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Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo mammals

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Abstract

The effect of individual differences on the behaviour and reproduction of zoo animals has long been recognised by zoo biologists, yet only recently has the quantitative assessment of personality been used to investigate some of the challenges faced in zoo animal management. We review the findings of animal personality studies carried out in zoos since 1995. Our results reveal that zoo animal personality is most commonly assessed using observer ratings, where people who are familiar with the animals are asked to rate them on various personality traits. The reviewed studies indicate that zoo keepers are able to reliably rate animal personality research and these ratings are valid and related to behaviour. We identify promising areas of development in zoo animal personality research and suggest applications of personality profiling to zoo animal welfare and management. We argue that a validated personality questionnaire is a valuable tool for zoo professionals and advocate the implementation of personality assessment into existing zoo management practices to inform decisions on welfare and captive breeding.

Keywords: animal behaviour, animal personality, animal welfare, captive breeding, conservation, zoo

Introduction

Since the 1930s, there has been increasing scientific interest in the study of personality in non-human animals (Gosling 2001; Freeman & Gosling 2010). Initially, the focus of this research was primarily anthropocentric, using animal models to investigate human personality (Gosling 2001; Réale et al 2007). These studies most frequently involved primate species, due to their close phylogenetic proximity to humans, and little attention was paid to the role of personality in the study of animal behaviour across different species (King & Figueredo 1997). During the last fifteen years, however, there has been an emerging field of research concerned with the study of animal personality and its implications for the breeding, management and welfare of captive animals (Powell & Svoke 2008). We suggest that now is a timely juncture to review the progress of this developing field and assess its prospects and pitfalls going forward, since early signs point toward the potential for both management and welfare benefits.

One of the goals of the modern zoo is to contribute to the conservation of threatened species by participating in captive breeding programmes, designed to maintain both the genetic diversity and the demographic composition of captive populations (Wedekind 2002; Ballou *et al* 2010; Asa *et al* 2011). The success of captive breeding programmes depends not only on the management of the

captive population as a whole, but also on the management and husbandry of individual animals. The captive environment itself has a profound effect on the behaviour of wild animals (Morgan & Tromborg 2007) and individuals vary in their responses to environmental variables (Carlstead *et al* 1999b; Jones & Gosling 2005; Kuhar *et al* 2006). Understanding this variation among individuals is the goal of animal personality research.

The effect of individual differences on zoo animal behaviour and reproduction has long been recognised by zoo biologists, and people who work with animals often describe their different character traits (Powell & Svoke 2008; Watters & Powell 2012). Temperament or personality is frequently proposed by zoo researchers as an explanation for the results of their investigations, even in studies which do not aim to investigate personality directly (Andersen 1992; Jurke *et al* 1997; Owen *et al* 2004; Zhang *et al* 2004; Miller & Kuhar 2008). Yet it is only recently that the quantitative assessment of personality has been used to investigate some of the challenges faced in zoo animal breeding, management and welfare.

In 1999, two papers were published in *Zoo Biology* by Carlstead and her co-workers (Carlstead *et al* 1999a,b), describing the assessment of personality using keeper ratings in black rhinoceros (*Diceros bicornis*) and its relationship with housing, mortality and breeding success.





Number of zoo animal personality studies, published since 1995, identified in our literature search.

These papers were closely followed by the publication of guidelines for constructing behavioural profiles for zoo animals, as part of the 'Methods of Behavioural Assessment' (MBA) project carried out by the American Zoo and Aquarium Association's Behaviour and Husbandry Advisory Group (Carlstead et al 2000). The MBA project focused on four species, of which the captive population is not self-sustaining: black rhinoceros, maned wolf (Chrysocyon brachyurus), great hornbill (Buceros bicornis) and cheetah (Acinonyx jubatus). The project attempted to assist captive breeding programme co-ordinators in identifying possible explanations as to why these species show reduced reproductive potential in captivity (Carlstead et al 2000). Following these publications (Carlstead et al 1999a,b, 2000), there has been an increase in the number of behavioural profiling, or personality, studies (Figure 1) as the potential effect of individual differences in behaviour on the welfare and management of zoo animals is becoming apparent.

Although researchers in this developing field share a common interest in personality, studies are carried out from assorted perspectives (Jones & Gosling 2005). Some researchers are interested in the comparison of human and animal personality, using primates as model species. Others investigate the reliability and validity of methods used to

assess animal personality and still others have focused on the influence of personality on behaviour, fitness and reproductive success. Consequently, papers are published in journals in areas ranging from psychology to animal welfare. It is therefore potentially difficult to keep up to date with the latest findings (Jones & Gosling 2005) and isolate areas of further investigation. Additionally, several authors identified the need for a standard method of zoo animal personality assessment (McDougall et al 2006; Whitham & Wielebnowski 2009; Watters & Powell 2012), yet there has been little effort to summarise the findings of personality research carried out in zoos to determine the feasibility of such a method. With this in mind, the purpose of this paper is to review and summarise the findings of recent zoo-based animal personality studies and to ascertain the potential applications of personality assessment to zoo animal management. In doing so, we aim to identify future research directions that will facilitate the implementation of personality assessment into current animal management practices.

Defining personality

The term 'personality' is considered by some authors to be too anthropomorphic to be used in the animal behaviour literature (Meagher 2009; Freeman & Gosling 2010). Consequently, there is inconsistency in the literature regarding the terms used when describing animal personality (Réale *et al* 2007; Freeman & Gosling 2010). Many researchers refer to 'temperament' (Freeman *et al* 2004), others use the phrase 'behavioural profiling' (Carlstead *et al* 1999a, 2000) and still others refer to individual differences (Wielebnowski 1999; Blumstein *et al* 2006) or 'individual distinctiveness' (Carlstead *et al* 1999b). These differing terms are sometimes used interchangeably in the same paper (eg Blumstein *et al* 2006). We use the term 'personality' hereafter and define personality as "individual differences in behaviour that are thought to be stable across time and situations" (Freeman & Gosling 2010; p 654). This is intended to be a broad definition encompassing the work of researchers who prefer 'temperament' or 'behavioural profile' (Freeman & Gosling 2010).

