for covariation between personality traits and individual plasmatic  
131 levels of corticosterone, quantified both in the field and in the laboratory after exposure to an  
132 acute stress. Rather than examining the correlation between physiology and a single  
133 personality trait (reviewed in Mathot and Dingemanse 2015), we measured several behavioral  
134 dimensions simultaneously, including activity, risk taking, sociability and aggressiveness.  
135 CIDs in behavior have been documented previously for activity, exploration, sociability and  
136 risk taking in juvenile common lizards (Cote and Clobert 2007; Le Galliard et al. 2013, 2015),  
137 and there is independent variation in activity, risk taking and sociability (Le Galliard et al.  
138 2015). In adults, measurements of SMR are repeatable and consistent over short time periods  
139 (e.g., Artacho et al. 2013). The link between SMR and behavioral activity has been explored  
140 in juvenile lizards but no significant correlation was found (Le Galliard et al. 2013). However,  
141 by taking into account intra-individual variation in metabolism and several behavioral traits,  
142 we expect to gain greater insight into the relationship between behavioral syndromes and  
143 metabolism. In addition, plasma corticosterone levels of common lizards are repeatable over  
144 several days in the laboratory (SM & J-FLG unpubl. data) and increased corticosterone  
145 secretion in response to a stressor modifies activity and foraging behaviors (de Fraipont et al.  
146 2000; Cote et al. 2006). Whether this intra-individual variation parallels inter-individual  
147 variation along a general proactive-reactive continuum remains to be tested.

148 **MATERIALS AND METHODS**

149 ***Study species***

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

163 ***Study 1: covariation between behavior and metabolism***

164 Thirty-nine adult males ( $n = 7$  two-years old and  $n = 32$  more than two-years old) were  
165 captured in 2011 between May 16 and 19 from ten enclosures and measured for snout-vent  
166 length (SVL, range=53-63 cm, mean = 57.7) and body mass. Right after their capture, all  
167 lizards were placed in individual terraria (25 x 16 x 15 cm) and kept under standardized day-  
168 night (16h night: 8h day) and temperature conditions (16°C night: 23°C day) with food and  
169 water *ad libitum* (see Le Galliard et al. 2003 for detailed protocols). Individuals were  
170 measured once for three behavioral traits, activity (N=29), boldness (N=30) and  
171 sociability(N=30) within eight days of capture. Then, from July 1 to July 10, the SMR was  
172 measured for each lizard at 15°C, 25°C and 35°C (see details below). These temperatures  
173 were chosen because they cover the range of variation of body temperatures experienced



## Covariation between physiology and personality in lizards

174 during different activities, including temperature at rest, preferred body temperature and an  
175 intermediate value (Le Galliard et al. 2003). We did not take repeated measurements of  
176 activity, boldness and sociability. However, short-term repeatability estimates were calculated  
177 at the same time from another sample of adult lizards maintained in the same conditions and  
178 tested twice for the same behaviors the same year. In the data set involving measurement of  
179 repeatability, behaviors were also recorded within eight days of recapture of individuals, and  
180 repeated measures were taken the same day a few hours apart.

### 181 *Study 2: covariation between behavior and stress response*

182 For this study, fifty adult males ( $n = 13$  two-year-olds and  $n = 37$  older than two years) were  
183 captured on March 31, 2014 from 10 different enclosures and measured for SVL (range=48-  
184 62 cm, mean =57.5 cm) and body mass. Blood samples were taken immediately following  
185 capture. In order to avoid biases due to capture and handling stress, we performed short visits  
186 to each enclosure (in general, less than 5 min) and collected all blood samples within less than  
187 3 min of capture. To account for potential stress due to our visits to the enclosures, we  
188 measured the time between each capture and the first visit for each lizard (hereafter called  
189 time spent in the enclosure). Lizards were then transferred into individual terraria and held  
190 under the same conditions as lizards experienced in study 1. Activity, boldness and  
191 aggressiveness were measured during a first series of behavioral tests starting on day 7. On  
192 day 7, half of the lizards were tested for activity and aggressiveness, while the other half were  
193 measured for boldness and aggressiveness. On day 8, each group was tested for the behavior  
194 not measured during day 7, and then fed with a standard quantity of live crickets to ensure  
195 similar digestive state before the next measurements. The second session started on day 9 and  
196 followed the same procedure as the first one to obtain repeated measures. At day 11, another  
197 blood sample was collected in order to assess the corticosterone stress response under  
198 laboratory conditions. To ensure that peak corticosterone levels were reached, lizards were  
199 exposed to handling and simulated predation stress by scaring them with a paint brush for 10

