

Individual variation in an acute stress response reflects divergent coping strategies in a large herbivore

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ABSTRACT

Individuals differ in the manner that they cope with risk. When these behavioral differences are manifested in risky or challenging environments (i.e. stressful situations), they are generally interpreted within the “coping style” framework. As studying inter-individual variability in behavior is particularly challenging in the wild, we used a captive facility to explore consistency in the individual behavioral response to an acute stress in roe deer (*Capreolus capreolus*). Using behavioral and physiological parameters measured six times across a calendar year, we first quantified individual repeatability and, second, explored the correlations among these parameters that might indicate a coherent stress response. Finally, we analyzed the link between the stress response and individual body mass, a reliable indicator of phenotypic quality in roe deer. We found that the measured parameters were highly repeatable across seasons, indicating that the individual stress response is consistent over time. Furthermore, there was considerable covariation among the stress response parameters, describing a proactivity-reactivity gradient at the individual level. Finally, proactive individuals had higher body mass than reactive individuals. We suggest that consistent individual differences in energy metabolism and physiology may promote consistent individual differences in behavioral traits, providing a mechanistic link between food acquisition tactics and demographic performance.

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1. Introduction

Consistent individual differences in behavior (Koolhaas et al., 1999; Réale et al., 2007; Sih et al., 2004) mediate the interactions between individuals and their environment, notably their response to human-induced rapid environmental change (HIREC, Sih et al., 2011). For instance, as bold individuals are assumed to be fast explorers that are highly aggressive, they might be expected to cope better with environmental change. However, they may also have

less flexible behavioral repertoires and often perform better in stable environments (Koolhaas et al., 1999), whereas shyer individuals are more neophobic, but more behaviorally flexible (Koolhaas et al., 1999; Sih et al., 2004). Moreover, the fitness outcomes of the two tactics may be context-dependant (Boon et al., 2007; Dingemans et al., 2004; Dingemans and de Goede, 2004; Monestier et al., 2015). Thus, the existence of inter-individual variability in behavior (i.e. different behavioral types) within a population may favor adaptation to a wide array of environmental changes (Fogarty et al., 2011; Pearish et al., 2013).

Behavioral differences manifested in risky or challenging environments (i.e. stressful situations) are generally interpreted within the “coping style” framework as “a coherent set of behavioral and physiological stress responses which are consistent over time and characteristic to a certain group of individuals” (Koolhaas et al., 1999). Two different phenotypes are well recognized: the proactive and the reactive types (Groothuis et al., 2005; Koolhaas et al., 1999). Proactive individuals are highly aggres-

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sive, take risks and adopt a 'flight-or-fight' response in the face of potential danger, whereas reactive individuals tend to react by freezing and, more generally, being passive (Koolhaas et al., 2010, 1999). Physiologically, proactive individuals predominantly display a high sympathetic reactivity and a low parasympathetic and hypothalamus-pituitary-adrenal (HPA) reactivity, whereas reactive individuals predominantly show a high HPA and parasympathetic reactivity, but a low sympathetic reactivity (Ellis et al., 2006; Koolhaas et al., 1999). However, a link between the neuro-physiological and behavioral dimensions of the stress response has been described only in a few species (in mice and rats: Koolhaas et al., 1999; birds: Carere et al., 2003; fish: Overli et al., 2005).

Inter-individual differences in behavior, and particularly in the stress response, may affect life-history traits and, ultimately, fitness (Smith and Blumstein, 2008). Some theoretical (Wolf et al., 2007) and empirical (Biro and Stamps, 2008; Careau et al., 2008; Stamps, 2007) studies have indicated a correlation between behavior and individual performance, generally indexed as growth rate or fecundity. Stamps (2007) and Biro and Stamps (2008) predicted a positive relationship between boldness, activity or aggressiveness and an individual's growth rate, body size and metabolic rate (Careau et al., 2008; Lantova et al., 2011). Although this information would contribute to a better understanding of behavioral tactics and life history evolution (Bell et al., 2007; Del Giudice et al., 2011; Smith and Blumstein, 2008), studies on the link between coping style, their neuro-physiological basis and individual performance are rare due to the difficulty of obtaining such detailed individual data in wild populations (Dingemans et al., 2002; Herborn et al., 2010).

