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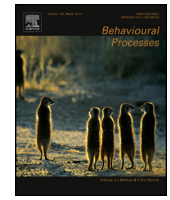

Individual variation in an acute stress response reflects divergent coping strategies in a large herbivore

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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.

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; Dingemanse et al., 2004; Dingemanse 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 adaption 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 neurophysiological 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 (Dingemanse 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 (Toïgo 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