



Personality predicts cognitive bias in captive psittacines, *Amazona amazonica*



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The prevalence of stable behavioural differences between individuals of a species (i.e. personality) is puzzling because it indicates that there are limits on animals' behavioural plasticity and, therefore, optimality of behaviour. Personality may result from individual state characteristics (e.g. morphology or physiology). In turn, these characteristics can lead to differential fitness outcomes for individuals. Cognitive processing of environmental information may be such a characteristic. We developed a subjective personality assessment for *Amazona amazonica*. We then assessed whether personality predicted a cognitive state difference in attention bias, as measured by the proportion of barks and errors when performing a spatial foraging task in the presence of a passive human observer. Attention biases occur either because individuals attend more quickly to certain environmental stimuli, or because they cannot disengage their attention from such stimuli. Two factors, 'neuroticism' and 'extraversion', accounted for 66% of the total variance in personality. There was individual variation between parrots' scores on both personality factors and both factors were temporally consistent over 1 year. There was a significant correlation between neuroticism and attention bias. Evolutionarily, attention biases are selected for because the fitness cost of failing to attend to potential threats is much greater than the cost of expending energy attending to benign stimuli. Therefore, cognitive biases such as attention bias are logical candidate cognitive states driving stable personality differences. Our findings show that differences in personality in *A. amazonica* are correlated with attention bias, a biologically relevant difference in cognition.

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Research efforts across a range of scientific fields are investigating the evolution (e.g. Dingemanse & Wolf, 2013; Foster, 2013), fitness effects (e.g. Dingemanse & Réale, 2005; Smith & Blumstein, 2008), genetics (e.g. van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005) and practical implications (e.g. Carere, Caramaschi, & Fawcett, 2010; Ijichi, Collins, & Elwood, 2013; Schuett, Dall, & Royle, 2011; Weinstein & Capitanio, 2008) of intraspecific differences in behaviour that are stable across multiple contexts (Gosling & Vazire, 2002). Such differences are referred to as 'personality' in the comparative personality literature (Gosling, 2001) and 'behavioural syndromes' in the behavioural ecology literature (Sih, Bell, & Johnson, 2004). Individual personality traits can be grouped together based on the latent variables (dimensions) they reflect. Human personality traits are often explained by five dimensions, referred to as the 'big five' (Digman, 1990; McCrae & John, 1992).

Comparative personality research has identified three of these big five dimensions in animals (Gosling & John, 1999). Behavioural syndromes in animals also consist of correlated suites of behaviours (Dingemanse & Wolf, 2010). These may similarly reflect underlying behavioural organization (Wolf, van Doorn, & Weissing, 2008) akin to personality dimensions and, like personality dimensions, be generalizable across taxa (Groothuis & Carere, 2005).

The prevalence of personality/behavioural syndromes is puzzling because it indicates that there are limits on animals' behavioural plasticity and, therefore, optimality of behaviour (DeWitt, Sih, & Wilson, 1988; Sih et al., 2004; Wolf & Weissing, 2010). Our understanding of why personality types evolve and vary among individuals within a species is still limited (Wolf et al., 2008). Theoretical models suggest that between-individual state differences lead to consistent behavioural differences across time and contexts because animals adopt different behavioural strategies on the basis of their initial starting point for a particular state (Dingemanse & Wolf, 2010; Nettle, 2006). State differences can be morphological, physiological or neurobiological (Dingemanse & Wolf, 2010); examples include body size (e.g. McElreath &

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Strimling, 2006) and growth rate (e.g. Stamps, 2007). The resultant behavioural strategies could increase fitness through increased reproductive success and/or increased survivability (Both, Dingemanse, Drent, & Tinbergen, 2005; Dingemanse, Both, Drent, & Tinbergen, 2004; Smith & Blumstein, 2008). These models generate testable hypotheses about the effect of state differences on behavioural types. For example, if a difference in body size underlies a behavioural difference (e.g. shy versus bold), then altering relative body size should also alter the animals' behavioural type.

Cognition is another putative state underpinning personality differences in animals, but this has yet to be experimentally evaluated (Dingemanse & Wolf, 2010). Because cognition is a broad term, this evaluation would require hypotheses about how specific cognitive state differences drive differences in personality. In humans, certain personality traits (i.e. anxiety) are known to correlate with altered cognitive processing of environmental stimuli, known as attention biases (Mathews, Mackintosh, & Fulcher, 1997). It is thought that this relationship is bidirectional: personality renders certain individuals more susceptible to developing attention biases during periods of stress, and such biases can then have a positive feedback on personality traits such as anxiety (MacLeod, Rutherford, Campbell, Ebsworthy, & Holker, 2002). Attention biases occur either because individuals more quickly attend to environmental stimuli, or because they cannot disengage their attention from such stimuli, or both (Cisler, Bacon, & Williams, 2009). Evolutionarily, such biases are selected for because the fitness cost of failing to attend to potentially important environmental stimuli is much greater than the cost of expending energy attending to benign stimuli (Haselton & Nettle, 2006). Therefore, cognitive biases such as attention bias for environmental stimuli are logical candidate cognitive states driving stable personality differences.

