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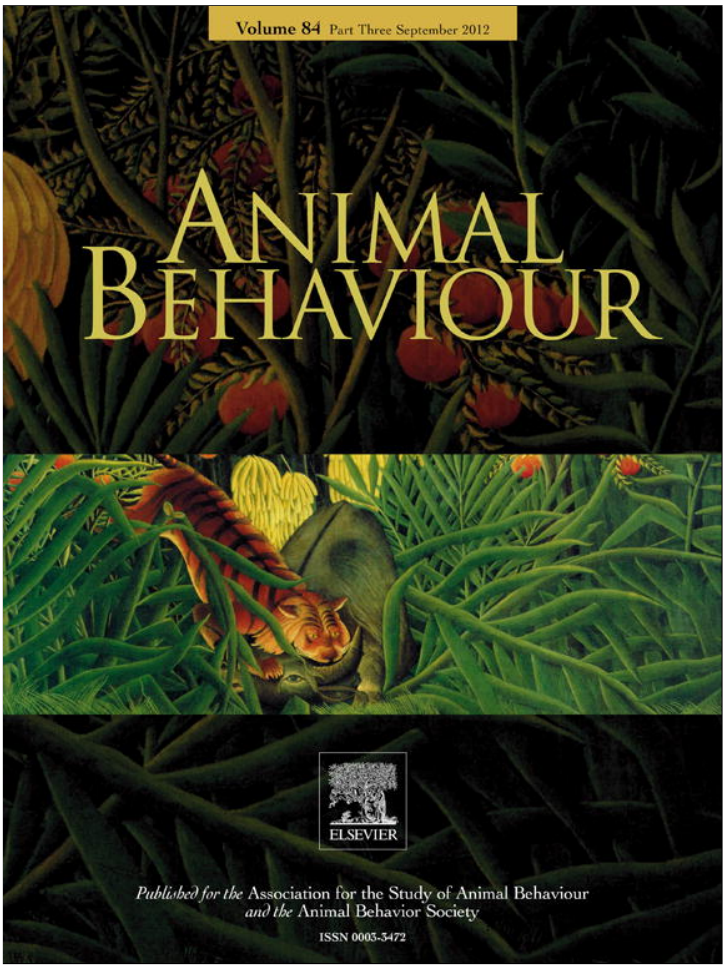

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How not to measure boldness: novel object and antipredator responses are not the same in wild baboons

Alecia J. Carter [a,b,*], Harry H. Marshall [b,c], Robert Heinsohn [a], Guy Cowlishaw [b]

[a] The Fenner School of Environment and Society, The Australian National University, Australia
[b] The Institute of Zoology, Zoological Society of London, London, U.K.
[c] Division of Ecology and Evolution, Department of Life Sciences, Imperial College London, U.K.

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Boldness in animal personality studies is measured using a range of different behavioural assays, including responses to novel objects, novel environments and threatening stimuli. These assays should be correlated if they all reflect boldness, but this assumption has rarely been tested. We investigated experimentally whether presentation of threatening stimuli (a taxidermic puff adder, *Bitis arietans arietans*) and novel object (an unfamiliar food item) both assayed the same personality trait in wild chacma baboons, *Papio ursinus*. We recorded individual responses to both the snake model and novel foods for 57 baboons encompassing all age–sex classes in two study troops over 3 years. Surprisingly, those individuals that showed the greatest alarm responses to the model snake, that is, the least bold responses, also inspected it for longer. Furthermore, individuals' threat responses did not correlate with their response to the novel food. Thus, boldness according to one definition was not related to boldness using another definition. We suggest that threat-directed behaviours did not reflect individual boldness, but instead were indicative of another personality dimension: anxiety. These findings highlight that current boldness assays may not be interchangeable, and in some cases may not measure boldness at all. We stress the value of using multiple assays to measure the personality trait of interest.
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Contrary to the expectation that flexible and responsive behaviour should be selected for within a population (Wilson et al. 1994), investigations into animal personality have found that individual behaviour tends to be consistent across contexts (Réale et al. 2007). Consistent, cross-context correlations in behaviour are particularly interesting from an evolutionary standpoint, as it may mean that some individuals employ suboptimal behaviour in some situations. For example, bolder male rock agamas, *Agama planiceps*, spend more time basking, which may lead to increased feeding rates compared with shy individuals; however, bolder individuals may also suffer higher predation as a result of spending less time hiding in shelters (Carter et al. 2010).