Generally speaking, the stress response involves a chain reaction from the nervous system to behavior (Boonstra, 2013; Romero et al., 2009). The most obvious response is an individual's behavior (Reimoser, 2012), however, variation in heart rate, temperature and glucocorticoids are considered reliable indicators of an acute stress response from a physiological point of view (Carere and van Oers, 2004; Moberg, 1985; Moe and Bakken, 1997; Zethof et al., 1994). In addition, the levels of hematocrit, hemoglobin concentration and red blood cell counts (Mentaberre et al., 2010; Montané et al., 2007) may also accurately index stress. With regard to the immune response, an acute stress provokes an increase in neutrophils within 1–2 h after the rise in glucocorticoids, and a decrease in lymphocytes (Davis et al., 2008; Mentaberre et al., 2010; Montané et al., 2007). Hence, the neutrophil/lymphocyte (N/L) ratio is also used in many species to index physiological stress (Davis et al., 2008).

Our first aim in the present study was to highlight inter-individual differences in the acute stress response of adult roe deer using behavioral and physiological parameters. Because Koolhaas et al. (1999) emphasized that coping styles should be consistent over time, we first explored individual repeatability in the behavioral and physiological measures recorded six times across a calendar year. The stress response should also be consistent across a set of behavioral and physiological parameters (Koolhaas et al., 1999), thus, we quantified the relationships among these parameters. More precisely, we expected to observe a gradient in the stress response, from proactive individuals which should exhibit a marked response to an acute stress in terms of both behavioral and physiological parameters (high values for rectal temperature, behavioral score, hematocrit level and N/L ratio), compared to reactive individuals. Then, we explored the relationship between these measures of the stress response and individual body mass which constitutes a reliable indicator of an individual's body condition and phenotypic quality in roe deer (Toigo et al., 2006). Individuals were fed ad libitum in captivity so that they were under no obvious energetic constraint. However, because proactive (or bold) individuals are known to prioritize energy intake over risk avoidance (Bonnot

et al., 2015), we expected proactive individuals to achieve higher body mass.

2. Material and methods

2.1. Study site and population

Because studying inter-individual variability in behavior is particularly challenging in the wild, we used a captive facility for roe deer, the INRA experimental station of Gardouch, located in south-western France, about 30 km south-east of Toulouse and about 100 km north of the foothills of the Pyrénées mountains. The station is located on the slopes of a hill, around 230 m above sea level. The climate is of the 'Aquitaine' Atlantic type, although subject to a strong Mediterranean influence, especially in summer.

The roe deer were bred in the experimental station in accordance with European directive (2010/63/UE) for care and use of animals (agreement N° 31-2012-17 for the station and agreement N° 311255504 for H. Verheyden). Roe deer were housed in enclosures of about 0.5 ha containing between 1 and 4 individuals according to their status and sex. Each enclosure consists of a meadow and a hut where individuals are artificially fed with pellets (600 g per individual) and can obtain shelter. The current experiment included a total of 10 adult individuals: 4 males and 6 females aged from 4 to 10 years old. Of these, four individuals were hand-reared for the first two months of their life and were housed alone, whereas the other six were maternally-reared and housed in two groups of three individuals. All deer had some degree of habituation to humans.

2.2. Data collection

For the experiment, each individual was caught 6 times, once every two months across a calendar year, from March 2013 to January 2014. The animals were directed into their hut by slowly approaching them and then pushed through a trap door into a retention box. In the box, the animals were tranquilized with a low dose intramuscular injection of acepromazine (calmivet 3 cc) to reduce risk of injury, as recommended by Montané et al. (2003). The use of acepromazine may attenuate the stress response, but not suppress it. We, hence, made the explicit assumption that all individuals were similarly affected by the tranquilizer in terms of their stress response. Indeed, to ensure comparability among individuals, behavioral measurements and blood samples were taken within a standardized time window (see below). The animal was left in the box for at least 30 min before being restrained and placed on a table for sampling. During each capture event, individuals were weighed with an electronic balance (with a precision of 0.1 kg). Then, we continuously measured their rectal temperature during handling (using a Ecoscan thermometer YSI 400 and flexible probe with a precision of 0.2 °C) until stabilization. We also recorded behavior at capture and during handling and calculated a behavioral score describing a stress profile gradient. We attributed a score for vocalization on the table during handling (1 or 0 if not), and for struggling and panting on the table during handling (1 for both, 0.5 for struggling only, otherwise 0). An index of the behavioral stress response was then calculated as the mean of the scores for each of these three components, describing a stress profile gradient ranging from 0 to 1, with 1 indicating a priori proactive individuals (see Bonnot et al., 2015; Debeffe et al., 2014; Monestier et al., 2015 for a similar approach). We also took blood samples from each individual from the left jugular vein using manual compression. On average, the blood sample was taken 40 min (range = [32–48]) after capture. Four tubes (4 mL stabilized with EDTA) were collected and then shaken gently a dozen times to avoid blood clotting and