200 minutes before blood sampling (Dauphin-Villemant and Xavier 1987). Plasma corticosterone  
201 levels were assessed using an immuno-enzymatic reaction following protocols previously  
202 used in (Meylan et al. 2003).

203 ***Collection of behavioral data***

204 We used a neutral arena test to investigate exploratory behavior and locomotor activity (Le  
205 Galliard et al. 2013). All tests were done during the daily activity period between 10 am and 5  
206 pm. Each lizard was placed in a plastic box (44.5 cm x 24 cm x 26 cm) maintained in a room  
207 at a standard temperature of 23-25°C with one heat source (40 W bulb) at the centre and two  
208 white light sources (Iguana Light 10.0 UV-B, ZooMed, 40 W). The soil was covered with  
209 clean sand before each trial to avoid interference with odors from conspecifics. Each lizard  
210 was placed in the plastic box for a 10 min acclimation period, and then filmed from above for  
211 30 min with a webcam (Hercules Deluxe). The film was downloaded using Virtual Dub 1.7.8  
212 and image sequence from each video was obtained (one frame per second). From these  
213 videos, we recorded lizard position (x-y coordinates) in ImageJ v1.40  
214 (<http://rsbweb.nih.gov/ij/>) using a particle analysis procedure (Mallard et al. 2013). We  
215 calculated the percentage of time spent walking and the travel distance during each trial. For  
216 study 2, we also calculated the total time spent basking and the total time spent scratching the  
217 wall with real-time recordings of behaviors.

218 We measured risk-taking (or boldness) behavior based on the behavior of a lizard after a  
219 simulated attack by a human (e.g., López et al. 2005; Le Galliard et al. 2015). Plastic boxes  
220 were equipped with a cardboard shelter on one corner to provide a refuge and with a heat  
221 source on the opposite corner to provide a stimulus for basking. After the acclimation period,  
222 we simulated several consecutive predator attacks with a paintbrush, softly touching the tail to  
223 force the lizard into the shelter. If the lizard was already inside the shelter, we simulated  
224 attacks around the shelter to force the head of the lizard into the shelter. We then filmed the  
225 behavior from above and calculated the time spent hiding (body and head inside the refuge)

## Covariation between physiology and personality in lizards

226 before leaning out of the refuge (body inside the refuge but tip of the nose emerging from the  
227 shelter), the time spent before emerging from the refuge (body and head outside the refuge),  
228 and the time spent before basking under the heat source on the opposite side of the box.

229 Recordings stopped after 60 min. This procedure allowed for "censoring" of boldness scores  
230 for one lizard in each study (i.e., less than 3% of recordings). We replaced boldness scores by  
231 the maximum value (3,600 secs) for these animals.