Boldness is one of the most commonly studied personality traits (Réale et al. 2007; Conrad et al. 2011) but is perhaps the trait with the least unanimous definition. Boldness has perhaps most often been interpreted as being the propensity to take risks, especially in novel situations (Coleman & Wilson 1998; Toms et al. 2010). However, others have defined boldness in alternative ways, such as an individual's response to a risky situation, excluding reactions to novel situations and stimuli altogether (e.g. Réale et al. 2007).

In light of the importance of risk in the concept of boldness, it is unsurprising that boldness is often assayed experimentally by predator-related behaviours. These can include activity under predation risk (Magnhagen & Borcherding 2008), latency to return to a feeder after a simulated predation event (Bell & Stamps 2004; reviewed in Sih et al. 2004a; Bell 2005) and time orienting towards and investigating a predator (Huntingford 1976; Bell et al. 2010). In these cases, bolder individuals are defined as those that are more active, return to a feeder faster and approach the predator more often. However, in reflection of the diversity of definitions, boldness is also frequently assessed through other means, including individual responses to novel objects (Mettke-Hofmann et al. 2005) and novel environments (Brown & Braithwaite 2004; Dingemanse et al. 2004), and by observer assessment under natural conditions (Wielebnowski 1999; Bergvall et al. 2011; Carter et al. 2012; these methods are reviewed in Gosling 2001; Vazire et al. 2007; Uher 2008a; Toms et al. 2010). This raises the question of how comparable boldness in a risky context might be to boldness measured in other contexts (Burns 2008; Toms et al. 2010). This is a significant question, because if these measures of boldness are not comparable, it raises the possibility of what psychologists term a 'jingle'

* Correspondence: A. J. Carter, Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.
E-mail address: ac854@cam.ac.uk (A. J. Carter).

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fallacy: that two traits that are labelled similarly may actually be very different in practice (Thorndike 1903; Block 1995). Block (1995) highlighted the fact that jingle fallacies are pervasive and misleading within differential psychology (the study of individual differences in behaviour), but this issue has received little attention in studies of animal personality in the field of behavioural ecology.

Evidence from behavioural ecology, however, is suggestive of existing but currently overlooked jingle fallacies. For example, Fox et al. (2009) suggested in their study of personality in the chickadee, *Poecile gambeli*, that novel object exploration and exploration of a novel environment are not interchangeable traits, as proposed by other researchers. Furthermore, Dingemanse et al. (2007) encountered a similar problem when attempting to assay boldness in the three-spined stickleback, *Gasterosteus aculeatus*, using antipredator behaviour. They measured the behaviour of sticklebacks when exposed to a predator housed in an adjacent compartment and compared this to behaviour when exposed to an empty compartment. The authors found no significant difference in stickleback behaviour between the experiment and the control, and relabelled this behaviour a measure of 'exploration − avoidance of a novel environment'. Importantly, if the control had not been carried out, it might have been interpreted that individuals showed a marked response to predators when in fact they were explorative. The study by Dingemanse et al. not only highlights the importance of using controls, but also that the phenomenon of incorrectly ascribing personality traits may be more common than anticipated in animal personality research.

Other studies have found mixed results. For example, a correlation between novel object exploration and emergence tests (i.e. latencies to emerge from a shelter into a novel environment) was found in a poeciliid fish, *Brachyraphis episcopi* (Brown et al. 2007), but no correlation was found between response to a novel food and response to a threat in the pumpkinseed sunfish, *Lepomis gibbosus* (Coleman & Wilson 1998). However, these studies did not directly investigate the correspondence between measures of boldness. We know of only one study that directly compared experimental assays of boldness to determine whether they were comparable. Burns (2008) tested guppies, *Poecilia reticulata*, in a novel object test and two types of novel environment test, and found that the novel object test did not correlate with either of the novel environment tests, suggesting that this was a different trait. There is thus a pressing need to investigate whether the different assays designed to measure boldness are actually measuring the same trait in practice (Burns 2008; Uher et al. 2011).

