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Testing for the presence of coping styles in a wild mammal

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Coping styles represent alternative response patterns in reaction to a stressor. The coping style model provides a set of predictions about correlations between behavioural and neurophysiological reactions to a stressful situation. According to this model, high levels of activity should be correlated with high levels of aggressiveness at the behavioural level, and to high sympathetic reactivity, low parasympathetic reactivity (higher heart rate levels) and low hypothalamus–pituitary–adrenocortical (HPA) axis reactivity (low production of glucocorticoids in response to a stressor). More recent versions of the model, however, are challenging this view and consider the possibility of independent axes of coping style and stress reactivity. The coping style model has mainly been tested on artificially selected or inbred lines in laboratory settings. Such a situation restricts its generalization to a larger number of species and there is a need for studies testing it in the wild under more natural situations. Here, we test the predictions of the coping style model in a wild alpine marmot, *Marmota marmota*, population. We show that several behavioural (i.e. exploration in an open field, impulsivity and docility) and neurophysiological traits (i.e. heart rate, breathing rate and cortisol production) assumed to represent individual differences in coping style were significantly repeatable over 2–3 years. Not all the correlations between traits predicted by the coping style model were found in marmots, which supports the more recent two-axes model. Furthermore, most correlations were observed at the between-individual level, and the within-individual correlations (i.e. phenotypic plasticity) were weaker. Overall, our results support the prediction of the coping style model, but highlight the fact that the association between traits found in artificial conditions may be weaker in a more natural setting.

Coping styles are defined as alternative response patterns to a stressor (Koolhaas et al. 1999, 2010). Conceptual studies on coping style generally assume that the coping style model is represented by a set of strongly intertwined traits representing two different strategies: the proactive and the reactive type (Koolhaas et al. 1999; Groothuis & Carere 2005; Ellis et al. 2006; Cockrem 2007). According to these studies, we should find strong correlations between physiological and behavioural reactions to a stressor. Compared to reactive individuals, proactive individuals are fast explorers, highly aggressive, actively avoid stressors form routines easily and show little flexibility and sensitivity to cues in their environment (Koolhaas et al. 1999, 2010). Links between the expression of coping styles at the behavioural and neurophysiological levels have been described for several model species (e.g. *Mus musculus* and *Rattus norvegicus*: Koolhaas et al. 1999; Veenema et al. 2003), and more recently in artificially selected strains of wild species (e.g. *Parus major*: Drent et al. 2003; Carere et al. 2003; Stöwe et al. 2010; *Taeniopygia guttata*: Roberts et al. 2007; *Oncorhynchus mykiss*: Øverli et al. 2005). Proactive individuals (i.e. bold, active and aggressive animals) are assumed to show high sympathetic reactivity and low parasympathetic reactivity, leading to an increase in noradrenaline concentration in the blood, and a high but consistent heart rate under stressors (Koolhaas et al. 1999; Ellis et al. 2006). Proactive individuals are thus assumed to actively cope with the source of stress through a 'flight-or-fight' response. In contrast, reactive individuals (i.e. passive, shy and minimally aggressive) show the opposite physiological patterns and tend to react by freezing (Koolhaas et al. 1999). Compared to reactive individuals, proactive ones are assumed to show lower hypothalamus–pituitary–adrenal (HPA) axis activity and reactivity (Koolhaas

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et al. 1999; Ellis et al. 2006). As a consequence, proactive individuals show lower basal glucocorticoids levels (e.g. cortisol or corticosterone) and lower increases in these hormones under a restraint test than reactive individuals (Carere & van Oers 2004; Cockrem et al. 2009; Koolhaas et al. 2010). In an updated version of their model, Koolhaas et al. (2010), inspired by Steimer et al. (1997), proposed the existence of two independent axes: coping style and stress reactivity. In other words, behavioural reaction in an open-field (i.e. level of exploration/activity) and docility may reflect coping style and may not be related to glucocorticoid response to a stressor (called stress reactivity in Koolhaas et al. 2010 or fearfulness in van Reenen et al. 2005).

A good description of the relationships between facets of coping styles at the neurophysiological and behavioural levels is necessary to understand the mechanisms underlying consistent behavioural differences among individuals in a population (Koolhaas et al. 1999) and to generalize the occurrence of coping strategies across taxa. Most of the work on coping styles identification in animals has been done on artificially selected strains, under controlled laboratory conditions (Koolhaas et al. 1999; Veenema et al. 2003; Øverli et al. 2005; Martins et al. 2007; Roberts et al. 2007). Field tests of the coping style model are much rarer and in most cases, have been conducted on semifree-ranging populations (Rödel et al. 2006; Kralj-Fiser et al. 2007; Hoffman et al. 2011). The artificial selection approach has the advantage of highlighting the contrasts between the two most extreme phenotypes/genotypes of a population, and to establish clear genetic correlations between the traits under selection and other traits (Falconer & Mackay 1996; Fuller et al. 2005).