Literature review

The aim of the literature search was to identify research papers, published since 1995, reporting the results of animal personality studies that had been carried out in zoo environments, with mammals as their subjects.

Literature search procedure

Due to the variation in terms used in the literature, the keywords 'zoo' and 'temperament', 'zoo' and 'personality' or 'zoo' and 'behavioural profile' were used to search the Web of Science, Academic Search Premier, Zetoc and Scopus databases. The resulting articles were examined for their relevance and the references section of each article was checked to ensure that further papers of potential interest were not overlooked. The literature search yielded 30 empirical personality studies that had been carried out on mammalian species, partly or entirely in zoos. The resulting papers were published in thirteen different journals in the fields of psychology, animal behaviour and primatology. In their recent review of primate personality research, Freeman and Gosling (2010) identified 210 studies, 59% of which were conducted in laboratories and 14% in zoos. Our search was focused entirely on zoo-based research published within the last fifteen years and the small number of papers we indentified is indicative of a field still in its infancy. A summary of the results of the literature search is provided in Table 1.

Species and research focus

Primate species were the most commonly studied; sixteen papers (53%) had primates as their subjects and included work chimpanzees (Pan troglodytes), orangutans on (Pongo pygmaeus and Р. abelii), gorillas (Gorilla gorilla gorilla), bonobos (Pan pansicus) and liontailed macaques (Macaca silenus). Five papers focused on felid species, including cheetahs, clouded leopards (Neofelis nebulosa), snow leopards (Uncia uncia) and tigers (Panthera tigris). Elephants (Loxodonta africana and Elephas maximus, four papers), black rhinoceros (two papers), giant pandas (Ailuropoda melanoleuca, two papers) and Vancouver Island marmots (Marmota vancouverensis, one paper) were also studied. This represents an extremely small proportion of the vast number of mammalian species currently maintained in zoological collections and is related to the areas of investigation of each particular study.

The main focus of the reviewed work carried out on primates was to assess the reliability and validity of personality assessments (eg Rouff et al 2005; Weiss et al 2007; Uher & Asendorpf 2008), and to compare primate personality with human personality (eg King & Figueredo 1997). Zoos provide excellent opportunities to study exotic species and zoo primates are often chosen for this type of study due to their accessibility, rather than to investigate personality specifically in the zoo environment. Nonetheless, these studies provided information and insight into the overall components of personality found in these species and their general importance in ecological and evolutionary terms, even though their specific focus was not the application of personality information to zoo animal management. Researchers interested in the application of personality assessments to the management of zoo animals chose to study species prone to behavioural problems in captivity. For example, studies focusing on the relationship between personality and breeding success had species displaying inconsistent reproduction in captivity as their subjects (eg black rhinoceros: Carlstead et al 1999a,b; cheetahs: Wielebnowski 1999; giant pandas: Powell et al 2008).

Methods of data collection

Animal personality can be assessed using two methods: trait rating by knowledgeable informants and coding of the animals' behaviour (Gosling 2001; Meagher 2009; Freeman & Gosling 2010; Highfill *et al* 2010; Watters & Powell 2012). The literature search revealed that zoo animal personality is most commonly assessed through the use of observer ratings (87% of studies; Figure 2), where people who are familiar with the animals (zoo keepers, for example) are asked to rate them on various personality traits. This typically involves the use of a questionnaire consisting of a list of adjectives sometimes accompanied by a definition of each, and raters are asked to score individuals on these adjectives using a scale defined by the researcher (Meagher 2009, but see Dutton *et al* 1997).

Only four studies used behavioural coding alone in their assessment of personality (Figure 2). Coding consists of more conventional observations of behaviour using ethograms, and observations are recorded and analysed in the context of personality traits (Gosling 2001; Highfill et al 2010). Most studies using this method record the behaviour of animals when presented with novel objects (Rouff et al 2005; Blumstein et al 2006; Powell & Svoke 2008), or during specific behavioural tests (Uher et al 2008). Behavioural coding is considered to be more objective than keeper ratings, however observers who are coding the behaviours must still use their own judgement to ascertain whether the behaviours they are observing are those defined in the ethogram (Jones & Gosling 2005; Meagher 2009). This is true of all behavioural research, yet the reliability and repeatability of studies in which occurrences of behaviour are recorded are rarely questioned (Jones & Gosling 2005; Vazire et al 2007; Meagher 2009; Highfill et al 2010). Furthermore, Vazire and colleagues (2007) found that trait rating was more reliable