In this study, we explored whether behaviour in the presence of a threat might reflect boldness. We considered two such behaviours: threat-inspection behaviour and alarm responses. In the first case individuals in many group-living species often undertake seemingly paradoxical behaviours, such as approaching a threat to inspect it (Walther 1969; Dugatkin & Godin 1992b; Fishman 1999) or to mob it (Kobayashi 1994, 1996). However, these behaviours are thought to confer advantages through information gathering and risk assessment, or predator deterrence (e.g. Dugatkin & Godin 1992a, b; Fitzgibbon 1994). Predator inspection has received attention as a cooperative behaviour (for examples, see Dugatkin & Alfieri 1991; Dugatkin & Godin 1992b; Croft et al. 2006; Thomas et al. 2008), as it can provide advantages to group members at the expense of the inspecting individual (Dugatkin 1992; Fitzgibbon 1994; but see Godin & Davis 1995), which suggests that inspecting individuals may be bolder than others. In addition, evidence from fish suggests that individual differences in inspection behaviour are consistent through time (Magurran 1986; Murphy & Pitcher 1991), and can thus be classed as a personality trait. In the second case, alarm responses to threatening stimuli have also been used to classify boldness. For example, Nelson et al. (2008) quantified male fowl, *Gallus gallus domesticus*, crouching behaviour and alarm calls in response to a simulated overhead-soaring hawk. Furthermore, stickleback behaviours such as type of swimming performed and position of spines in response to presentation of a predator have also been used as measures of boldness (Huntingford 1976).

In this study we tested the hypothesis that behaviour in the presence of a threat reflects boldness in wild, group-living chacma baboons, *Papio ursinus*. Our hypothesis generated three predictions: (1) that individuals are consistent in their reaction to a threat, in both their alarm response and threat-inspection times; (2) that the extent of an individual's alarm response will be negatively correlated with how long it spends inspecting the threat (e.g. Bell et al. 2010); and (3) that boldness in a threat context correlates with boldness towards a novel object.

METHODS

Study Area and Species

We studied chacma baboons from May to November 2009, May to October 2010 and June to September 2011 at Tsaobis Leopard Park, Namibia (15°45′E, 22°23′S). Two groups of chacma baboons ($N = 44$, 31 in 2009) have been habituated to the presence of observers at close range and are individually recognizable (see Huchard et al. 2010 for general methods of behavioural data collection at this site). We collected data annually from 57 adult, subadult and juvenile baboons (we did not test individuals under 2 years of age) over the 2009–2011 period. Our experimental protocols were assessed and approved by the Ethics Committee of the Zoological Society of London, and approved by the Ministry of Environment and Tourism in Namibia (Research/Collecting Permits 1379/2009, 1486/2010 and 1486/2011).

Presentation of Stimuli

Like other primates (Cook & Mineka 1989; Vitale et al. 1991; Ohman et al. 2001), chacma baboons will both alarm-call and inspect pythons and venomous snakes when they are encountered (Cheney & Seyfarth 2007). We used a taxidermic coiled puff adder, *Bitis arietans arietans*, as our threat stimulus. Puff adders are venomous snakes that naturally occur at the site, and the taxidermic specimen was sourced locally in Namibia. To control for any confounding effects of the experimental protocol on the baboon's behaviour during the stimulus presentations, a subset of baboons was also presented with a control stimulus, a dry domestic cow, *Bos* sp., pat. These are the same size and shape as a coiled puff adder and are regularly encountered by the baboons in their environment. The stimuli were presented by one observer (A.J.C.) on the edges of game trails and paths regularly used by the baboons during foraging. Although every effort was made to present the stimuli to an individual while it was walking alone, in some cases the baboons were unexpectedly running (usually a slow canter) and/or accompanied by another baboon. Instances in which the subjects were running fast and jumped over the snake were excluded. All experiments were filmed to facilitate data extraction (Panasonic SDR-SW20, Kadoma Osaka, Japan; see Supplementary Movie Files S1–S4).

