Do opposites attract? Effects of personality matching in breeding pairs of captive giant pandas on reproductive success

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ARTICLE INFO

ABSTRACT

Successful and cost-effective conservation breeding programs rely largely on animals doing what should come naturally: mate & reproduce. Behavioral management, especially that targeting mate compatibility and choice, will be important to achieve breeding goals efficiently. The endangered giant panda, *Ailuropoda melanoleuca*, was once notorious for its poor reproductive performance in captivity. Although the panda breeding program has experienced great improvement in recent years, we hypothesized that a better understanding of the role personality traits play in mating behavior could further improve reproductive performance. We used animal caretaker surveys and novel object tests to characterize pandas according to several personality traits—including exploratory, aggressiveness, excitability, fearfulness, and general activity—and tested how variation in these traits influenced mate compatibility and offspring production. Our findings indicate that specific combinations of personality traits showed better reproductive performance than others. Sometimes personality trait similarity enhanced reproduction and sometimes it impaired reproduction, depending on the trait. For example, Excitable males paired with Low-Excitable females had better reproductive outcomes, but pairs with Low-Fearful males regardless of the female's Fearfulness performed better. Males that were more Aggressive than their female partner were more likely to mate and produce cubs than when the female had a higher level of Aggressiveness than the male. Applying these results to breeding management strategies should result in higher reproductive rates and the production of more candidates for China's panda reintroduction program. These results highlight the potential importance of associative mating patterns based on personality for conservation breeding programs for a large number of other species.

1. Introduction

As wildlife species become imperiled at increasingly rapid rates (Barnosky et al., 2011), conservation managers increasingly turn to ex-situ conservation breeding programs to mitigate species loss and/or supplement dwindling wild populations (Conde et al., 2011; Fa et al., 2011). However, efforts to create self-sustaining populations through ex-situ conservation breeding have often failed to produce animals to replacement (Lees and Wilcken, 2009) let alone to provide a surplus of animals for reintroduction programs. This failure may be due, in part, to breeding methods used in captive-breeding programs.

Typically mates are chosen on the basis of minimizing inbreeding and maintaining founder representation, goals that are widely recognized as important (Ballou and Lacy, 1995), but may emphasize genetic suitability at the expense of behavioral compatibility (Asa et al., 2011; Rabin, 2003; Swaisgood and Schulte, 2010). If a pair is behaviorally incompatible and does not mate, then the potential genetic benefits of producing offspring from that pair are entirely lost to the captive population. Thus, improving behavioral mate compatibility to increase reproductive success is particularly important in conservation breeding.

Personality—repeatable consistent individual differences in behavior across time and situations (Carter et al., 2013)—has an important but relatively untapped role to play in conservation (Blumstein et al., 2006; Bremner-Harrison et al., 2004; McDougall et al., 2006). Once rooted in the field of human psychology, personality is now an accepted phenomenon across an array of taxa (Gosling, 2001; Sih et al., 2004). Personality is now recognized to play an important role in a variety of

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ecological and evolutionary processes, including population persistence, individual fitness, movement ecology, invasion biology, speciation, and species distribution and abundance (Dall et al., 2004; Ingley and Johnson, 2014; Réale et al., 2007; Sih et al., 2004; Sih et al., 2012).

Personality also plays an important role in mate selection, compatibility and other aspects of reproduction governed by sexual selection (Schuett et al., 2010). It is therefore surprising that efforts to define and manage compatible personality types for conservation breeding has not figured more prominently, and has rarely been subjected to rigorous testing, although a recent review suggests that personality may play a large role in mate compatibility, thus warranting further investigation (Powell and Gartner, 2011). Mates may choose partners with specific personality traits because of genetic compatibility, because some personality characteristics indicate quality, or because certain personality types might be able to provide more effective parental care (Schuett et al., 2011). Matings between compatible personalities may therefore confer fitness benefits. Although few studies address this question, most point to assortative mating among certain personality combinations (typically similar personalities; reviewed in Schuett et al., 2010) which increase reproductive success and offspring survivorship. For example, great tit pairs that display similar exploratory behaviors raise chicks in better physical condition (Both et al., 2005) and produce more offspring than dissimilar pairs (Dingemanse et al., 2004), and stellar jay pairs similar in 'explorative tendencies' and in 'willingness to take risks' are more likely to fledge offspring than dissimilar pairs (Gabriel and Black, 2012). However, to date these tests of personality similarity have only been applied to species that exhibit biparental care, not species that exhibit solely maternal care as seen in most mammals. On theoretical grounds, mutual mate choice and compatibility are thought to be more important for monogamous, biparental species because pairing involves a greater investment than in polygynous species without paternal care (Clutton-Brock and McAuliffe, 2009).