stored in an ice box. The next morning, we used a manual reading of the blood sample to obtain the hematocrit level (Ht). The slides were stained (May-Grünwald-Giemsa staining) using the RAL 555 kit according to the protocol provided by the manufacturer (RAL Reagents, Martillac, France) and 100 white blood cells were examined microscopically to estimate the proportion of each cell type. We used these values to calculate the N/L ratio.

2.3. Statistical analyses

2.3.1. Repeatability of stress response parameters

Individual consistency in behavioral score, temperature, hematocrit level and N/L ratio was estimated by calculating individual repeatability with mixed models (Nakagawa and Schielzeth, 2010). To control for differences in the number of repetitions per individual for a given stress response parameter, we calculated adjusted repeatability estimates (sensu Nakagawa and Schielzeth, 2010) by including the fixed effect of the number of repetitions per individual in the linear mixed models. The resultant values estimate repeatability as if all measurements were taken for a fixed number of repetitions (Nakagawa and Schielzeth, 2010). Repeatability was estimated as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor) using R version 2.15.1 software (R Development Core Team, 2013). We obtained at least two repetitions per individual for all measured parameters (temperature: range = [2.0–6.0] and median = 3.5 repetitions; behavioral score: range = [2.0–6.0] and median = 4.0 repetitions; hematocrit: range = [2.0–6.0] and median = 3.5 repetitions; N/L ratio: range = [2.0–6.0] and median = 3.5 repetitions; body mass = [3.0–6.0] and median = 4.0 repetitions). Similarly, we calculated a repeatability estimate for body mass using the same method as described above.

2.3.2. Inter-individual variability in stress response parameters

Prior to evaluating inter-individual variation in the stress response parameters, because our small sample size precluded complex model construction, we conducted preliminary analyses to investigate potential confounding effects linked to differences in age, sex and rearing conditions of the individual deer (i.e. hand-reared and housed alone vs. maternally-reared and housed in groups). For this, we first constructed univariate models (linear or beta regressions, see below) with either age, sex or rearing conditions as an explanatory variable and each stress response parameter as the dependent variable. We retained the model with the lowest Akaike's Information Criterion for small sample size (AICc, Burnham and Anderson, 2002). For three of the four stress response parameters (rectal temperature, N/L ratio and hematocrit level), the model selected included the rearing conditions, whereas for the behavioral score the constant model was the best. Therefore, we then standardized each stress response parameter (except the behavioral score) in relation to the individual's rearing conditions. To do so, we subtracted the mean value of the given stress response parameter for a given type of rearing conditions from each observed value of that parameter for all individuals that experienced those conditions. Consequently, in all subsequent analyses of rectal temperature, N/L ratio and hematocrit level (but not behavioral score), data were standardized for rearing conditions.

To investigate inter-individual variability in the four stress response parameters, we constructed four sets of models with each of the four stress response parameters as the dependent variable and individual identity as a fixed explanatory factor. Prior to analysis, the N/L ratio was log-transformed to achieve normality. For rectal temperature, hematocrit level, and N/L ratio (log transformed), we used linear models, while for the behavioral score which took values between 0 and 1, we used a beta regression. As

beta regression models assume that the dependent variable takes values within the interval]0,1[(only (Cribari-Neto and Zeileis, 2009), we first transformed the behavioral score to exclude the extreme values 0 and 1 (with a classical transformation, see (1); Smithson and Verkuilen, 2006).

$$BS' = \frac{BS \cdot (n - 1) + 0.5}{n}, \quad (1)$$

where n is the sample size and BS the mean behavioral score.

In addition, to control for possible seasonal variation in the stress response parameters, we included the period at which the capture event occurred (categorical variable, 6 modalities: March, May, July, September, and November 2013, January 2014) as a fixed effect.