Upon encountering the stimulus, whether the individual stopped, backed away, vocalized, tail flagged, performed self-directed behaviour or bared its teeth were recorded as binary responses (see Table 1 for definitions). All of these behaviours are indicative of outward signs of alarm (Cheney & Seyfarth 2007), and were recorded only when the individual was within 5 m of

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Table 1
Definitions of the binary responses that were recorded when individual baboons were presented with a model snake

Behaviour	Definition
Stop	The individual stops travelling when it sees the stimulus
Back away	The individual backs away from the stimulus; individuals that change their direction of movement, but do not travel backwards, score 0
Bare teeth	The individual bares its teeth at the stimulus
Tail flag	The individual raises its tail on seeing the stimulus; only individuals that raised their tail through more than 20 degrees are included in this definition
Vocalize	The individual makes a noise on seeing the stimulus
Self-directed behaviour	The individual performs a self-directed behaviour on seeing the stimulus; self-directed behaviours comprised self-scratching, self-touching, body shaking and yawning

the stimulus. Only one other behavioural response was observed (threatening the snake model); however, as this was observed only once, we did not systematically record it as a behaviour. All individuals stopped all responses on leaving the immediate vicinity (2.5 m) of the stimulus, demonstrating that that this distance was sufficient. We also recorded the time (maximum value 30 s) that individuals remained in the area inspecting the stimulus (following Bell et al. 2010). Inspection behaviour was defined as the individual looking in the direction of the stimulus while within 5 m of it. Finally, we recorded both the speed of the approaching individual (walking or running) and the presence of other individuals (alone or in the presence of others within 2.5 m) when the subject noticed the stimulus (or passed close to it, in those cases where the subject showed no response), as well as the distance at which the individual noticed the stimulus (within 2 m, further than 2 m or when travelling parallel but within 2 m of the stimulus). Presentations were thus defined as: slow or fast; social or solitary; and near, far or parallel. If more than one baboon saw the stimulus during a given presentation, we extracted data for both of the individuals if the second individual did not respond to the reaction of the first individual (and in one case third individual). A baboon was recorded as responding to another individual if it looked in the direction of and/or approached the individual who initially saw the stimulus.

The baboons were also presented with a novel food item to investigate individual boldness towards a novel object. Individuals were presented with a novel food item as they were moving between food patches, and all individuals were presented with the stimulus when they were solitary. Novel food items comprised: (1) hardboiled eggs with the shell on or removed or (2) a small egg-shaped bread roll, all of which were dyed red or green (Moir's food dye) in 2009; (3) semidried eighths of apple or (4) pear dyed red in 2010; and (5) eighths of an orange or (6) equivalent-sized pieces of butternut squash in 2011. Any naïve individual that saw another individual interacting with a novel food was presented with a different novel food when they were tested. To control for any confounding effects of the experimental protocol on the baboon's behaviour during the stimulus presentations, a subset of baboons was also presented with a control stimulus, the seed pod of an *Acacia erioloba*. Baboons will eat the seeds of *A. erioloba* pods; thus this stimulus presents a familiar, locally abundant food source the same size and shape as the fruit and vegetable stimuli. All experiments were filmed as above (see Supplementary Movie Files S5–S8) and the following data were recorded: the latency to handle the item, the time spent inspecting the item and the time spent handling the item.

Statistical Analyses

Our statistical analysis took four steps, outlined below. All analyses were conducted in R (R Development Core Team 2011). Data are presented as means ± SE.

It was first necessary to obtain individual values for behavioural reactions to threats and novel foods. Reactions to threats comprised threat-inspection behaviour and alarm responses. Individual threat-inspection behaviour was measured simply as the time spent inspecting the snake. Individual alarm responses were measured as the number of alarm behaviours expressed, resulting in a score from 0 to 6. Thus, individuals that showed a greater alarm response had higher scores than those that showed a weaker response. Individual behavioural responses to novel foods were assessed from a principal components analysis on the three response measures (latency, inspection time, handling time), in which each year's novel food responses were centred and standardized to have a mean of 0 and a standard deviation of 1 so that data between years could be compared on the same scale. The differentially weighted scores of the first two components, PCs 1 and 2, were retained for investigation following parallel analysis (Horn 1965).

