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Independence between coping style and stress reactivity in plateau pika

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ABSTRACT

The concept of coping style represents the way individual animals react to a stressful situation, both behaviourally and neurophysiologically. Over the last decades coping style has been linked to the development of research on animal personality. Based on this concept, we should find a proactive-reactive continuum in animal populations, with proactive individuals being fast explorer, bold, aggressive, and show high sympathetic reactivity (higher heart rate), as well as low hypothalamus-pituitary-adrenocortical (PHA) axis reactivity to external stressor (higher plasma glucocorticoid level). At the other extreme, shy, lowly aggressive, reactive individuals should be slow in their exploration, and show a low sympathetic reactivity and a high HPA axis reactivity. However, a recent two-tier model proposed that coping style and stress reactivity should be independent of each other. In this study, we tested the two-tier model in a wild plateau pika (*Ochotona curzoniae*) population on the Tibetan Plateau, by quantifying the associations between several behavioural and physiological traits at the among- and within-individual levels. We repeatedly measured exploration, docility, boldness, heart rate and plasma cortisol concentration in individuals between April and September of 2013. All traits tested were repeatable. At the among-individual level, all behavioural traits were correlated with each other and with heart rate, but were independent of both basal level and variation of plasma cortisol concentration. Most correlations were negligible at the within-individual level. In support of the two-tier model, these results suggest that coping style (i.e. behaviour and heart rate associations) is independent of stress reactivity (i.e. glucocorticoid reactivity) in that species.

1. Introduction

Animals regularly face challenges in their life [1]. Food can be difficult to find and when it is found it may need to be defended [2]. Reproduction often requires that individuals either monopolise areas containing resources or sexual partners [3]. Predators may attack at any moment, and when they attack, fight or flight decisions make the difference between life and death [4,5]. It has been proposed that individuals differ in a consistent way in their behavioural and physiological responses to these challenges and that these responses are associated with each other to form different coping styles [6]. In support of this model, an increasing number of studies have found consistent differences among individuals in behaviour traits across time and situations [7,8]. Correlations between behavioural traits have also been found in many taxa, and they are generally organised along a proactive (i.e. bold, highly active, and aggressive individuals) / reactive (i.e. shy, lower active, and less aggressive ones) continuum [2,9–11]. In addition, several studies have shown links between animal behaviour and physiological responses to a stressful situation. Differences in glucocorticoid concentrations in response to stress have also been reported to be repeatable [12–15] or heritable [16], and proactive individuals have been found to produce less glucocorticoids than reactive ones in several studies [9,14,17]. In addition, studies in both vertebrates and invertebrates have reported that a positive link between boldness and activity, and heart rate, a proxy for sympathetic autonomic reactivity [7,14,18]. This has led Koolhaas et al. [6] to consider that coping style was represented by one full syndrome of behavioural and physiological traits (see also Sih et al. [19] for behavioural syndromes).

However, with their more recent the two-tier model, Koolhaas et al. [20] have proposed a new organisation of the response of animals to stressful situations, with two independent dimensions: on one hand, coping style would represent individual differences along a proactive-

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reactive axis composed of several behavioural traits (such as activity, exploration, boldness and aggressiveness) and the reactivity of the sympathetic autonomic nervous system; on the other hand, the activity of the hypothalamic-pituitary-adrenal axis (HPA), and the production of glucocorticoids would represent stress reactivity, a second independent dimension to coping style [20,21]. In support of this model, a few recent studies have found independent reactions of the HPA axis and behaviour traits [12–14,22,23]. It is therefore equivocal yet whether coping style and stress reactivity form one same and unique continuum or if individuals can be distributed along two independent dimensions of stress reaction.

The reasons for studying trait associations into a syndrome are both related to their proximal and ultimate causes. From a proximal point of view, traits involved in coping styles or behavioural syndromes may form modules of phenotypically, genetically, physiologically, and developmentally associated traits [19,24], and studying these associations may help us understand the causal pathways that lead two traits to be associated or not. From an ultimate point of view, traits within a module are assumed to be involved in the same biological function and thus to have coevolved as a result of natural selection, which itself supposed to have led to and to have maintained independence of traits belonging to different modules or biological functions [25]. However, studies of the modularity of behaviour and physiological traits that would permit to understand how these traits are involved in one or more stress response modules are still lacking.