2.3.3. Relationships among stress response parameters and the link with individual body mass

To explore inter-individual variation in the stress response within the coping style framework, we assumed that the behavioral and physiological parameters should be inter-related at the among-individual level. Thus, we constructed a Pearson's correlation matrix and then performed a centered and scaled Principal Component Analysis (PCA) on the individual-specific means of the four stress response parameters (rectal temperature, hematocrit level and N/L ratio and behavioral score) to generate one or more synthetic variable(s) (i.e. Principal Components) summarizing variation in the overall individual stress response using the "dudi.pca" function in the ade4 package (Dray et al., 2015). Finally, we used linear models (LM) to examine the relationship between the overall individual stress response (Principal Component scores for a given individual) and mean body mass (over the 6 capture events; note that adult body mass is achieved by 2–3 years of age (Hewison et al., 2011) and is thereafter generally stable over the prime-age stage in roe deer (Hewison et al., 1996), while sexual dimorphism is low in this species (ca. 10%); Andersen et al., 2000) as the dependent variable.

All analyses were performed in R version 3.1.0 (R Development Core Team, 2013). We used a model selection approach based on the Akaike's information criterion (AIC), retaining the model with the lowest AIC value (AICc, i.e. AIC corrected for small sample size), reflecting the best compromise between precision and accuracy (Burnham and Anderson, 2002). We also calculated AICc weights as a measure of the likelihood that a given model fitted the data best among the set of candidate models.

3. Results

3.1. Repeatability of stress response parameters

Rectal temperature was moderately repeatable for a given individual ($r = 0.24$, 95% confidence interval = [0.016, 0.774]). The N/L ratio was quite strongly repeatable ($r = 0.46$, 95% confidence interval = [0.178, 0.732]). The behavioral score ($r = 0.61$, 95% confidence interval = [0.365, 0.790]), the hematocrit level ($r = 0.72$, 95% confidence interval = [0.467, 0.860]) and body mass ($r = 0.79$, 95% confidence interval = [0.575, 0.859]) were highly repeatable across individuals.

3.2. Inter-individual variability in stress response parameters

For three of the four stress response parameters (behavioral score, hematocrit level and N/L ratio), the model with the highest support contained individual identity as the only explanatory factor (Table 1), indicating no seasonal variation in the stress response across the year, but marked variability among individuals in the severity of the response (Fig. 1). In contrast, for rectal temperature, the best model was the constant model (Table 1).