To investigate individual consistency in behaviour, as a key criterion of personality (prediction 1), we calculated the repeatability of alarm responses and inspection times for all individuals who were presented with the stimulus on multiple occasions ($N = 49$). We also calculated repeatability in responses to novel foods for all those individuals that were presented with a novel food in more than one year ($N = 55$), as it is important to verify that these responses also reflected a personality trait (see also Carter et al. 2012). We calculated link scale repeatability r using the R package rptR (Nakagawa & Schielzeth 2010). In all cases, a log link was used, and count data with multiplicative overdispersion was specified. To transform PC1 to a count (as it followed a logarithmically skewed distribution), we used the integer of PC1 + 1 (to make all the values positive) multiplied by 10 (to increase the spread of the integer values). As PC2 was bimodally distributed and could not be analysed in rptR, we calculated the intraclass correlation coefficient of this variable in the R package irr (Gamer et al. 2010) for the 49 baboons who had been tested in all 3 years.

We investigated the relationship between the alarm response and the time spent investigating the snake using a generalized linear mixed effects model (GLMM) with Gaussian error and a log link function (prediction 2). We used inspection time as the response and included the reaction score as a fixed effect. To control for other possible determinants of individual differences in inspection times, we also included as fixed effects each baboon's sex (male/female), age class (following Huchard et al. 2010) and whether female individuals had offspring in the troop or not (as a binary response; males were listed as not having offspring) and for each trial the approach speed, social condition (0/1) and approach distance. To control for multiple trials, individual identity was included as a random effect, as were year and troop. We minimized the model as follows. We started with a model with all main fixed effects and, owing to overparameterization, we first investigated the significance of all possible three-way interactions between age class, sex, offspring and social condition of the presentation separately in this model. We also investigated the interaction between social condition, approach speed and approach distance in a model that had no other interactions. After three-way interactions were considered, we investigated all two-way interactions between the above-mentioned variables, while retaining any significant three-way interactions. Once we had identified all the interactions that were individually important, we specified them all in a single model. We then reduced this model by

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sequentially dropping the least significant terms to find the minimum adequate model. Model residuals were checked for normality.

To investigate whether antithreat boldness correlated with novel-object boldness (prediction 3), we first had to obtain a single measure of each individual's antithreat and novel-object boldness across presentations and years. In the first case, we only considered individual alarm responses, as threat-inspection times did not show individual consistency (see Results). We therefore used the best linear unbiased predictors (BLUPs) from a GLMM with alarm score as the response variable and presentation type, approach distance and approach speed as fixed effects, as each individual's measure of antithreat boldness. (Alternatively, the median alarm response score across presentations could have been taken for each individual, but this would not have allowed us to control for other variables such as presentation type, approach distance and speed.) In the second case, we took the median value of PC1 (response to the novel food items) across years as each individual's measure of novel-object boldness. With these scores, we ran a linear model using the alarm score BLUPs as the response variable and the median of PC1 as a predictor variable. We further included age class and sex and their interaction as fixed effects, and troop as a random effect. We then sequentially dropped the least significant of these further fixed terms but retaining the variable of interest, in this case the median PC1 score.

RESULTS

Snake Presentations

We extracted 153 individual snake encounters from 139 successful presentations on 57 individual baboons (mean = 2.7, median = 3, range one to five presentations per individual); 110 presentations (72%) were 'solitary' and 129 (84%) were 'slow'; in 90 (59%) presentations, the baboons noticed the stimulus when they were in front of it and close to it, whereas in 35 (23%) and 28 (18%) presentations the baboons noticed when they were more distant from it or parallel to it, respectively. The most common response to the snake model was to stop (63% of cases), followed by tail flagging (27%), backing away (26%), baring teeth (14%), self-directed behaviours (13%) and finally vocalizing (8%). The median inspection time was 6 s (range 1–30).

Novel Food Presentations

We completed 168 novel food presentations on 58 individual baboons (mean = 2.8, median = 3, range one to three per individual). Every individual present was tested in all 3 years; however, owing to emigration and disappearances between years, 55 and 50 individuals were tested in 2010 and 2011, respectively. The first and second principal components of the PCA on the novel food experiments explained 55% and 35% of the variation in the experimental data (Table 2). Higher PC1 scores were associated with higher inspection and handling times. These scores are thus indicative of bolder behaviour, that is, individuals that were willing to spend longer in close proximity to, and in contact with, the novel object. By contrast, higher PC2 values were associated with longer latencies to handle the food item.