We integrated predictions generated from theoretical models with the methodology of comparative personality in order to assess the relationship between cognitive state differences and personality in *Amazona amazonica*. Psittacines are an ideal system for this question because they possess complex cognition (e.g. Emery, 2006; Huber & Gajdon, 2006; Pepperberg, Koenke, Livingston, Girard, & Hartsfield, 2013) and display consistent variability in behaviour between individuals (Mettke-Hoffman, Winkler, & Leisler, 2002), and because their longevity allows temporal stability of personality to be assessed over long periods. We developed a multidimensional personality assessment for *A. amazonica* using subjective ratings, and then experimentally tested our prediction that a state difference in cognition would correlate with personality differences. For our cognitive measure we chose to evaluate differences in attention bias during a foraging task, because this has potential implications for fitness and such biases are related to personality in humans.

METHODS

Subjects and Housing

All animal care and experimental procedures were approved by the University of California, Davis Institutional Animal Care and Use Committee (protocol numbers 15046 and 17002). We hatched 20 parrots (11 female, 9 male) from an established breeding colony of *A. amazonica*. Chicks were parent-reared with human interaction until fledging at approximately 60 days post hatch. They were then removed from the breeding colony and individually housed in wire cages (91.4 × 91.4 × 121.9 cm) in visual and auditory contact with their cohort members. Cages contained multiple perches: one softwood; one Manzanita; one concrete; one grape vine. A softwood cube for chewing and a plastic dish with water (changed

daily) for soaking food were also provided. We fed the parrots an extruded complete ration (Roudybush Lowfat Maintenance Pellets, Roudybush Inc., Woodland, CA, U.S.A.) and provided drinking water via water lines with nipple drinkers, both ad libitum.

We socialized the chicks to human contact for 15 min per day, 6 days per week. Socialization consisted of positive human–parrot interactions (e.g. feeding treats, time outside of home cage, allowing flight around the room, etc.). All chicks had additional foraging devices or toys in their cage during these socialization sessions. The socializers were the first author, another graduate student, and approximately 20 undergraduate students, and all of the parrots were exposed to all of the socializers. In addition to the unstructured socialization, we used a positive reinforcement protocol to train the parrots to respond to verbal commands, such as to move to a particular cage location. These training sessions lasted 5–10 min per bird, 3 days per week. The first author and two of the socializers conducted the training. Training lasted a minimum of 2 months, while socialization occurred throughout the study period.

Personality Instrument and Assessment

The personality inventory was adapted from one developed by Gosling (1998) for spotted hyaenas, *Crocuta crocuta*. That inventory was sent to four psittacine experts and, based on the input received from three of the experts, the trait definitions were revised to be unambiguous and appropriate for parrots. The revised inventory consisted of 36 personality traits and four physical traits (see Results, Table 1) that were scored from 0 (complete absence of the trait) to 7 (extreme amount of the trait).

Two raters, the first author and one of the trainers, each completed the personality inventory twice for each bird: an initial rating and a second rating 1 week later. These ratings were carried out independently, and the raters did not discuss their ratings with one another. Ratings were based on the raters' aggregate experiences with the parrots from both the structured training and free-form socialization sessions. Raters were required to wait at least 24 h after interacting with a parrot before completing the inventory for that parrot to minimize the chance that they were biased by contextual cues or interactions that occurred shortly before they rated the parrots. The second rating allowed an assessment of intra-rater reliability. The parrots hatched over the course of three breeding cycles (Winter 2008/2009, Winter 2009/2010 and Winter 2010/2011). All initial personality assessments occurred during the autumn of 2011, so the parrots were juveniles (12–32 months of age) at the time of initial personality assessment, depending on the breeding cycle of hatch. Raters varied in the length of time they were acquainted with the parrots, but all raters had socialized and trained the parrots for at least 2 months. Ratings were absolute (i.e. parrots were not rated in relation to the other individuals in their cohort), and raters were encouraged to use the entire scale from 0 to 7 as necessary (Capitanio, 1999). For each rater, the initial and 1-week rerate scores were averaged; these scores were then averaged across raters, resulting in a composite average personality trait score for each trait for each bird, which was then used in the factor analysis. Such composite scores help to minimize measurement error (J. Capitanio, personal communication).

Reliability and Agreement

For each trait on the inventory, we assessed intra-rater reliability using Spearman rank correlations comparing the results of the 1-week rerate with the initial rating. Because we used a composite trait score, inter-rater reliability for each trait on the inventory was calculated using the Spearman–Brown prophecy formula (Capitanio, 1999). In addition to assessing inter-rater

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