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A comparison of animal personality and coping styles in the red junglefowl

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There is an increased focus in biology on consistent behavioural variation. Several terms are used to describe this variation, including animal personality and coping style. Both terms describe between-individual consistency in behavioural variation; however, they differ in the behavioural assays typically used, the expected distribution of response variables, and whether they incorporate variation in behavioural flexibility. Despite these differences, the terms are often used interchangeably. We conducted experiments using juvenile and adult red junglefowl, *Gallus gallus*, as subjects to explore the degree to which animal personality and coping styles overlap. We demonstrate that animal personality and coping styles can be described in this species, and that shyer individuals had more flexible responses, as expected for coping styles. Behavioural responses from both personality and coping style assays had continuous distributions, and were not clearly separated into two types. Behavioural traits were not correlated and, hence, there was no evidence of a behavioural syndrome. Further, behavioural responses obtained in personality assays did not correlate with those from coping style tests. Animal personality and coping styles are therefore not synonymous in the red junglefowl. We suggest that the terms animal personality and coping style are not equivalent and should not be used interchangeably.

Several terms are used to describe consistent between-individual variation in animal behaviour, such as 'animal personality' (Dall, Houston, & McNamara, 2004; Sih, Bell, Johnson, & Ziemba, 2004), 'coping style' (Koolhaas et al., 1999) and 'temperament' (Boissy, 1995; Clarke & Boinski, 1995; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Common features of animal personality and coping styles are that behavioural responses are expected to show consistent variation between and within individuals, and that this variation can be biologically meaningful. However, despite these similarities, there are fundamental differences in how behavioural variation and consistency are investigated, including the behaviours recorded, their distribution and the assays used to measure variation in behaviour.

Defining Animal Personality and Coping Styles

Animal personality is commonly defined as between-individual differences in behaviour that are consistent over time and/or across context (Dall et al., 2004; Sih, Bell, Johnson, & Ziemba, 2004; Table 1). Wild and captive animals of both sexes have been studied in stressful and not stressful situations, and variation in activity, aggression, boldness, exploration and sociability are described for multiple taxa (Carere & Maestripieri, 2013; Gosling, 2001; Réale et al., 2007). A coping style is typically defined as a set of correlated behavioural and physiological stress responses that are consistent over time (Koolhaas et al., 1999; Table 1). In contrast to studies of personality, laboratory male rodents have been the main focus of coping style studies (Carere, Caramaschi, & Fawcett, 2010; but see e.g. Castanheira et al., 2015; Table 1). Coping styles differ somewhat from the broader definition of animal personality by describing behavioural strategies to handle stressful situations in which several behaviours are intercorrelated and correlate with physiological mechanisms, such as stress response and androgen levels (e.g. Castanheira et al., 2015; Cervantes & Delville, 2007; Coppens, de Boer, & Koolhaas, 2010; Koolhaas, de Boer, Coppens, & Buwalda, 2010; Koolhaas et al., 1999; Øverli, Sørensen, Pulman, Pottinger & Korzan, 2007). In contrast, physiological measures are rarely included in descriptions of personality, although a few studies relate variation in personality to stress physiology (Baugh, Schaper, Hau, Cockrem, & Goede, 2012; Cockrem, 2007; Kralj-Fišer, Weiß, & Kotrschal, 2010). Furthermore, personality traits

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Table 1
A comparison of similarities and differences between 'animal personality' and 'coping styles'

	Animal personality	Coping style
Definition	Between-individual behavioural differences consistent over time and/or across context (1, 2)	A coherent set of behavioural and physiological stress responses (3)/ characteristics (4) consistent over time (3) and over context (4)
Subjects	Wild and captive species ranging from insects to primates. Often research is conducted on both sexes (1)	Primarily (but not only (3)), male rodents in a laboratory setting (4)
Assays used	Exposure to unfamiliar or familiar environments, novel objects, simulated predators, conspecifics (1, 2, 9). Tonic immobility test (6)	Exposure to unfamiliar or familiar environments, novel objects, conspecifics, electrical probe (3). Operant conditioning tasks, where after reaching a stable task performance, the reaction to a small change is studied (5, 4). Back test or tonic immobility test (7, 8)
Response types	Spontaneous behaviour, often when exposed to some challenge	Spontaneous behaviour or reactions to changes in operant tests. Reactions to challenges (4) that allow different response patterns (5)
Response gradients	Shyness-boldness, exploration–avoidance, activity, aggression, sociability (1)	Proactive–reactive (4), aggression (5), active–passive response to test situation, aspects of initiative (3)
Response structure	Quantitative, normally distributed responses along a unidimensional gradient ((1), but see 'behavioural syndromes' (9))	Multidimensional, correlated gradients with both qualitative and quantitative aspects (5, 4), clustered in reactive–proactive phenotypes (3, 5, 4). Responses are typically bimodal or non-normal (3)
Flexibility	Personality can partly be explained by limitation in behavioural flexibility (2, 9), and behavioural flexibility is complementary (11, 12) or a separate personality gradient (13)	Behavioural flexibility is typically included as an important aspect (3, 4, but see 10 for when it is not). Reactive individuals are more flexible, and proactive individuals have stronger routine formation (3, 4)