Table 2
Component loadings of behaviours observed on the first and second principal components

Behaviour	Loadings	
	PC1	PC2
Time inspecting the food item	0.71	0.17
Time handling the food item	0.70	−0.28
Latency to handle the food item	<0.10	0.95
Variation explained	54.8%	34.9%

Control Experiments

We completed 59 snake control presentations on 41 individual baboons (1.4 ± 0.1 presentations, range one to four presentations) and 110 novel food control experiments on 52 individual baboons (2.1 ± 1.0 presentations, range one to four presentations). For all of the threat control presentations (cowpats), no positive binary responses were recorded, and in only three of the 59 trials did the baboons look in the direction of the cowpat as they walked past it. However, we could not define this as 'investigating' the stimulus as the baboons merely glanced in its direction. Thus we are confident that the experimental protocol had no confounding effects on the response of the baboons to the model snake. Similarly, no targeted baboons investigated the *A. erioloba* pod when it was presented. Thus we have not included the control responses in the following analyses.

For those 43 baboons for whom we had repeated the snake model presentation more than once (prediction 1), the individual alarm scores were found to be repeatable (link scale $r = 0.34$, CI = 0.12–0.51, $P = 0.005$); however, individual inspection times were not (link scale $r = 0.16$, CI = 0.00–0.37, $P = 0.075$). Novel-object boldness (PC1) was also found to be repeatable ($r = 0.26$, CI = 0.18–0.63, $P = 0.02$), as was latency to approach the food item (PC2; ICC(1) = 0.33, CI = 0.16–0.52, $P < 0.001$).

Contrary to our prediction (2), across the 153 individual threat encounters, those individuals that inspected the snake model for longer, and might therefore be interpreted as showing higher levels of boldness, did not show lower intensity alarm responses. Rather, the opposite pattern was found: longer inspection times were associated with greater intensity alarm responses (GLMM: $\beta \pm SE = 0.17 \pm 0.03$, $t_{136} = 5.64$, $P < 0.0001$). The minimal model also included social context, approach distance, approach speed, age class, sex and the interaction between social context, age class and sex (Table 3).

Contrary to our prediction (3), across the 57 individual baboons, we found no relationship between how boldly an individual behaved in the snake presentation (alarm response score BLUP) and how boldly it responded to a novel food (PC1; $\beta \pm SE = 0.012 \pm 0.04$, $t_{54} = 0.30$, $P = 0.76$).

DISCUSSION

We tested the hypothesis that an individual's reaction to a threat is a reflection of its boldness. In partial support of our first

Table 3
Parameter estimates for the minimal model describing the relationship between the threat-inspection time (log-transformed; 1–30 s) as the response variable and the alarm response as the predictor variable

Parameter	Estimate	SE	*t*	*P*
Alarm response score	0.25	0.05	5.14	0.0001
Sex	−1.75	0.99	−1.76	0.08
Age class	0.12	0.26	0.46	0.65
Social condition	0.60	0.16	3.71	0.0004
Approach speed	0.48	0.14	3.41	0.001
Approach distance (far)	0.60	0.14	4.09	0.0001
Approach distance (parallel)	−0.04	0.16	−0.26	0.80
Sex : Age class	1.83	0.67	2.73	0.008
Sex : Social condition	2.12	0.79	2.69	0.009
Age class : Social condition	0.08	0.26	0.31	0.76
Sex : Age class : Social condition	−3.09	0.86	−3.58	0.0006

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prediction, we found that both the alarm response to a threatening stimulus and boldness towards a novel food were repeatable through time, and therefore indicative of individual personality traits, but that inspection time was not. However, contrary to our second prediction, those baboons that showed a more intense alarm response to the threat also inspected the threat for longer. Furthermore, contrary to our third prediction, the alarm response to the threat did not correlate with that individual's response to a novel object. These results suggest that when chacma baboons are faced with a threatening situation such as a venomous snake, their response does not reflect their boldness. Below we discuss which personality trait this assay could be measuring, and the implications for those studies that use antipredator assays to measure boldness.