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Table I	Research	on zoo ani	mal person	ality publishe	d since	1995.
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Study	Species	Focus of study	Method	Reliability	Validity
Dutton et al (1997)	Chimpanzee	Novel rating method	Rating	Not assessed; different raters used different instruments	Not assessed
King & Figueredo (1997)	Chimpanzee	Comparison of chimpanzee personality with human Five Factor Model	Rating	Intra-class correlation, ICC $(3, k)$ from 0.67 to 0.83	Examined correlations between factors
Murray (1998)	Chimpanzee	Influence of early rearing and social group size	Rating	Assessed but not described	Not assessed
Carlstead et <i>al</i> (1999a)	Black rhinoceros	Behaviour, breeding success in relation to housing	Rating	Kendall's coefficient of concordance (W), mean of 0.62	Novel object tests
Carlstead et al (1999b)	Black rhinoceros	Breeding success	Rating	Kendall's coefficient of concordance (W), mean of 0.62	Novel object tests
Wielebnowski (1999)	Cheetah	Individual breeding success	Rating	Kendall's coefficient of concordance (W), from 0.57 to 0.98	Mirror-image stimulation test
Wielebnowski et al (2002)	Clouded leopard	Assessment of adrenal activity, behaviour and husbandry	Rating	Kendall's coefficient of concordance (W), excluded if < 80% agreement	Compared ratings with faecal corticoid concentration
Weiss et al (2002)	Chimpanzee	Heritability, relationship between Dominance and subjective well-being	Rating	Intra-class correlation, ICC (3, <i>k</i>) 0.90	Examined correlations between factors
King & Landau (2003)	Chimpanzee	Relationship to subjective well-being	Rating	Intra-class correlation, ICC $(3, k)$ from 0.70 to 0.90	Behavioural observation
McKay (2003)	Cheetah	Individual breeding success	Rating	Spearman's rank correlation coefficients from 0.72 to 0.98	Novel object tests
Freeman <i>et al</i> (2004)	African and Asian elephant	Relationship between behaviour and ovarian cyclicity	Rating	Not assessed	Not assessed
King et al (2005)	Chimpanzee	Comparison of zoo and sanctuary-housed chimpanzees	Rating	Intra-class correlation, ICC $(3, k)$ from 0.74 to 0.92 (zoo), from 0.77 to 0.94 (sanctuary)	Examined correlations between factors
Martin (2005)	Chimpanzee	Influence of early rearing	Rating	Kendall's coefficient of concordance (W), reliable if $P < 0.01$. Spearman's rank correlation coefficient, rater considered reliable if $P < 0.01$	Not assessed
Pederson et al (2005)	Chimpanzee	Validation of HPQ	Rating	Intra-class correlation, ICC $(3, k)$ from 0.72 to 0.90	Behavioural observation
Rouff et al (2005)	Lion-tailed macaque	Novel method of analysis	Coding	Cohen's Kappa, from 0.88 to 1.00	Not assessed
Blumstein et al (2006)	Vancouver Island marmot	Survival following reintroduction	Coding	Not assessed	Not assessed
Kuhar et al (2006)	Gorilla	Age, social housing, behaviour	Rating	Not assessed	Behavioural observations
Weiss et al (2006)	Orangutan	Relationship to subjective well-being	Rating	Intra-class correlation, ICC $(3, k)$ from 0.40 to 0.91	Examined correlations between factors
Phillips & Peck (2007)	Tiger	Keeper/animal interactions	Rating	Friedman's test, $P < 0.001$ for 13 of 27 adjectives	Behavioural observation
Weiss et al (2007)	Chimpanzee	Comparison of zoo-housed and laboratory-housed chimpanzees	Rating	Intra-class correlation, ICC $(3, k)$ from 0.38 to 0.88	Not assessed
Dutton (2008)	Chimpanzee	Reliability and stability of ratings	Rating	Spearman's correlation, between 0.39 and 0.59 for five dimensions	Not assessed
Powell et al (2008)	Panda	Relationship between personality, husbandry and socio-sexual behaviour	Coding	None stated	Behaviour during novel object trials compared with keeper survey of sexual behaviour

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Table I (cont)

Study	Species	Focus of study	Method	Reliability	Validity	
Powell & Svoke (2008)	Panda	Use of environmental enrichment to assess personality	Rating and coding	Rating: Kendall's coefficient of concordance (W) all P < 0.001. Coding: 92% agreement between observers	Novel object trials	
Uher et al (2008)	Bonobo, chimpanzee, gorilla, orangutan	Reliability of coding during behaviour tests	Coding	Cronbach's α , median 0.96	Not assessed	
Uher & Asendorpf (2008)	Bonobo, chimpanzee, gorilla, orangutan	Comparison of methods of assessment	Rating	Cronbach's α , median 0.90	Behavioural observations	
Freeman <i>et al</i> (2009)	African elephant	Relationship between social behaviour and ovarian cyclicity	Rating	Kendall's coefficient of concordance (W), excluded if P > 0.05	Ratings compared with ovarian cyclicity	
Weiss et al (2009)	Chimpanzee	Personality assessment in Japan	Rating	Intra-class correlation, ICC $(3, k)$ from 0.06 to 0.82	Not assessed	
Freeman et <i>al</i> (2010a)	African elephant	Social rank and ovarian cyclicity	Rating	Kendall's coefficient of concordance (W), all $P < 0.05$.	Ratings compared with ovarian cyclicity	
Freeman et al (2010b)	African elephant	Comparison of keeper ratings and direct observations of social behaviour	Rating	Kendall's coefficient of concordance (W), excluded if P > 0.05	Behavioural observations	
Gartner & Powell (2012)	Snow leopard	Comparison of keeper ratings and behavioural observations	Rating	Kendall's coefficient of concordance (W), between 0.211 and 0.660. Spearman's rank-order coefficient (r_{s}), $P < 0.05$	Novel object tests	

Figure 2



than behavioural coding in an assessment of chimpanzee personality, and suggested that behavioural codings can in fact be difficult to measure reliably.

Previous reviews of animal personality research revealed that behavioural coding is the most common method of data collection (Gosling 2001; Smith & Blumstein 2008; Freeman & Gosling 2010). Indeed, Freeman and Gosling (2010) found that 89% of primate personality studies used behavioural coding. Thus, it would seem that the choice of method in most zoo animal personality research is in contrast to methodological trends in other animal personality studies. Studies of zoo animal personality often involve several institutions, to enable researchers to compare environmental effects and husbandry factors and to obtain information on a large number of animals. Studies identified in the present review that used keeper ratings alone (n = 24) had a mean of 83.9 subjects, whilst studies using only behavioural coding (n = 4) had a mean of 32.5 subjects. The use of questionnaires eliminates the need for researchers to visit every collection participating in the study, whilst simultaneously increasing sample size and allowing data to be collected on many animals from multiple collections (Carlstead et al 1999b, 2000; Kuhar et al 2006; Meagher 2009). In contrast, behavioural coding is time consuming and often not logistically possible in zoobased studies, depending on the number of collections taking part, as it requires direct observations of behaviour. This may explain the apparent tendency for zoo researchers to rely on keeper ratings alone (Figure 2).

