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Boldness towards novel objects predicts predator inspection in wild vervet monkeys

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Although the number of studies documenting animal personalities has increased over the last decade, ecological validations of animal personality traits remain relatively rare in the behavioural ecology literature. I examined whether wild vervet monkeys, *Chlorocebus pygerythrus*, were consistent in their responses to diverse novel objects, and tested whether experimentally assayed boldness predicted the number of times individuals were observed inspecting naturally occurring snakes at close range. Boldness was repeatable across three novel object tests, and boldness scores were correlated with the number of snake inspections. An additional novel object, a toy lizard, elicited antipredator behaviour and was reclassed as a potential predator stimulus; both novel object boldness and the number of snake inspections predicted approach of this item. Age–sex class differences in boldness and in predator approach and inspection were found to be highly consistent across these different contexts. Subadult males were bolder than adult females and had higher snake inspection counts. These age–sex differences fit well with expected variation in risk–reward ratios of exploratory risk-taking behaviour considered within a life history framework for this species. The results of this study provide a crucial ecological validation of using novel object tests to assay boldness in a wild primate.

Interindividual behavioural variation that is stable over time, consistent across contexts and related to fitness outcomes has been documented in a number of taxa (Dall & Griffith, 2014; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih & Bell, 2008; Smith & Blumstein, 2008). The majority of studies on animal personality have, however, been conducted in captive populations or with wild-caught individuals held and assayed in a captive setting. Since captive environments may have substantial effects on the expression of behaviour, ecological or evolutionary interpretations of these studies' results may be problematic (Archard & Braithwaite, 2010; McCowan, Mainwaring, Prior, & Griffith, 2015; McPhee, 2004; Niemelä & Dingemanse, 2014). It is therefore important to validate personality traits in wild populations by testing animals in their natural habitats (Niemelä & Dingemanse, 2014).

Recently, several researchers have criticized the lack of validation testing in most studies of animal personality within behavioural ecology (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Dochtermann & Nelson, 2014; Uher, 2011; Weiss & Adams, 2013). Validation of personality measures is a standard procedure in personality studies conducted in other fields (e.g. comparative psychology), along with assessments of repeatability or reliability (Gosling, 2001; Weiss & Adams, 2013). Testing the validity of animal personality traits can be undertaken by comparing measurements from multiple tests that target a given trait or by comparing different methods of assessing the given trait, for example by testing for correlations between behaviour in a test setting and observations of naturalistic behaviour (Carter et al., 2013; Gosling, 2001; Weiss & Adams, 2013). Other factors also considered to support the validity of personality traits are correlations of personality measures with markers of neurobiological or physiological functioning, with health outcomes, or with certain life history variables (Fairbanks & Jorgensen, 2011; Gosling, 2001; Weiss & Adams, 2013). Réale et al. (2007) suggested that behavioural ecologists should be concerned with both biological and ecological validation of personality traits, where the former involves testing for relationships between personality and aspects of physiology and the latter for ecological correlates. Ecological validation of personality traits, such as establishing that these

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phenotypes are correlated with other traits of ecological significance (e.g. dispersal, home range size), is an integral step in studying the ecology and evolution of personality in natural populations (Réale et al., 2007).

One example of a personality trait for which biological validity (but not ecological validity) is well established is that of 'novelty seeking' in captive vervet monkeys, *Chlorocebus sabeaus* (Fairbanks & Jorgensen, 2011). Individual differences in captive vervets in responses to novel objects (commonly referred to as 'boldness' in the animal behaviour literature) are repeatable and highly heritable and are further associated with a polymorphism in the dopamine D4 receptor gene (Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007; Fairbanks et al., 2011). Novelty seeking is also correlated with cortisol levels measured in hair (which reflects long-term cortisol release), with bolder animals showing lower cortisol levels (Laudenslager, Jorgensen, Grzywa, & Fairbanks, 2011).