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

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

### 250 *Measurement of metabolic rate*

251 The standard metabolic rate (SMR) is defined as the minimum rate of energy expenditure

## Covariation between physiology and personality in lizards

252 under post-absorptive conditions in a resting phase at dark and at a given temperature within  
253 the animal's range of activity (Andrews and Pough 1985). Metabolic rates were estimated  
254 with a multiple-channel flow-through respirometry system (Qubit Systems, Canada) coupled  
255 with a differential O<sub>2</sub> analyzer (DOX; S104 Differential Oxygen Analyzer) and a CO<sub>2</sub>  
256 analyzer (S157) connected to respirometry software (QS Research). Metabolic records were  
257 processed by a macro program recorded in ExpeData software (Sable Systems) to transform  
258 the measurements from parts per million to milliliters per hour, taking into account the flow  
259 rate (140 mL/min). SMR was measured once at each of three body temperatures (15°C:  
260 minimum temperature, 25°C: intermediate body temperature during activity and 35°C: inside  
261 the range of preferred body temperature) after a fasting period of 72 hours to ensure post-  
262 absorption conditions. Individuals were placed in a room at a constant temperature of 15°C  
263 the night before recording, and were kept in the dark until being weighted and placed in the  
264 measurement chamber for an hour of acclimation at the test temperature. Excurrent O<sub>2</sub> and  
265 CO<sub>2</sub> concentrations were then measured continuously for 45 minutes at the same temperature.  
266 The average respiratory quotient of the population, calculated from the production of CO<sub>2</sub> and  
267 consumption of O<sub>2</sub> obtained from all individuals, was then used to convert the values of CO<sub>2</sub>  
268 production (mL/h), averaged over the recording, into energy expenditure (J/h).

### 269 *Statistical analyses*

270 All statistical analyses were carried out in R 3.0.3 (<https://www.r-project.org/>). Repeated  
271 measurements of the three focal behaviors, activity, risk taking and aggressiveness, were  
272 analyzed with linear mixed-effects models (LMM) using the *lme* function (Pinheiro and Bates  
273 2000). The LMM fitted to each behavioral variable included a fixed time effect to control for  
274 changes in behavior across repeated measures and a random individual effect. From this, we  
275 assessed the significance of random effects with likelihood ratio tests (LRT) and calculated a  
276 repeatability coefficient as the intra-class correlation coefficient (Wolak et al. 2012), which  
277 equals to the ratio of between-individual variance to total (between-individual and residual)

278 variance. Since the between-individual variance can take only positive values, the  $\chi^2$  statistics  
279 of the LRT is distributed as an equally weighted mixture of  $\chi^2$  distributions with one and zero  
280 degrees of freedom (Careau et al. 2014 and references therein). Thus, we halved the P-values  
281 obtained from the standard  $\chi^2$  distribution with one degree of freedom (equivalent to  $\chi^2_{0:1}$  in  
282 results below). In addition, behavioral syndromes were explored using principal component  
283 analyses (PCAs) of the mean, individual values of each behavioral trait. PCAs were  
284 implemented with the function *dudi.pca* in the R package *ade4* using a correlation matrix  
285 implicitly rescaling all variables (Chessel et al. 2004). The number of principal components  
286 retained for the analysis was determined on the basis of the broken-stick method (Legendre  
287 and Legendre 1998). We identified statistically significant contributions to the different PCs  
288 by calculating the inertia attributed to each variable. The contribution of the variable was  
289 considered significant when its inertia was greater than the mean inertia.

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

301 We used the PC scores obtained from the PCAs described above to explore the  
302 covariation between behavioral traits and physiology (SMR and plasma corticosterone levels).  
303 For SMR, we fitted a linear model with the SMR as a dependent variable and the individual

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

## 316 ***RESULTS***

### 317 ***Consistent individual differences in behavior***

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

330 the variables related to aggressiveness.

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

### 338 *Covariation between metabolism and personality*

339 The SMR increased significantly and almost linearly with body temperature on the log scale  
 340 (mixed-effects model, body temperature effect: slope =  $0.10 \pm 0.0048$ ,  $F_{1,79} = 437.1$ ,  $p <$   
 341  $0.001$ ; Fig. 1A). According to individual regressions, slopes (log SMR, mean =  $0.10 \pm 0.009$   
 342 SD) and intercepts at 15°C (log SMR, mean =  $1.65 \pm 0.47$  SD) were strongly negatively  
 343 correlated (Pearson moment-correlation :  $r = -0.85$ ,  $p < 0.0001$ ). Given this pattern of  
 344 crossing thermal sensitivity curves (Fig. 1A), the thermal repeatability of SMR was small ( $R_T$   
 345 =  $0.052$ ) and not significant ( $\chi^2_{0:1} = 0.30$ ,  $p = 0.27$ ). The best model (adjusted  $R^2 = 0.126$ )  
 346 describing metabolic variation (intercept at 15°C) included the PC2 score measuring variation  
 347 in sociability (slope =  $-0.103 \pm 0.05$ ,  $F_{1,36} = 4.21$ ,  $p = 0.047$ , Fig. 1B) and a marginal negative  
 348 effect of PC1 score (slope =  $-0.08 \pm 0.04$ ,  $F_{1,36} = 3.30$ ,  $p = 0.077$ ). This effect of PC1 did not  
 349 hold when we removed one outlier for boldness score (Table S2).