Powell and Svoke (2008) attempted to devise a method for assessing the personality of giant pandas, using behavioural coding when the pandas were presented with novel objects. To test this method, they compared the results of behavioural coding during novel object tests alongside keeper ratings. Both methods enabled the authors to construct personality profiles for each individual, and those constructed using behavioural coding were qualitatively similar to those constructed using keeper ratings. However, the small sample size of four pandas meant there was insufficient power to detect a personality-behaviour relationship (Powell & Svoke 2008). Since personality is most strongly expressed when animals are presented with novelty (Réale et al 2007), observing and quantifying animals' reactions to environmental enrichment trials such as these may provide insight into personality (Watters & Meehan 2007; Powell & Svoke 2008). This method could be useful for quickly assessing specific personality traits with implications for management and welfare, such as fearfulness, in a few individuals (Watters & Powell 2012). If these assessments are to be relevant, however, the overall components of personality in the given species must first be identified. This requires a large-scale, multi-institutional study, similar to those carried out by King and Figueredo (1997) on chimpanzees and Wielebnowski (1999) on cheetahs, in which ratings provided by experienced keepers would be essential for identifying complex traits that may not be easily distinguishable using behavioural coding alone.

In order for the information provided by a personality study to be useful, the assessment of personality must be both reliable and valid (Gosling 2001; Gosling & Vazire 2002; Kuhar et al 2006; Meagher 2009; Freeman & Gosling 2010). Raters scoring the animals, or coders observing them, must agree in their assessments or observations. This can be confirmed by testing inter-rater (or inter-observer) reliability (Gosling 2001; Gosling & Vazire 2002; Martin & Bateson 2007; Meagher 2009). Therefore, it is important that as many people as possible provide ratings for each animal, and that those providing the ratings do so independently and do not confer on their answers (Gosling 2001). Studies that reported rater numbers employed between one and sixteen raters (n = 22, median = 3.7). Whilst it is not possible to assess inter-rater reliability with only one rater, this should not be considered a barrier to personality research, especially in a multi-zoo study. Animals rated by one person can still be included in overall analyses, and inter-rater reliability calculated for those animals rated by more than one keeper (eg Dutton 2008). Additionally, retest reliability (Carlstead et al 1999a) or correlating the ratings with behaviour can indicate the reliability of ratings provided by one person.

Using keeper ratings to assess personality has been criticised for being too subjective, anthropomorphic and not scientific (see Gosling & John 1999; Gosling 2001; Meagher 2009 for reviews), as it requires keepers to use their judgement to rate the animals based on their own knowledge and impression of the animals and their behaviour (Wemelsfelder 1997; Gosling 2001; Highfill et al 2010). However, the increasing body of evidence suggesting that observer ratings are both reliable and valid has added weight to the argument that this method is scientifically acceptable (Gosling 2001; Meagher 2009; Highfill et al 2010). Moreover, there is little evidence supporting the contention that ratings are tainted by anthropomorphism. Kwan et al (2008) found little correlation between self-personality ratings and ratings of dogs (Canis familiaris) provided by the same person, suggesting that the raters were not projecting their own characteristics onto their pets. Similarly, Weiss et al (2009) found no cross-cultural differences between ratings of chimpanzee personality obtained from American and Japanese observers, indicating that the cultural backgrounds and experiences of raters do not influence ratings.

Observer ratings have been used to great effect in assessing the welfare and personality of farm animals (Hessing *et al* 1994) and the personality of companion animals (Feaver *et al* 1986; Hsu & Serpell 2003). Indeed, the assessment of personality in domestic dogs has been used to indicate the suitability of individuals for roles as guide dogs (Serpell & Hsu 2001) and police dogs (Slabbert & Odendaal 1999), or as family pets (Hennessy *et al* 2001; Hsu & Serpell 2003). In the same way, keeper ratings can be used to investigate the welfare and personality of zoo animals.

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Inter-rater reliability was examined in 93% of studies using observer ratings (Table 1). The most common tests for interrater reliability were Kendall's coefficient of concordance (W) (eg Wielebnowski *et al* 2002; Martin 2005) and intraclass correlations within a General Linear Model, or GLM (eg King & Figueredo 1997; Weiss *et al* 2007; Uher & Asendorpf 2008). All authors found that inter-rater reliability was sufficiently high, indicating that raters are able to reach a statistically confirmed agreement on the expression of traits in individual animals.

The many different statistical methods used to test the reliability of keeper ratings make the comparison of results from different studies problematic (Freeman & Gosling 2010). The literature search revealed as many as five different methods of assessing inter-rater reliability (Table 1) and not all authors reported specific reliability data. Of those that did, some reported reliability for individual traits and others for personality dimensions. There is, therefore, a need for a standardised method of reporting reliability to enable comparisons to be made between studies (Freeman & Gosling 2010), especially when the same rating instrument is being used by different researchers. We strongly encourage researchers to report the total number of raters employed, the number of raters per animal (or a mean of this number), the specific reliability tests used and the results of those tests. In addition, it would be beneficial if researchers stated the criteria used to determine whether ratings were considered reliable or not.

To ensure that the personality dimensions extracted from trait ratings are as accurate as possible, traits with low interrater reliability (ie those that keepers are unable to agree on) should be excluded. Inter-rater reliability therefore needs to be examined *a priori* further analysis. The most appropriate reliability test will depend on the study design, so it is not possible for researchers to use a single, standard measure of reliability. Furthermore, checking whether reliability tests are significant is often problematic in zoo research, where small sample sizes can mean that the tests are underpowered (Powell & Svoke 2008). Researchers therefore need to use their own judgement in deciding whether the ratings obtained are reliable or not. For example, Martin (2005) considered raters to be reliable if their ratings correlated with those of another rater.