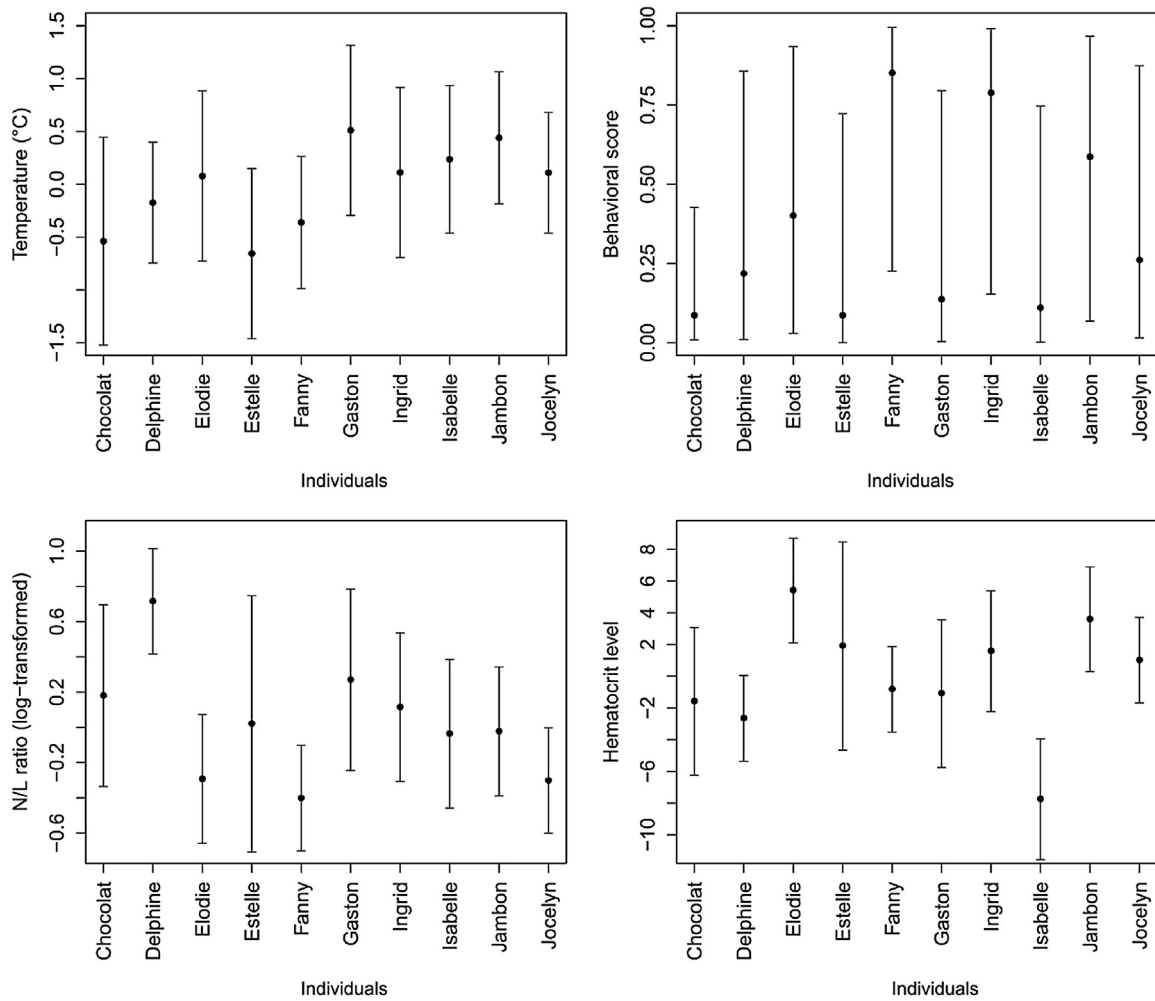


Fig. 1. Inter-individual variability in the four stress response parameters (rectal temperature, behavioral score, N/L ratio, hematocrit level). We constructed linear models for rectal temperature, N/L ratio and hematocrit level and we standardized these three dependent variables in relation to the rearing condition of the individuals (see text). We used beta regression models for the behavioral score which was transformed to exclude extreme values (0,1, see text). The graph presents the predicted values for each individual and the associated confidence interval (95%) from the best models for each of the parameters with individual identity ($N = 10$ individuals) as the explanatory variable.

Table 1

Candidate linear models (rectal temperature, N/L ratio, and hematocrit level), beta regression (behavioral score) fitted to investigate seasonal and individual variation in the four stress response parameters. Both the individual identity and the period of the year were used as fixed effect. AICc is the value of the corrected Akaike's Information Criterion and K is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for Δ AICc and on the Akaike weights.

Dependent variable	Models	K	AICc	Δ AICc	AICcWt
Temperature	constant model	2	82.06	0.00	0.96
	period	7	88.56	6.50	0.04
	individual	11	95.26	13.20	0.00
	individual + period	16	110.84	28.79	0.00
Behavioral score	individual	11	-43.00	0.00	0.97
	individual + period	16	-37.10	5.90	0.03
	constant model	2	-19.50	23.60	0.00
	period	7	-12.40	30.60	0.00
N/L ratio	individual	11	42.86	0.00	0.99
	constant model	2	52.92	10.06	0.01
	individual + period	16	60.42	17.56	0.00
	period	7	63.95	21.09	0.00
Hematocrit level	individual	11	205.69	0.00	1.00
	constant model	2	215.60	9.91	0.00
	period	7	225.94	20.26	0.00
	individual + period	16	227.64	21.96	0.00

Table 2

Scores on the four axes (PC1, PC2, PC3, and PC4) of the PCA performed on the four stress response parameters. Projections of all the variables on the different principal components and percentage of total inertia captured by each principal component.

Stress response parameters	PC1	PC2	PC3	PC4
Rectal temperature	0.64	0.60	0.03	-0.25
Behavioral score	0.80	0.17	-0.10	0.51
Hematocrit level	0.79	-0.21	0.42	-0.20
N/L ratio	-0.76	0.24	0.32	0.36
Variance explained (%)	53.8	25.6	11.2	9.4

3.3. Relationships among stress response parameters and the link with individual body mass

In the PCA of the four stress response parameters, the first principal component (PC1) captured 53.8% of the total inertia and was much more informative than all lower order axes (Table 2). Rectal temperature, hematocrit level and behavioral score were all positively correlated with PC1, whereas the N/L ratio was negatively correlated with it (Table 2). Thus, this axis represented a gradient of stress response, with positive values indicating a rapid and marked response to the stress induced by capture, and negative values indicating a low level of response. This interpretation was supported by the correlation matrix which showed that rectal temperature,

Table 3
Matrix of the Pearson's correlation coefficients among the four stress response parameters (rectal temperature, behavioral score, hematocrit level and N/L ratio).