The first step to study modularity is to analyse the sources of covariance between traits. Covariance between two traits at the phenotypic level can be decomposed into an among- and a within-individual component [26]. The among-individual component corresponds to differences in the average individual levels of the trait, and is caused by genetic, permanent environmental, and maternal effects affecting the phenotypes of both traits in a constant manner; the within-individual component corresponds to the combined response of the two traits to changes in the environment and results from phenotypic plasticity and measurement errors [27]. Covariance estimates between behavioural traits are often reported at the phenotypic level. However, phenotypic covariance may hide important associations, when its two components, the among- and the within-individual covariance, show antagonistic patterns [13,28]. The two components of covariance thus reflect totally different biological phenomena: the among-individual correlation component represents behavioural syndromes and is important for the study of coevolution of integrated traits, whereas within-individual component reflects integrated phenotypic plasticity of traits under identical environmental changes [27]. Partitioning phenotypic covariance into among- and within-individual correlation is thus important to study the ecological and evolutionary processes of traits (co)variation [28]. However, only a few studies have provided estimates of covariance or correlation at the three levels [10,13,14].

In this study, we tested whether the behavioural and physiological responses of plateau pikas (*Ochotona curzoniae*) to challenges are associated following the two-tier model of coping style and stress reactivity [12,14,15,20]. Plateau pika is a dominant lagomorph which is the primary prey for almost all predators on the plateau [33], thus, it bears high predation stress and is a good species to test the two-tier model. We repeatedly measured behavioural and physiological traits widely used in personality studies [7,10]: we used the reaction in an open-field arena as an index of exploration, behavioural reaction and heart rate under restraint as indices of docility and of reactivity of the sympathetic nervous system, respectively. Furthermore, we measured flight initiation distance over the summer as an index of boldness [4]. We measured plasma cortisol from repeated blood samples as an index of the reactivity of the Hypothalamic-pituitary-adrenal (HPA) axis [29]. First, we tested whether behavioural and physiological traits were repeatable over the summer (i.e. analysis of the relative importance of among- vs within-individual variance). Second, we tested whether behaviour traits were correlated to heart rate and plasma cortisol concentration. Following the two-tier model we expected that boldness (i.e. undocile, fast explorers with short flight distance) was positively related with heart rate, but not related to either baseline plasma cortisol concentration or changes in cortisol concentration during an acute stress (Table 1). Using repeated measures on individuals over the whole summer, we decomposed the phenotypic variance and correlations into an among-individual and a within-individual component and tested whether the traits were repeatable and the correlations occurred among individuals rather than within individuals [12,14]. Finally, using structural equation modelling (SEM) we compared different scenarios of covariance among different behavioural and physiological traits and tested for the occurrence of modularity between behavioural and physiological reactions to environmental challenges.

Table 1
The summary of previous findings about the correlations between pairs of behaviour and physiological traits.

	Docility	Boldness	Heart rate	Body mass
Exploration	– [7,13,26]	+ [7]	+ [7,14]	+ [59–61]
Docility		– [18]	– [18]	– [4,14], + [59]
Boldness			+ [18]	– [4], + [59,60]
Heart rate				None [14]

Note: +, −, none represent positive, negative and non-significant correlations, respectively.

2. Methods

2.1. Study species and study site

The plateau pika (henceforth, pika) is a small diurnal lagomorph, that is widely distributed in alpine meadows of the Tibetan Plateau [30]. Pikas have evolved for > 1.2 million years in this region with the uplift of the plateau [31]. Their preferred habitat is low alpine meadows characterised by short vegetation (3–5 cm) and deep soil where they can dig burrows [32]. Pikas dominate the Tibetan alpine ecosystem, whereas the other small-sized herbivores, including the woolly hare (*Lepus oiostolus*), the Himalayan marmot (*Marmota himalayana*), and the plateau zokor (*Myospalax baileyi*), are patchily distributed and encountered infrequently. Pikas represent the primary prey for most predators in the area [33].

This study was conducted on an alpine meadow, 17 km southeast of Dawu, Guoluo, China (34°24′ N, 100°21′ E, 3946 m) during the breeding (25th April–12th June) and the non-breeding (20th August–12th September) seasons of 2013. The study site was a 200 m × 200 m grid dominated by *Kobresia humilis* and grazed by sheep and yaks all year long. The main predators of pika, including upland buzzards (*Buteo hemilasius*), red foxes (*Vulpes vulpes*), and Tibetan foxes (*V. ferrilata*), are commonly seen in this area. See Qu et al. [34] for more details on the study site and our long-term research (since 2005) on the life history of individually-marked pikas [35].

2.2. Pika trapping

Pikas were live-trapped using string nooses anchored at burrow entrances with chopsticks [32]. Traps were set near all the burrow entrances in the study site to enhance the capture probability. Four assistants helped to set and monitored about 50 traps at the same time. Traps were set from ~07:00 until ~12:00 and monitored from 30 m away. Trapped pikas were removed from the nooses within ~3 min after captured and brought to a central location (around 30 m away) where we recorded their ID, trapping location, sex, and age. Soon afterwards, pikas were gently transferred into a cylinder-shaped, cotton handling-bag, weighted with a hand-held spring balance to the nearest 2 g (Pesola, Switzerland). Pikas captured for the first time were individually marked using ear tags (i.e., ID) and two plastic-coloured