Research by King and colleagues (King & Figueredo 1997; Weiss *et al* 2002; King & Landau 2003; King *et al* 2005; Pederson *et al* 2005; Weiss *et al* 2006, 2007, 2009) has focused on the reliability and validity of primate personality assessments and the comparison of non-human primate personality dimensions with human personality. As well as providing information on the personality of zoo-housed chimpanzees and orangutans, this body of research has yielded important insights into the methods of assessing personality in zoo animals by using the same questionnaire, developed initially by King and Figueredo (1997), and the same inter-rater reliability tests. The Chimpanzee Personality Questionnaire was first used by King and Figueredo in 1997 to assess the personality of

100 chimpanzees, housed at twelve zoos. The results suggested that chimpanzee personality is composed of five dimensions that are comparable to human personality (the human Five Factor Model: Extraversion, Agreeableness, Dependability, Openness and Emotionality) plus one extra dimension: Dominance (King & Figueredo 1997). Interrater reliability was high and there were no significant differences between zoos among the ratings, suggesting that chimpanzee personality remains consistent across different collections (King & Figueredo 1997). The Chimpanzee Personality Questionnaire has since been developed and applied to other species (Weiss et al 2006, 2009), and is now known as the Hominoid Personality Questionnaire (HPQ, available online at http://extras.springer.com/2011/978-1-4614-0175-9).

Powell and Svoke (2008) argued that it may take many months of working with a particular animal before a keeper's ratings are reliable. This issue was briefly addressed by King et al (2005) in their comparative study of the personality of zoo-housed chimpanzees and chimpanzees housed in a naturalistic habitat at an African sanctuary. Zoo keepers had known the animals for an average of 6.5 years, whereas sanctuary staff had a mean of 6.9 months experience with the animals. Inter-rater reliability, assessed by intra-class correlations (King & Figueredo 1997), showed that the reliability of an individual's ratings was lower among the sanctuary raters (between 0.17 and 0.51) than the zoo raters (between 0.43 and 0.76). However, each sanctuary chimpanzee was rated by a mean of 16.2 raters, so the reliability of mean ratings across all raters was higher (between 0.77 and 0.94). The limited experience of the sanctuary raters was therefore mitigated by the large number of people providing the ratings (King et al 2005).

The experience of raters clearly affects their ability to provide reliable ratings (Dutton *et al* 1997; King *et al* 2005; Weiss *et al* 2007). Researchers should therefore endeavour to obtain information about the experience of those providing ratings and include rater experience as a factor in their analyses (Carlstead *et al* 2000; Gosling 2001; Meagher 2009).

Multi-institutional studies can require keepers from different countries and cultures to provide animal personality ratings, which may affect the reliability of those ratings. Two studies (King et al 2005; Weiss et al 2009) investigated the effects of the language and culture of raters on the reliability of ratings. King et al (2005) translated the HPQ into French to allow the keepers at a French-speaking sanctuary in Africa to rate their animals. This resulted in minor differences in the observed personality structure of the sanctuary chimpanzees, as two factors, Openness and Emotionality, observed in zoo-housed chimpanzees, did not replicate in the sanctuary chimpanzees. This discrepancy may have been caused by the small number of adjectives defining the Openness and Emotionality factors (King et al 2005). However, the authors also noted that these differences may have been due to inconsistencies in the translated questionnaire, as no back-translation was carried out to

check that the definitions of the adjectives provided in the English version of the questionnaire were the same as those provided in the French version (King *et al* 2005).

Chimpanzee personality ratings obtained by Weiss *et al* (2009) in a sanctuary in Japan were compared with those obtained by King and Figueredo (1997) in North America. Unlike the French version of the questionnaire (King *et al* 2005), the Japanese questionnaire was back-translated to correct inconsistencies. The ratings obtained by Weiss *et al* (2009) were as reliable as those obtained by King and Figueredo (1997), and also resulted in six personality dimensions, providing evidence that chimpanzee personality can be reliably assessed by raters of different cultures (Weiss *et al* 2009). These findings have important implications for future personality assessments in zoos, which must be comparable and consistent when ratings are provided by different cultures of keepers and in different languages.

Validity of ratings

The validity of a personality assessment refers to its ability to accurately measure animal personality (Gosling 2001; Meagher 2009). The results must therefore relate to the 'real world' and predict outcomes such as behaviour or breeding success (Gosling & Vazire 2002; Pederson *et al* 2005; Uher *et al* 2008).

Discriminant validity examines the lack of correlation between measures of two traits that are theoretically unrelated (Campbell & Fiske 1959; Meagher 2009; Freeman & Gosling 2010). Few studies described the assessment of discriminant validity, although King and Figueredo (1997), Weiss *et al* (2002) and King *et al* (2005) argued that ratings made using the HPQ were theoretically valid because the results demonstrated factor independence, as there were weak correlations between the six personality factors.

Convergent validity examines the relationship between a personality trait and other measures to which it is theoretically similar (Campbell & Fiske 1959; Meagher 2009; Freeman & Gosling 2010), and was tested in fifteen of the studies reviewed (Table 1). Fearfulness in cheetahs was positively correlated with the amount of time taken to approach a mirror, and cheetahs rated as more aggressive were significantly more likely to growl, hiss and stare at their mirror image (Wielebnowski 1999). Similarly, fearfulness was positively correlated with the amount of time taken for black rhinoceros to approach a paper towel (Carlstead et al 1999b). Convergent validity can also be demonstrated by correlating traits with biological factors, for example adrenal activity (eg Wielebnowski et al 2002) or ovarian cyclicity (eg Freeman et al 2009), or with quantitative records of behaviours related to the trait (eg King & Landau 2003; Pederson et al 2005). Interestingly, in the study carried out by Powell et al (2008), keeper ratings of socio-sexual behaviour were used to validate personality profiles obtained from behavioural coding during novel object tests, rather than the more conventional method of using ratings to construct personality profiles. This study uncovered a link between shyness and the frequency of socio-sexual behaviour in female pandas, which suggests that the personality profiles were validated by keepers' ratings of behaviour.