### 350 *Covariation between glucocorticoid stress response and personality*

351 Mean plasma corticosterone levels were higher in the field than after exposure to a handling  
 352 stress in the laboratory (mean level in the field:  $56.3 \text{ ng/mL} \pm 2.33$ , range: 21.4-92.8; mean  
 353 stress-induced level:  $35.0 \pm 2.66$ , range: 6.98-117.6, paired t-test:  $t_{49} = 7.35$ ,  $p < 0.001$ ; Fig.  
 354 2A). We found no significant effects of behavioral score, SVL, time spent in the enclosure  
 355 and age class on plasma corticosterone concentration in the field (all  $p > 0.21$ ). The best



## Covariation between physiology and personality in lizards

356 model (adjusted  $R^2 = 0.16$ ) selected to describe variation in stress-induced corticosterone  
357 levels in the laboratory included two variables, a positive effect of field corticosterone (slope  
358  $= 0.41 \pm 0.15$  SE,  $F_{1,47} = 6.32$ ,  $p = 0.015$ ) and a marginal, negative effect of PC3 score, which  
359 is positively correlated to aggressiveness (slope  $= 3.60 \pm 1.92$  SE,  $F_{1,47} = 3.49$ ,  $p = 0.068$ , Fig.  
360 2B). The removal of one "outlier" for corticosterone titer (Fig. 2A) weakened the effect of  
361 PC3 (slope  $= 2.69 \pm 1.60$  SE,  $F_{1,46} = 2.85$ ,  $p = 0.099$ , Fig. 2B), as well as the correlation  
362 between field corticosterone and the stress response (slope  $= 0.21 \pm 0.13$  SE,  $F_{1,46} = 1.94$ ,  $p =$   
363  $0.17$ , Fig. 2A).

### 364 *DISCUSSION*

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



## Covariation between physiology and personality in lizards

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

399

400 Regarding the individual variation in the standard metabolic rate (SMR), we found variation  
401 among individuals at the lowest body temperature (intercept), in addition to showing that  
402 lizards with a low intercept had a greater increase of their SMR with body temperature.

403 Although these results must be considered with some caution, as we only tested animals once  
404 at each temperature, they suggest crossing thermal sensitivity curves for SMR (Careau et al.  
405 2014). This could indicate that lizards that minimize basal energy expenditure at rest (low  
406 body temperatures) have higher basal expenditures at activity (high body temperatures). The  
407 robustness and generality of this pattern remains to be tested in larger samples of common

408 lizards and in other species, and with several repeated measures at each temperature. In  
409 addition, we found that individuals with high values of sociability, and to some extent  
410 activity, were characterized by a lower SMR at 15°C.