We propose that the antithreat assay used in our study measures anxiousness rather than boldness. Fear of snakes is learned more rapidly in humans and monkeys than fear of neutral stimuli such as flowers (Cook & Mineka 1989; LoBue & DeLoache 2008). Similarly, humans and monkeys detect threatening stimuli such as snakes and spiders more rapidly than nonthreatening stimuli (Ohman et al. 2001; LoBue & DeLoache 2008; DeLoache & LoBue 2009). These patterns suggest that fear of snakes represents an evolved trait in primates (Cook & Mineka 1989; Ohman & Mineka 2001; LoBue et al. 2010). Further research has explored how individual variation in detecting threatening stimuli such as a snake might be related to personality. Dot-probe experiments quantify the latency to find a dot after the presentation of two stimuli, one threatening and one nonthreatening. These experiments revealed that people who were more vigilant for threatening stimuli were also more anxious individuals (Mogg et al. 1997, 2004). This result has been further supported by attentional-bias studies, which use the latency to find a threatening stimulus and the duration of attention to the same stimulus to assess differences in individual responses. It is commonly found in humans that highly anxious individuals show attentional bias towards threatening stimuli and that nonanxious individuals tend to bias their attention away from threatening stimuli (Macleod et al. 1986; Macleod & Mathews 1988), and that this tendency is evident even in young children (Vasey et al. 1996; Bar-Haim et al. 2007). As those baboons that showed more extreme responses to the threat also spent longer inspecting it, and anxious humans attend to threatening stimuli for longer, we suggest that the antithreat assay used in this study measures anxiousness rather than boldness as we initially intended.

Anxiety has been found to be part of a behavioural coping style/syndrome (Sih et al. 2004a) as it correlates with other personality traits in rats and mice. For example, mice bred for high and low levels of aggression also display low and high levels of anxiety in behavioural tests, respectively (Nyberg et al. 2003). Furthermore, anxious rats display higher levels of panicking during high acoustic stimulation (de Paula et al. 2005) and show lower exploration and movement in an open-field test (Liebsch et al. 1998). Altogether, these findings are indicative of anxiety as a personality trait within a behavioural syndrome in rats and mice. The neurological bases and behavioural outcomes of fear and anxiety have been studied extensively in nonhuman primates (reviewed in Lang et al. 2000; Barros & Tomaz 2002; Kalin & Shelton 2003). Although these studies do not investigate the connections between boldness and anxiousness, they do support our finding that individual patterns of response to a novel food do not correlate with corresponding measures of fear/anxiety. In particular, using factor analysis, latency to inspect a novel food loaded on a separate factor to anxiety traits in captive rhesus macaques, *Macaca mulatta* (Williamson et al. 2003). Finally, Weiss et al. (2011) described the uncorrelated traits anxiety and confidence (similar to boldness) in their study of free-ranging rhesus macaque personality using observer ratings. This line of evidence suggests that boldness and anxiety are separate traits; threatening situations may measure anxiety, not boldness. This is an interesting suggestion, not least because the trait 'anxiety' is not currently considered in many studies of animal personality within behavioural ecology (Réale et al. 2007).

It is important to note that behaviour in response to a threat may be different for different species, potentially complicating definitions of boldness, and between-species comparisons of animal personality. For example, Fitzgibbon (1994) enumerated three main reasons that prey species may approach and inspect predators or potential threats: acquiring information, deterring the predator and informing others. In this study, baboons could be acquiring information about the threat. Thomson's gazelles, *Gazella thomsoni*, by contrast, may inspect predators to deter them (Fitzgibbon 1994). This further raises the issue of how comparable personality traits are between species (discussed in Réale et al. 2007; Weiss & Adams, in press), which is another issue in animal personality studies that is frequently overlooked.

We used a standard assay to measure boldness and found what appears to be a measure of anxiousness. This may have significant implications for animal personality research, and begs the question: How many studies that set out to assay one personality trait inadvertently assay another? Our findings demonstrate a jingle fallacy within our own animal personality research, and indicate that such further jingle or jangle (where two different labels are used for the same trait) fallacies may exist in the animal personality literature. 'Validity' is a concept that comes from the psychology literature and refers to the degree to which an assay measures the targeted trait (see also Réale et al. 2007; Burns 2008). One way to ensure the validity of a trait is to use multiple measurements for multiple traits: the multitrait, multimethod approach (Campbell & Fiske 1959). Consequently, we suggest that future research on animal personality should carefully consider the terminology adopted and/or use multiple assays to measure the targeted personality trait (Campbell & Fiske 1959; Gosling 2001; Vazire et al. 2007; Uher & Asendorpf 2008; Uher 2008b; Weiss & Adams, in press).

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Supplementary Material

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