Applications of personality ratings to zoo animal management

Given that zoo keepers are able to reliably rate animal personality traits, and that these ratings are valid, knowledge of animal personality has the potential to inform important management decisions relevant to breeding and welfare.

Personality and captive breeding: individual breeding success

One focus of recent research into zoo animal personality has been the effect of personality on individual breeding success and the literature in this area is dominated by studies on those species that display poor reproductive success in captivity (Carlstead *et al* 1999a,b; Wielebnowski 1999; McKay 2003; Powell *et al* 2008), which might indicate underlying welfare concerns.

In her 1999 study, Wielebnowski found that cheetahs in North American zoos that were rated as more fearful by their keepers were less likely to breed successfully. However, in a further UK study, McKay (2003) reliably assessed cheetah personality using keeper ratings at nine zoos, but found no differences in the personality scores of breeders and non-breeders. The aim of McKay's study was to compare the personality and breeding success of individuals with environmental factors and husbandry routines, and an individual's breeding success was only analysed for the time spent at their current institution at the time of the study. This resulted in a small number of breeding individuals within the sample that did not allow an effect of personality on breeding success to be detected (McKay 2003).

In their study of black rhinoceros breeding success and environmental variables, Carlstead and her colleagues (Carlstead et al 1999a) analysed breeding success at the institutional level, rather than the individual level. Zoos with larger rhino enclosures were more successful in breeding black rhinoceros, and male Dominance scores were lower for males housed in larger enclosures. In a separate study, Carlstead et al (1999b) found that Dominance scores for males were negatively correlated with individual breeding success, and Dominance scores for females were positively correlated with breeding success. In addition, the number of births per year spent together was higher in pairs of rhinos consisting of a submissive male and a dominant or aggressive female (Carlstead et al 1999a,b). Taken together, these results suggest that the optimum conditions for breeding black rhinoceros in captivity include large enclosures, which facilitate submissive behaviour in males, which in turn affects pair compatibility.

Powell *et al* (2008) discovered a relationship between 'shyness' and socio-sexual behaviour in female pandas. This study is of particular interest because the authors used novel object and scent tests to assess the personality of the pandas, then compared these results to keeper ratings of socio-sexual behaviour. They found that females scoring highly on the 'shy' personality component were judged by their keepers to display fewer socio-sexual behaviours than females that were more 'confident' or 'bold'. This study also revealed that access to den sites within enclosures and

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interaction between keepers and pandas resulted in lower 'shyness' scores. The authors were therefore able to recommend simple measures to reduce shyness and increase socio-sexual behaviour, including increased keeper-panda interactions, which in turn could improve the reproductive success of female pandas (Powell *et al* 2008).

The results of some zoo animal personality studies have led researchers to make recommendations to reduce fearfulness to improve reproductive success (eg Powell et al 2008) and, since personality is heritable (Weiss et al 2000; Drent et al 2003), there is a danger that artificial selection is occurring for traits that predispose adaptation to a captive environment. Those same traits might be detrimental to survivorship of individuals in reintroduction programmes (McDougall et al 2006). There is, therefore, an emerging tension concerning the relationship between personality and fitness in wild and captive animals. In captivity, fearfulness appears to be a predictor of reduced reproductive success (Wielebnowski 1999; Powell et al 2008; Smith & Blumstein 2008) and chronic stress, characterised by increased faecal corticoid concentrations (Wielebnowski et al 2002). Conversely, fearful individuals in the wild are more likely to avoid predators and their chances of survival are therefore enhanced (Bremner-Harrison et al 2004; Watters & Meehan 2007). These examples demonstrate how monitoring personality in captivity could provide important insights into the effects of captive breeding and selection (McDougall et al 2006). A balance must be found between improving welfare and reproduction in captivity and conserving natural behaviours that improve the prospects of survival for reintroduced individuals.

Personality and captive breeding: pair compatibility

To maintain the genetic health of captive populations, recommendations for breeding pairs are made on the basis of kinship (Wedekind 2002; Ballou *et al* 2010; Asa *et al* 2011). However, individuals that are a good genetic match for one another may not necessarily produce offspring and behavioural incompatibility is often cited for the failure of a recommended pair to breed successfully (Carlstead *et al* 1999b; McDougall *et al* 2006; Freeman *et al* 2009; Lees & Wilcken 2009). This often results in an increased number of costly, time-consuming animal transfers, which can cause unnecessary distress to the individuals being moved (Lees & Wilcken 2009; Asa *et al* 2011). An important avenue of investigation in future studies should be the combination of personalities that might compose a successful breeding pair.

Personality may be linked with sexual selection (Schuett *et al* 2010, 2011) and some studies in birds have begun to explore this link. In a recent study by Schuett *et al* (2011), pairs of zebra finches (*Taeniopygia guttata*) with similar personality profiles raised healthier chicks than pairs whose personality profiles did not match. These finches were more exploratory and aggressive. The authors suggested that the personality of a male might indicate his strengths as a parent, and that females may choose mates on this basis (Schuett *et al* 2011). These findings seem to contrast those of Carlstead and her colleagues (Carlstead *et al* 1999a,b)

that black rhinoceros pairs with opposite personalities (a dominant female and a submissive male) were the most successful. This may be due to differences in the socioecology of the two species; since male rhinoceros have no involvement in parental care, females may use different characteristics to choose suitable mates. Little is currently known about the effects of personality combinations on the reproductive success of zoo mammals, despite the findings of Carlstead and her colleagues that personality is a good predictor of pair compatibility in black rhinoceros. Studies of animals with similar mating systems, and other behaviours, may be useful in understanding the link between personality and breeding success. Experimental studies in which the personality combinations of foster parents are manipulated (eg Schuett et al 2011) can be used to inform zoo researchers about the potential for pair compatibility to influence reproductive success. However, such manipulations are not possible in the zoo environment, so further research in this area will remain retrospective in its analysis of successful breeding pairs.