411 At first glance, the negative relationship obtained between the SMR at 15°C and the  
412 sociability-activity axis seems to support the allocation model of energy management, where  
413 SMR constrains the expression of energetically costly behaviors (Careau et al. 2008; Careau  
414 and Garland 2012; Mathot and Dingemanse 2015). However, a more detailed examination of  
415 the results cautions against such a straightforward explanation. First, PC1 and PC3 scores  
416 directly related to risk taking and activity were not correlated with SMR even though these  
417 may reflect variation in energetically costly behaviors (Mathot and Dingemanse 2015).  
418 Second, even after accounting for the effect of PC2 score, much variation in SMR remained.  
419 Third, despite good evidence that SMR represents a significant part of total energy  
420 expenditure in lizards (e.g., Niewiarowski and Waldschmidt 1992), no empirical study has yet  
421 examined among-individual partitioning of energy into maintenance, activity and other  
422 energetic expenses. Given that an increased SMR does not seem to impair mean growth,  
423 survival or reproduction in this species (Le Galliard et al. 2013; Artacho et al. 2015), we  
424 cannot tell with certainty that differences in SMR represent a significant energetic constraint  
425 at the individual level. Fourth, our study indicates that conclusions from correlation patterns  
426 between behavior and physiology obtained with measures of SMR at one body temperature  
427 may be misleading. Since low SMR at 15°C was strongly, negatively associated with the  
428 thermal sensitivity of RMR, more sociable and active lizards did not necessarily have the  
429 lowest SMR at the highest body temperatures. Thus, when thermal repeatability of RMR is  
430 low, correlative studies linking animal personality and energetics may lead to results  
431 supporting the allocation model, the performance model or none of them, depending on  
432 temperature used during measurements. While estimates of SMR at one body temperature are  
433 generally repeatable over time (Nespolo and Franco 2007), the thermal repeatability of SMR

## Covariation between physiology and personality in lizards

434 can be low when individuals vary in the thermal sensitivity of their metabolism (Careau et al.  
435 2014). This suggests that relevant aspects of thermal biology should be considered when  
436 examining behavioral and physiological syndromes in ectotherms. In particular, we advocate  
437 for future investigations of covariation patterns between behaviors and physiology by  
438 repeatedly measuring all traits at several body temperatures.

439

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

453         These results contradict the hypothesis that the glucocorticoid stress response  
454 constitutes a causal proximate mechanism behind the activity-aggressiveness-risk taking  
455 behavioral syndrome, since we found no correlation with activity and boldness. In addition,  
456 the weak correlation found for aggressiveness, if real, contrasts with findings in some bird and  
457 mammal species, where more aggressive individuals have a lower HPA axis activity and  
458 reactivity in response to a stressor (i.e., proactive coping style, Koolhaas et al. 1999;  
459 Groothuis and Carere 2005; Cockrem 2007). For example, house mice selected for low

460 aggression have higher basal corticosterone levels during daytime and prolonged  
461 corticosterone secretion in response to a strong stressor (Veenema et al. 2003). Similarly,  
462 great tits (*Parus major*) selected for slow exploration speed are less aggressive and have more  
463 elevated corticosterone in response to a social stress than birds selected for fast exploration  
464 (Carere et al. 2003; Groothuis and Carere 2005; Baugh et al. 2012). The short-term increase  
465 of corticosterone concentration in response to a stressor also differs among individual birds,  
466 with stronger increase in slow than in fast explorers in *Parus major* and *Passer domesticus*  
467 (Lendvai et al. 2011; Baugh et al. 2013).

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

477

478 Overall, our study uncovered some (albeit weaker than expected) relationships between  
479 behavior and physiology that we expected under the Pace Of Life Syndrome hypothesis,  
480 which states that behavioral syndromes are generally associated with physiological syndromes  
481 of the pace-of-life. The SMR at rest (measured at the lowest body temperature) was  
482 negatively correlated with behavioral variation in sociability and activity, and the plasma  
483 corticosterone level after an acute, handling stress increased slightly but not significantly with  
484 aggressiveness. Thus, correlations between physiology and behavior were trait-dependent and  
485 less consistent than predicted. In addition, even though we had reasonable sample size in this

486 study, the observed correlations should be treated with some caution, because behavioral traits  
487 most likely to be correlated with physiology were not observed, correlations between  
488 behavior and physiology could be sensitive to a few extreme values, and the ranking of  
489 individual scores of metabolic expenditure was temperature-dependent. This suggests that  
490 stress physiology and metabolism drove only a small part of the inter-individual variation in  
491 behavior in the common lizard.