	Rectal temperature	Hematocrit level	N/L ratio	Behavioral score
Rectal temperature	1.00			
Hematocrit level	0.58	1.00		
N/L ratio	-0.27	-0.79	1.00	
Behavioral score	0.36	0.50	-0.51	1.00

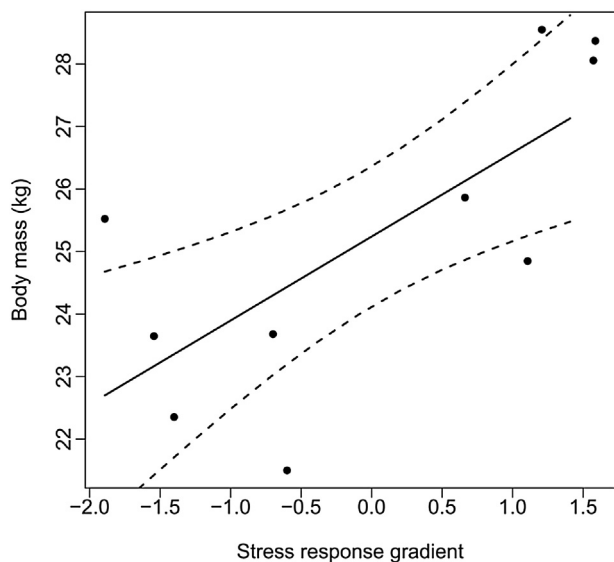


Fig. 2. Relationship between individual mean body mass (dependent variable) and the overall stress response gradient (PC1). Positive values for the overall stress response gradient indicate a high rectal temperature, a high behavioral score, a high hematocrit level and a low N/L ratio. Dashed lines represent the 95% confidence intervals.

hematocrit level and behavioral score were quite strongly and positively inter-correlated, and all were negatively correlated with the N/L ratio (Table 3).

To explore the link between body mass and the stress response at the individual level, we retained the individuals' scores on the first Principal Component (PC1) from the above PCA as a descriptor of an individual's overall stress response. We found that the best model describing variation in individual body mass included the PC1 (AICc weight 0.80, Δ AICc to constant model = 3.43). Body mass increased with increasing values of the PC1 score ($R^2 = 0.57$), suggesting that heavier individuals expressed a more acute stress response (high rectal temperature, high behavioral score, high hematocrit level, low N/L ratio) compared to lighter individuals (Fig. 2).

4. Discussion

Our overall aim was to quantify inter-individual variation in the stress response in captive roe deer and to explore the link between this variation and individual condition or quality. Firstly, we showed that the four stress response parameters, rectal temperature, behavioral score, hematocrit level and N/L ratio, were all highly repeatable across seasons, indicating that the stress response of individuals appears to be consistent over time. From a meta-analysis, Bell et al. (2009) reported that behavioral traits are generally repeatable, with an average value of 0.37, whereas the repeatability of our behavioral score was substantially higher ($r = 0.61$, 95% confidence of interval = [0.365, 0.790]). Published information on the repeatability of other stress parameters is scarce (Biro and Stamps, 2010; Szafranska et al., 2007). For instance,

although a stress-induced rise in temperature has been extensively studied on model organisms in controlled environments (Cabanac and Guillemette, 2001; Cabanac, 1975; Carere and van Oers, 2004; Moe and Bakken, 1997), consistency in this parameter was only clearly demonstrated recently in eastern chipmunks (*Tamias striatus*, Careau et al., 2011). In this study, repeatability of rectal temperature was somewhat lower than that of Careau et al. (2011) (0.24 vs. 0.40 respectively). However, the values that we obtained for repeatability of temperature and behavioral score were in line with those of previous studies on wild roe deer (Debeffe et al., 2015; Monestier et al., 2015), suggesting that measures of the stress response in captivity are representative of responses in the wild. For the haematological parameters, we demonstrated an extremely high level of consistency in hematocrit level, as was previously found in several taxa (Escribano et al., 2013; Hatch and Smith, 2010). However, we were unable to find any published information concerning repeatability of the N/L ratio. Indeed, our study is the first, to our knowledge, to provide estimates of individual consistency in this parameter for large ungulates. Finally, body mass was highly repeatable ($r = 0.79$, 95% confidence of interval = [0.575, 0.859]) which is consistent with the fact that body mass of adults is extremely stable over the year in roe deer (Hewison et al., 1996).