Personality and social groups

Appropriate social housing is crucial for the success of captive breeding programmes (Mellen 1991) and can have a substantial impact on the welfare of zoo-housed mammals (De Rouck *et al* 2005; Morgan & Tromborg 2007). Since personality affects the compatibility of breeding pairs, it follows that the personality of individuals within a social group can affect the social compatibility, stability and success of that group (Hessing *et al* 1994; Watters & Meehan 2007; Miller & Kuhar 2008; Freeman *et al* 2010b). Thus, the assessment of personality can be used to inform decisions about which individuals could be placed together when planning the introduction of individuals into social groups (Stoinski *et al* 2004; Kuhar *et al* 2006; Powell & Svoke 2008).

A few studies investigated the effects of personality on social group cohesion. In their assessment of gorilla personality in North American zoos, Gold and Maple (1994) described four factors of gorilla personality: Extroverted, Dominant, Fearful and Understanding (the Gorilla Behaviour Index, or GBI), and suggested that their instrument for rating gorilla personality could be used to inform management decisions. However, due to the small number of individuals on which behavioural data were collected, few correlations between these personality factors and behaviour were observed.

Kuhar *et al* (2006) attempted to validate the GBI and reassessed 119 male gorillas, collecting behavioural data on a subsample of 25 individuals at seven zoos. Their results indicated a stronger relationship between the GBI and observed behaviours. Furthermore, the Understanding factor was related to social housing conditions, as males scoring highly on this factor were more likely to be housed in social groups, displaying high rates of affiliative behaviour and little contact aggression, whilst solitary males that had been removed from social groups due to frequent instances of aggression scored lower on the Understanding factor (Kuhar *et al* 2006). This result raises the question of cause and effect; it is possible that solitary gorillas scored lower on this dimension because they were housed alone. However, the authors argue that, in either case, the Understanding factor appears to be predictive of those gorillas that might benefit from solitary housing (Kuhar *et al* 2006). In addition, the authors reported two instances of the successful introductions of juvenile male gorillas to a silverback male. In both cases, the silverbacks scored highly on the Understanding personality factor.

Freeman and her colleagues (Freeman et al 2004, 2009, 2010a,b) used information obtained from keeper questionnaires to investigate relationships between social behaviour, dominance status and ovarian activity in captive Asian and African elephants. In this body of work, the term 'temperament' is used to describe social behaviour and dominance, and the results have shown that elephant keepers are able to reliably rate the behaviour of female African and Asian elephants and predict the social rank of elephants in their care (Freeman et al 2010a,b). Keeper ratings of social behaviour correlated strongly with direct observations of social interactions among African elephants (Freeman et al 2010b) and females rated as dominant by their keepers were significantly more likely to approach, push and displace other elephants in the herd (Freeman et al 2010a). Freeman et al (2004) suggested that a female's personality may determine her social rank, since more aggressive females were more likely to be dominant. When viewed alongside the findings of Freeman et al (2009), that dominant females were more likely to show ovarian acyclicity, the results of this research indicate the importance of social factors in the success of captive breeding programmes, and illustrate how keeper ratings could be used to further our understanding of the effects of individual differences in personality on social group behaviour and reproductive success among socially housed mammals.

Discussion — incorporating personality assessment into zoo animal management

Recently, several authors identified the need for zoo animal personality assessment to be incorporated into existing zoo management practices (McDougall *et al* 2006; Whitham & Wielebnowski 2009; Watters & Powell 2012), yet little effort has so far been made to summarise the findings of personality research carried out in zoos. In the present paper, bringing together research from various fields allowed the reliability and validity of zoo animal personality studies to be investigated, with a view to evaluating the feasibility of using keeper ratings to assess zoo animal personality to complement existing zoo record-keeping techniques.

The small number of papers identified in our literature search is surprising, considering that zoos are an excellent resource for studying animal personality. Zoo keepers are familiar with their animals and zoos provide researchers the opportunity to conduct longitudinal investigations into various aspects of personality, including heritability and environmental effects (Watters & Powell 2012). The general reduction in non-human animal personality studies between the 1960s and the 1990s, highlighted by Weinstein *et al* (2008), may explain the lack of published research into zoo

animal personality. Only recently has interest in non-human animal personality research increased and its potential applications to animal welfare are now becoming clear.

The literature search revealed that keeper ratings are most commonly used to assess the personality of zoo animals. The majority of studies used keeper ratings as a method of data collection and evidence from the growing body of research into zoo animal personality demonstrates that zoo keepers are able to reliably rate animal personality traits based on their knowledge and long-term observations of the animals in their care (King & Figueredo 1997; Carlstead et al 1999a,b; Wielebnowski 1999; Wielebnowski et al 2002; Kuhar et al 2006; Whitham & Wielebnowski 2009; Freeman et al 2010b). The ratings of zoo keepers working in different zoos, in different countries, speaking different languages can be reliable indicators of animal personality (King & Figueredo 1997; King et al 2005; Weiss et al 2009), although further research is required on the effects of zoo keepers' experience on the reliability of their ratings. Using keeper ratings to assess personality facilitates the collection of data on many individuals at different institutions, whilst behavioural coding can give a quick appraisal of a particular trait in a few individuals. There is great potential for personality assessments to be incorporated into zoo management practice to improve the welfare and breeding success of zoo mammals.