The aims of the present study were two-fold. The first aim was to test for repeatability of behavioural responses of wild vervet monkeys towards novel objects, in an attempt to validate behaviour observed in a laboratory setting against behaviour expressed in a natural setting. The second aim was to determine whether boldness towards novel objects among wild vervets is correlated with ecologically relevant behaviour of predator inspection. Boldness is generally defined as the propensity to take risks in the face of threatening and/or novel situations (Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Smith & Blumstein, 2008). Exploration of novel objects involves an inherent degree of risk taking, as stimuli that have never been encountered have the potential to be dangerous. Individuals that are more willing to approach or interact with novel objects are therefore also expected to show greater risk-taking behaviour in other situations, such as those involving exposure to potential predators. In animal personality studies, boldness is alternatively assayed using novel object tests or predator exposure tests (Carter et al., 2013). However, to date, few studies have investigated the relationship between individual differences in responses to novel objects and to predators or predator cues (Carter et al., 2013, 2012). Of the studies that have compared individuals' behaviour across these contexts, some have found correlations (e.g. David, Auclair, & Cézilly, 2011; Garamszegi, Eens, & Török, 2009), while others have not (e.g. Carter et al., 2012; Coleman & Wilson, 1998). These mixed findings could reflect interspecific differences (Garcia-Longoria, Garamszegi, & Moller, 2014), intraspecific variation between populations in different environments (Bell, 2005; Dingemanse et al., 2007), or methodological differences between studies in the tests they employ or in the specific behavioural variables that were measured (Carter et al., 2013; Gosling, 2001; Uher, 2011). However, the most common concept of boldness, which combines elements of risk taking and exploration, leads to the expectation that variation in behaviour towards potentially threatening novel stimuli will also be expressed in contexts involving non-novel but motivationally salient stimuli, such as predators or other animals that pose risks of injury or mortality to an animal.

Here I test the hypothesis that boldness in terms of novel object responses reflects a personality trait in wild vervet monkeys, *Chlorocebus pygerythrus*, and that this trait is correlated with predator inspection behaviour. I predicted that individuals would be consistent in their responses to different novel objects, and that boldness towards novel objects would predict approach and inspection of a novel predator model in a test context. I also predicted a relationship between boldness and the number of times that individuals inspected naturally occurring snakes under naturalistic conditions. I further explored sex and age differences in boldness and predator inspection, including exploring the consistency of patterns of age–sex class differences across contexts. Finally, given a relationship between dominance rank and some aspects of behaviour in vervet monkeys (Cheney & Seyfarth, 1992), I additionally explored whether boldness towards novel objects was related to dominance rank in the study population.

METHODS

Study Site and Subjects

The study was conducted in the Soetdoring Nature Reserve in the Free State Province, South Africa (28°50′S, 26°2′E). The region has an arid steppe climate (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006), with rainfall averaging 400–600 mm per annum (Janecke, 2002). The predominant vegetation is grassland, with riparian vegetation dominated by *Acacia karoo* occurring along the river that bisects the reserve (Janecke, 2002; Janecke & du Preez, 2005). Several vervet monkey troops are found in the reserve, and two of these (a large group averaging ~60 individuals over the course of the study, and a small group averaging ~20) were followed and habituated to human observers. The study subjects were all adult and subadult individuals in each group (Table 1), all of whom were individually recognizable based on distinctive facial and body features. Juveniles were not all individually recognizable and are not included in this study.

Following previous studies in vervets (e.g. Isbell & Pruetz, 1998; McDougall, 2010; van de Waal, Borgeaud, & Whiten, 2013), I classified females as adults after they had given birth. At the beginning of the study, multiparous females were recognized on the basis of their elongated nipples, indicative of having previously nursed offspring. Subadult females were recognized by their larger body size compared to juveniles. Five of the seven females classified as subadults in early 2012 gave birth in late 2012 during the period of novel object tests and snake inspection observations. The age classification of these females therefore varied over the relevant study period, but for simplicity they are treated as adults in analyses. Adult males were recognized on the basis of a large body size and fully developed testes, and subadult males were those males that were the same size as or larger than adult females, but smaller than adult males and with smaller testes.

The vervet troops under study subsisted on an almost exclusively natural diet, with seeds, leaves, flowers, berries, gum and insects forming the bulk of their diets. Infrequently eaten foods included eggs, small birds, honeycomb, small lizards and food scraps found in refuse bins or on the ground at picnic sites in each group's home range. Soetdoring is a small provincial nature reserve, and visitors to picnic sites within the study groups' home ranges were uncommon. Human-made materials were occasionally seen in other parts of the reserve; these were generally plastic waste (e.g. plastic bottles, bits of plastic), which had washed down the

Table 1
Study subjects participating in each novel object test, by age–sex class

Age–sex class	Subjects	Plants	Grasshopper	Scorpion	Lizard[a]
Females					
Adult	22/21[b]	19	21	17	17 (11)
Subadult	2	2	2	2	2 (2)
Males					
Adult	7	6	6	6	6 (3)
Subadult	9	7	8	9	9 (7)
Total	**40/39**[b]	**34**	**37**	**34**	**34 (23)**

[a] Numbers in parentheses show the number of individuals who first saw the lizard from at least 1 m away.
[b] One of the adult females disappeared from the large group in mid-November; she was present for the plants test, but not for any of the other novel object tests.