492 **COMPLIANCE WITH ETHICAL STANDARDS**

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Covariation between physiology and personality in lizards

659 **TABLES**

660

661 **Table 1** Repeatability estimates (REP), likelihood ratio test (LRT) statistics and associated p-  
 662 values computed to assess the significance of the random, inter-individual variance for each  
 663 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	$\chi^2_{0:1}=4.49,p=0.017$	<b>0.48</b>	$\chi^2_{0:1}=15.4,p<0.0001$	<b>0.51</b>
	Time spent walking	$\chi^2_{0:1}=0.29,p=0.29$	0.27	$\chi^2_{0:1}=20.9,p<0.0001$	<b>0.58</b>
	Time spent scratching	/	/	$\chi^2_{0:1}=25.2,p<0.0001$	<b>0.71</b>
	Time spent basking	/	/	$\chi^2_{0:1}=35.3,p<0.0001$	<b>0.63</b>
Risk taking	Time head hidden	$\chi^2_{0:1}=17.3,p<0.0001$	<b>0.52</b>	$\chi^2_{0:1}=0.97,p=0.32$	0.14
	Time body hidden	$\chi^2_{0:1}=3.69,p=0.027$	<b>0.45</b>	$\chi^2_{0:1}=19.0,p<0.0001$	<b>0.56</b>
	Time until basking	$\chi^2_{0:1}=2.95,p=0.043$	<b>0.43</b>	$\chi^2_{0:1}=20.9,p<0.0001$	<b>0.58</b>
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	/	/	$\chi^2_{0:1}=17.5,p<0.0001$	<b>0.54</b>
	Aggressiveness after risk taking	/	/	$\chi^2_{0:1}=18.4,p<0.0001$	<b>0.56</b>

664

Covariation between physiology and personality in lizards

665

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

671

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

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674 **FIGURE LEGENDS**

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

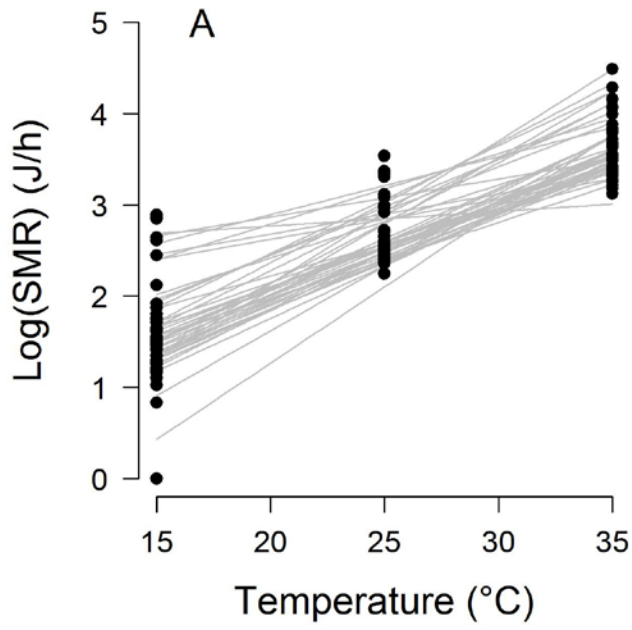
682

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

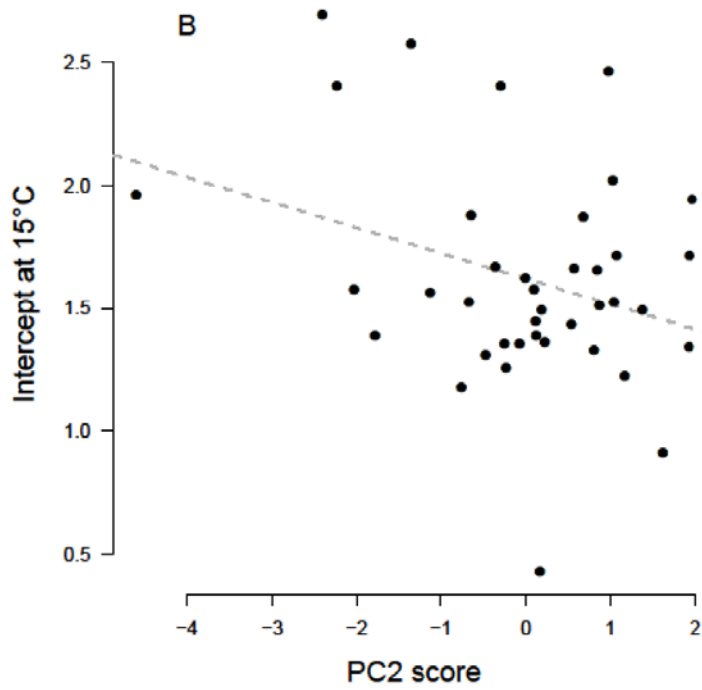
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691 **FIGURE 1**