The reviewed studies also provided evidence that the results of personality assessments can be validated and are related to behaviour, reproductive success and biological factors, such as adrenal activity and reproductive cyclicity in females. A validated personality questionnaire is a valuable instrument for zoo professionals and could help to identify possible explanations for the reproductive failure of individuals (Carlstead et al 1999a,b; Wielebnowski 1999; Powell et al 2008). Understanding individual differences in personality in species that are prone to reproductive problems in captivity might make clear the reasons why certain individuals do not fulfil their reproductive potential. In addition, this may lead to improvements in the captive environment for those species (Powell et al 2008). However, whilst encouraging reproduction is vital to the success of captive breeding programmes, care must be taken to avoid selection for traits that will be disadvantageous to those individuals should they be released into the wild (McDougall et al 2006).

If zoos are to be successful in their aim of conserving vulnerable species, the behaviours that are specific to those species must also be conserved (Markowitz 1997). In addition, zoo animals are integral to the educational role of the modern zoo and the behaviour and personality of animals may affect the perceptions of zoo visitors (Watters & Powell 2012). Since variation in personality exists in wild populations (Dingemanse & Réale 2005), maintaining variation in the captive population is integral to the success of captive breeding programmes. The effects of changes in personality due to selection remain largely unknown and further research in this area is required (Dingemanse & Réale 2005; McDougall *et al* 2006). Given that personality is heritable, the systematic monitoring of zoo animal

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personality in multiple institutions could be used to track changes in personality due to captive breeding through the generations, to assist the retention of natural behavioural characteristics and further our understanding of artificial selection in captive breeding.

Zoo professionals are often of the opinion that certain individuals are more compatible, which affects the success of breeding pairs (Carlstead et al 1999b), and this anecdotal evidence has been given some empirical backing (Carlstead et al 1999b; Schuett et al 2011). In addition to genetic analysis, personality assessments could therefore be used to recommend behaviourally compatible breeding pairs and improve reproductive success in captive breeding programmes. Of course, personality cannot override genetic considerations when recommendations for breeding pairs are made by studbook keepers, but they could give an indication of which pairs are likely to be successful. The issue of pair compatibility is an emerging topic in the field of animal personality research and further investigation is required before the effects of personality on the success of breeding pairs can be fully understood. Since there is little or no scope for experimentally manipulating pair compositions, zoo breeding records will be a valuable resource for retrospective investigations of pair compatibility. In addition, personality profiles could provide an indication of how an animal might react to events such as transfers between collections and introduction into new social groups. Socially housed species could therefore benefit from personality assessments, as social cohesion could be improved if the personalities of individuals to be housed together are known. Consequently, information about the personality of an individual could be invaluable to staff at institutions involved in co-ordinated captive breeding programmes.

Personality questionnaires have so far been devised and validated for some zoo-housed species (great apes: Gold & Maple 1994; King & Figueredo 1997; Murray 1998; Kuhar et al 2006; Weiss et al 2006; black rhinoceros: Carlstead et al 1999b; cheetahs: Wielebnowski 1999) and could prove useful tools for keepers of these species. Following the finding by Weiss et al (2007) that personality was consistent across laboratory and zoo-housed chimpanzees, questionnaires that have been validated for use with laboratory animals may be suitable for use with zoo animals. In order for personality assessments to be successfully implemented across multiple collections, there is a need for standardised keeper questionnaires to be devised for more zoo-housed species. We use the term 'standardised' here to denote a personality questionnaire for a specific species, that can be distributed to all collections holding that species. Reliability data must be obtained and we encourage researchers to report all aspects of their reliability analyses, including test results and numbers of raters. Questionnaires must also be validated by comparing the results to other measures, such as behavioural observations. Information from personality assessments could then be shared between collections, with the knowledge that the assessment has been carried out using the same rating instrument for all the individuals. Thus, the development of standardised questionnaires will

allow the results of personality assessments to be comparable between institutions and used alongside current animal record-keeping systems.

Questionnaire development will require much research in the first instance and will involve an initial, comprehensive investigation into a species' personality components. Following this, certain aspects of personality that are more relevant to welfare and management can be quickly assessed. The assessment of a salient personality characteristic that may be strongly correlated to welfare, such as fearfulness, can only be relevant if the overall components of personality have been identified. However, once a personality questionnaire has been validated for a particular species, many researchers and zoo professionals can benefit from it (Meagher 2009; Whitham & Wielebnowski 2009).

To make the research process more efficient, Watters and Powell (2012) suggest that questionnaires be developed at the level of family, rather than species, to which items could be added as required by individual projects. Indeed, the development of the HPQ, which has been used to investigate chimpanzee and orangutan personality (King & Figueredo 1997; Weiss *et al* 2002; King *et al* 2005; Pederson *et al* 2005; Weiss *et al* 2009), has shown that it is possible to use the same questionnaire to investigate personality across species. We agree that "the basic survey should be able to assess all the major dimensions of personality" (Watters & Powell 2012; p 10), and would therefore advocate that such questionnaires should be extensively validated to ensure that they accurately represent the fundamental personality traits of all the intended species covered.

Animal welfare implications

The importance of individual differences has long been recognised in the study of animal welfare. Animals vary in their responses to the captive environment and consequently there is variation in the degree of well-being experienced by individuals. Personality assessments can be used to provide insight into the subjective mental experiences, tendencies and dispositions of captive animals, and can inform important management decisions relevant to welfare. Information from personality assessments could be used to assess the reproductive failure of individuals, which might indicate underlying welfare concerns, and to improve captive breeding recommendations by identifying compatible breeding pairs. Social group cohesion could also be improved if the personalities of current and future group members are known. This could prevent chronic stress resulting from housing incompatible individuals together, and reduce the potential for aggressive interactions. The assessment of personality, with careful application, is a potentially valuable tool for zoo professionals for improving the welfare of the animals in their care.

Acknowledgements

CT is supported by a Graduate Teaching Assistantship in the School of Environment and Life Sciences at the University of Salford, UK. We are grateful to Nadja Wielebnowski and two anonymous reviewers for insightful comments that helped to improve this manuscript.

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