Second, as hypothesized, we identified considerable covariation among the behavioral and physiological parameters, suggesting a coherent overall stress response that may be interpreted within the coping style framework (Koolhaas et al., 1999), and strong evidence for substantial variation among individuals in the severity of this response. More precisely, rectal temperature, the behavioral score and hematocrit level were positively inter-correlated, whereas the N/L ratio was negatively correlated with these three parameters. Hence, within the coping style context, we identified a stress response gradient from reactive to proactive individuals, where the most proactive individuals have a higher hematocrit level, a higher behavioral score and a higher rectal temperature, but a lower N/L ratio, compared to more reactive individuals. These results are consistent with Koolhaas et al. (2010, 1999)'s studies where proactivity seems principally to depend on the sympathetic axis (Koolhaas et al., 2010, 1999) which notably involves a rapid increase of hematocrit in the blood in response to a stressful event (Koolhaas et al., 1999; Stockham and Scott, 2013; Weiss and Wardrop, 2011). A positive correlation between rectal temperature and the behavioral score was also previously interpreted in terms of a proactivity-reactivity gradient in a wild roe deer population (Monestier et al., 2015). Interpretation of the N/L ratio is rather more complicated because the response depends on the time lag between the stressful event and blood sampling. In our study, this lag was 40 min, on average, which is inferior to the latency period before which lymphocyte abundance is known to sharply decrease (see Montané et al., 2007 for roe deer). Consequently, the N/L ratio that we measured likely reflects the level of chronic stress expressed by the individual, rather than acute stress response to the capture event. In this case, the observed negative correlation of the N/L ratio with rectal temperature, the behavioral score and hematocrit level suggests that an individual with a higher basal N/L ratio (i.e. more chronically stressed) expressed a lower response to an acutely stressful event. This provides support for the hypothesis that when individuals must respond to repeated stressors and/or to a stressor for a long period of time (i.e. chronic stress), they are less able to adequately respond to a given acute stressor than individuals that are not chronically stressed (Romero et al., 2009).

Finally, we found evidence for a link between the overall stress response of an individual and its body condition such that body mass was higher among individuals that expressed a more marked overall stress response. That is, heavy individuals had a higher rectal temperature, a higher behavioral score, a higher hematocrit level and a lower N/L ratio. We suggest that proactive individ-

uals achieved higher body mass, despite equal access to feeding resources under captive conditions, due to a more persevering feeding tactic whereby they were more apt to feed than reactive individuals, even when disturbed. It is generally recognized that proactive individuals are more aggressive and bolder than reactive animals (Koolhaas et al., 2010, 1999; Réale et al., 2010). Consequently, they take more risk, notably to access resources of better quality, but may pay a cost in terms of survival for example (Smith and Blumstein, 2008). For example, in agricultural landscapes, the quality of food resources for roe deer is far better in open habitats (Abbas et al., 2011), hence, they achieve higher body mass than individuals living in forest habitat (Hewison et al., 2009). However, perceived risk (disturbance, predation) is likely higher in open than in closed refuge habitats such as forest (Mysterud et al., 1999a,b) so that only bolder individuals are able to tolerate this higher risk in order to exploit high quality resource patches (Bonnot et al., 2015). Indeed, consistent individual differences in energy metabolism might promote consistent individual differences in behavioral traits (Biro and Stamps, 2008; Careau et al., 2008) which are also linked to their performance (Biro and Stamps, 2008). Thus, individuals with a high basal metabolic rate may be more aggressive, active, dominant or bold (see Biro and Stamps, 2010 for a review), especially in contexts related to food acquisition, resulting in faster growth (i.e. larger size, higher mass) and higher fecundity (Biro and Stamps, 2008). Finally, chronic stress may lead to a decline in body mass (Boonstra, 2013) which may also explain why individuals with a higher N/L ratio (interpreted as a chronic stress response) had lower body mass than individuals with a higher acute stress response (and so a lower N/L ratio).

To conclude, we suggest that consistent individual differences in energy metabolism and physiology may promote consistent individual differences in behavioral traits, providing a mechanistic link between food acquisition tactics and demographic performance. A better understanding of these mechanisms and their consequences for individual fitness will shed light on the maintenance of behavioral variation in wild populations.

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