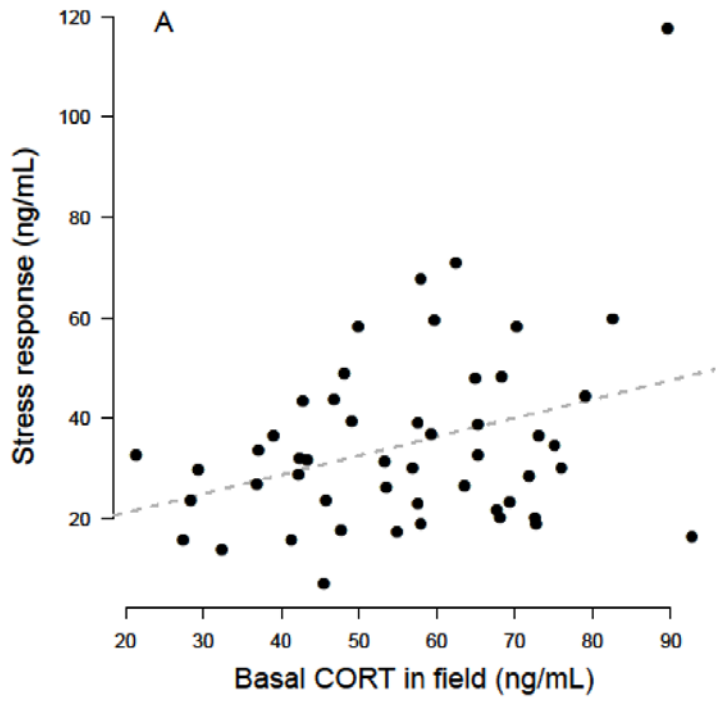


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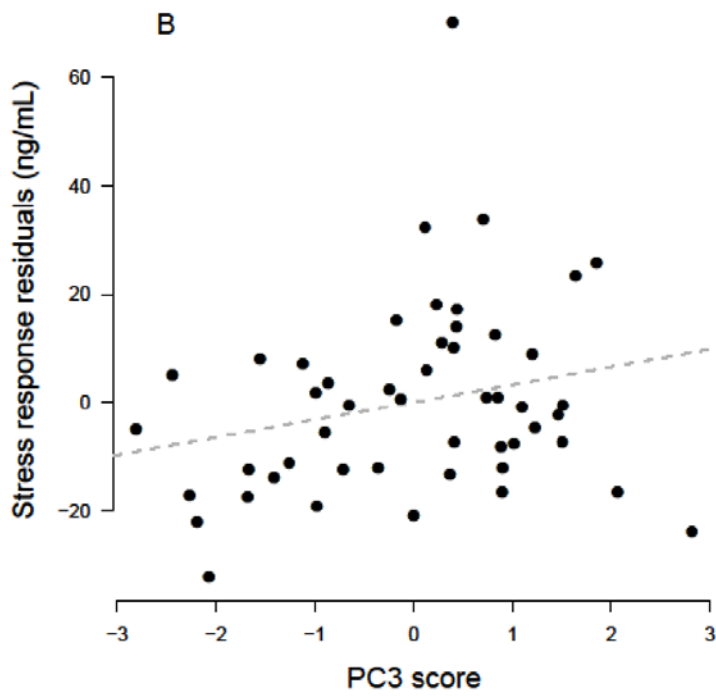


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694 **FIGURE 2**



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