Practical issues may explain the absence of tests of coping styles in the field: for example, noise caused by the presence of multiple uncontrolled stressors in the wild may hide the patterns of association among traits, or (co)variation in coping styles may not be as high as shown in artificially selected strains. Natural selection, the main driver of the evolution of associations among behavioural and physiological traits, is, however, assumed to work on coping styles at the phenotypic level, with consequences on these associations at the genetic level (Sih et al. 2004; Réale et al. 2007). Field studies are thus necessary to test whether coping styles are observed in natural conditions and still potentially the target of natural selection (Réale et al. 2007; Dingemanse & Réale 2011). Furthermore, the binomial distribution of coping styles (i.e. a proactive and a reactive type) may only result from the way the lines are artificially selected and this dichotomy may not always be found in natural populations (Réale et al. 2007). Field studies are also needed to generalize the coping style model to species that cannot easily be studied in captivity.

In this work, we test the coping style model in a wild population of alpine marmots, *Marmota marmota*. We examined whether consistent with this model, different behavioural and neurophysiological traits previously reported as expressions of coping styles in other models: (1) show consistent interindividual differences and (2) are correlated with each other at the between- and within-individual level. We measured the reactions of individuals to a novel environment using the open-field test adapted to sciurids (Boon et al. 2007; Martin & Réale 2008; Montiglio et al. 2010), and the reactions of individuals towards handlers, as an index of docility (Réale et al. 2000; Boon et al. 2008). We also measured several physiological reactions to stressful situations, namely cortisol production, heart rate and breathing rate under restraint. According to Koolhaas et al. (1999), proactive individuals are expected to be characterized by greater activity in the open-field, less docility, greater heart and breathing rates, and lower cortisol production under restraint, and that reactive ones will be at the other end of the spectrum of traits. Alternatively, in the updated two-tier model presented by Koolhaas et al. (2010; see also Steimer et al. 1997; van Reenen et al. 2005), open-field activity, docility, heart rate and breathing rate are not expected to be correlated with stress reactivity, measured as the cortisol response to a stressor.

Individual traits can be plastic, and plastic (co)variation at the within-individual level may reflect patterns of covariation at the between-individual level (van de Pol & Wright 2009). Differences between the within-individual correlation and the between-individual correlation may lead to a null correlation at the phenotypic level. Therefore, studies on coping style or behavioural syndromes using a phenotypic correlation approach may not be able to detect important patterns (Dingemanse & Dochterman 2012). We measured traits on 146 marmots captured repeatedly over 3 successive years. This design allowed us to use bivariate mixed models (Hadfield 2010) to estimate the (co)variation among traits at the within- and between-individual levels, and at the group level. This approach allows one to analyse data collected at different levels of aggregation and highlight different outcomes of selection on coping styles (van de Pol & Wright 2009). Separate estimates of within- and between-individual covariation provide a way of disentangling reversible environmental influences (i.e. within-individual) and permanent effects (e.g. genetic, maternal, or early environment) responsible for the association between two traits (Hadfield 2010). In this study we used bivariate models with a Bayesian approach, providing a new way to analyse coping style.

METHODS

Model Species and Study Area

Alpine marmots are large, diurnal, burrow-dwelling rodents inhabiting high alpine and subalpine meadows in Europe (Perrin et al. 1993). The basic social unit is a family group of 2–20 individuals composed of a territorial dominant breeding pair, mature subordinates (2–4 years old), yearlings and pups (Perrin et al. 1993; Allainé 2000). We will refer to these social units as colonies hereafter. Alpine marmots spend half of the year hibernating underground inside the group burrow and are active above ground from mid-April to mid-October (Arnold 1988; Perrin et al. 1993). The study area was located in Orvieilles (Valsavarenche, Aosta, Gran Paradiso National Park, North Western Italian Alps, 45°34′N, 7°11′E) at an altitudinal range of 1900–2400 m. The alpine meadow was characterized by coloured fescue (*Festuca varia*) and alpine meadow grass (*Poa alpina*). Natural predators, such as golden eagles, *Aquila chrysaetos*, and red foxes, *Vulpes vulpes*, are also present at high density in this region. In this area the marmot population has been studied since 2006 and most individuals have been marked and followed from birth (Ferrari et al. 2009; Pasquaretta et al. 2012).

Capture and Timeline of the Protocol

We live-trapped a total of 146 individuals from May to July in 2007, 2008 and 2009 using 19 Tomahawk traps (150 × 30 × 30 cm, Tomahawk Live Traps, Hazelhurst, WI, U.S.A.) and horse fodder (Omolene, Purina, Gray Summit, MO, U.S.A.) as food bait. Traps were observed at a distance of 300 m and were checked constantly. Once a marmot was trapped, two people transferred it to an opaque handling bag within 5 min and transported it to the handling area (mean ± SE time from the capture to first manipulation = 17 ± 5 min). Once at the handling area we used the following standard protocol for all marmots. No more than three people worked simultaneously, including one operator, who kept the marmot quiet inside the handling bag during the entire operation.

(1) A first blood sample (2 ml) was collected to measure cortisol (CORTISOL1 hereafter; see below).

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