Source: (1) Réale et al., 2007; (2) Dall et al., 2004; (3) Koolhaas et al., 1999; (4) Coppens et al., 2010; (5) Koolhaas et al., 2010; (6) Brust et al., 2013; (7) Bolhuis et al., 2004; (8) Forkman et al., 2007; (9) Sih, Bell, Johnson, 2004; (10) Øverli et al., 2007; (11) Dingemanse et al., 2010; (12) Wolf et al., 2008; (13) Carter et al., 2012.

can be intercorrelated and form 'behavioural syndromes' (Sih, Bell, Johnson, & Ziemba, 2004; e.g. great tits, *Parus major*, Verbeek, Boon, & Drent, 1996), but do not necessarily do so (e.g. three-spined stickleback, *Gasterosteus aculeatus*, Dingemanse et al., 2007; checkered pufferfish, *Sphoeroides testudineus*, Pleizier, Wilson, Shultz, & Cooke, 2015; fowl, *Gallus gallus* ssp., Favati, Leimar, & Løvlie, 2014; Favati, Leimar, Radesäter, & Løvlie, 2014; Favati, Zidar, Thorpe, Jensen, & Løvlie, 2016).

Distribution of Behavioural Traits

In contrast to the continuous distribution of most personality traits, coping styles were initially typically described as two distinct phenotypes; proactive and reactive, often with opposing behavioural and physiological features (for review, see Coppens et al., 2010; Koolhaas et al., 1999, 2010). It is often shown that reactive individuals respond passively by withdrawing from stressful situations ('conservation/withdrawal'), i.e. they try to avoid the stressor. Proactive individuals instead show an active approach ('fight/flight'), i.e. trying to counteract the stressor (for review, see Koolhaas et al., 1999; Øverli et al., 2007). Reactive individuals also tend to be more flexible and aware of environmental changes, whereas proactive individuals tend to be more rigid in their behaviour and easily form routines (e.g. mice, *Mus musculus*, Benus, den Daas, Koolhaas, & van Oortmerssen, 1990; pigs, *Sus scrofa*, Bolhuis, Schouten, de Leeuw, Schrama, & Wiegant, 2004; great tits, Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005, greylag geese, *Anser anser*, Kralj-Fišer, Scheiber, Blejec, Moestl, & Kotrschal, 2007).

Behavioural Flexibility

Both theoretical models (Coppens et al., 2010; Wolf, van Doorn, & Weissing, 2008) and empirical studies (e.g. mice, Benus et al., 1990; pigs, Bolhuis et al., 2004; rainbow trout, *Oncorhynchus mykiss*, Ruiz-Gomez, Huntingford, Øverli, Thörnqvist, & Höglund, 2011), support the hypothesis that behavioural flexibility is an important underlying aspect describing coping styles. Individuals that are less flexible are expected to be bolder and more proactive (Dingemanse, Kazem, Réale, & Wright, 2010; Koolhaas et al., 1999; Wolf et al., 2008). This has been observed, for example, in pigs where high resistance in the back test (describing proactive individuals) was negatively associated with behavioural flexibility (Bolhuis et al., 2004), and in rainbow trout where proactive individuals were less flexible in reversal learning (Ruiz-Gomez et al., 2011).

Behavioural flexibility has not traditionally been considered an important aspect of animal personality. More recently, individual plasticity has been discussed in relation to animal personality in the context of reaction norms (Dingemanse et al., 2010, 2012) and responsiveness (Wolf et al., 2008). Reaction norms describe individuals' differential responses to changes in the environment (e.g. perceived risk of predation, Dingemanse et al., 2010, 2012) and responsiveness describes flexible responses to varying situations (Wolf et al., 2008). Both reaction norms and responsiveness differ from coping style research where flexibility in specific (often operant) tasks is assessed (see below). Behavioural flexibility is therefore possibly an important aspect of animal personality, although this possibility has not yet been well explored empirically.

Behavioural Assays

Common personality assays include open field (arena without interior), novel arena (arena with interior encouraging exploration) and novel object tests (e.g. Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Carere & Maestripieri, 2013; Dingemanse et al., 2007; Réale et al., 2007; Walsh & Cummins, 1976). In these tests, the reaction of animals to novelty is measured.

Coping style assays can include the above as well as relatively more stressful tests such as responses to introduction of electric probes into the home pen (Koolhaas et al., 1999, 2010; Sluyter, Korte, Bohus, & van Oortmerssen, 1996) and forced swim tests (Koolhaas et al., 2010). Additionally, a commonly used test is the back test in which the individual is held on its back and resistance (Bolhuis et al., 2004) or latency to remain in tonic immobility, if that is induced, is measured (Forkman, Boissy, Meunier-Salaün, Canali, & Jones, 2007). However, the typical tests designed to capture coping strategies often include measures of responses to alteration of learnt tasks, often through maze or operant conditioning tests (Coppens et al., 2010).

In a maze test, the animal is typically trained to move through a maze to obtain a reward, and after it reaches a stable routine the maze is changed and the behavioural reaction of the animal is