The role of personality in mate compatibility has significant implications for ex-situ conservation breeding programs. Specific personality traits (such as aggressiveness and fearfulness) have been linked to reproductive success in some zoo-bred species (Carlstead et al., 1999; Wielebnowski, 1999; Powell et al., 2008), however the role of personality in mate compatibility has not been investigated previously in the conservation breeding context, despite its clear potential to increase reproductive rates. There are other potential benefits to investigating the role of personality in conservation breeding, As certain personalities may be more likely to prosper in captive settings, artificial selection for or against specific personality traits may expedite domestication processes, making conservation-bred animals less suitable for release back to the wild (McDougall et al., 2006).

Here, we investigate the role of personality in determining mating outcomes in an iconic endangered species, the giant panda (*Ailuropoda melanoleuca*). Previous research with this species has demonstrated that personality traits of individual pandas are associated with mating behavior and reproductive output (Ellis et al., 2006; Powell et al., 2008), but no studies have examined how the interaction of personality traits between the two individuals of a mating pair influences reproductive outcomes. Given how much study has been devoted to understanding the reproductive behavior and biology of this species (reviews in (Wei et al., 2015; Wenshi, 2014; Wildt et al., 2006), it is surprising that this question has remained unanswered for so long. As a relatively solitary species with no paternal care (Schaller et al., 1985) and strong male-male competition for mates (Nie et al., 2012), perhaps the role of mate choice and compatibility have been overlooked due to investigational bias (Martin-Wintle et al., 2015). Specifically, in the present study we tested whether similarity in personality traits such as Aggressiveness, Excitability, and Fearfulness—as determined by novel object tests and caretaker surveys—improve measures of reproductive success such as mating success and offspring production.

2. Methods

2.1. Study site and species

We conducted personality studies on 19 female and 10 male giant pandas during the non-breeding season (May–October) of 2012 and 2013 at the Chinese Conservation and Research Center for the Giant Panda at Bifengxia near Ya'An, China in the Sichuan Provence. All subjects were sexually mature, with ages ranging from 6 to 18 years, and all had previous mating experience prior to the study. Subjects included in the analysis were placed with one opposite-sex individual for mating purposes on at least three different occasions with no more than three separate individuals. Our resulting sample size for dyads, the unit used for analysis, was 30 unique dyads for keeper surveys and 18 unique dyads for novel object tests. Housing and animal husbandry practices are described in (Martin-Wintle et al., 2015). Animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998; Assurance #: A3675-01) were followed by all facility operators.

2.2. Personality trait evaluation

We assessed personality of giant pandas through animal caretaker personality surveys and novel object tests. Although some scientists may be skeptical of the validity of caretaker surveys, previous research has shown that they are a reliable method for assessing personality in several species (Gosling, 2001; Smith and Blumstein, 2008) including the giant panda (Powell et al., 2008). Evaluative surveys also have the advantage of providing an integrative summary of behavioral expression across time and contexts, thus incorporating the core requirement of repeatability in personality assessment into a single integrated variable. Primary caretakers for each panda completed a survey that included 23 behavioral adjectives reflecting personality (Table 1) rated on a 10-point Likert scale. Caretakers were instructed to score the subject compared to all pandas they have known. Surveys were developed after the methods of Wielebnowski (1999), Powell and Svoke (2008), and Shepherdson et al. (2013).

We investigated the consistency of inter-individual differences in behavioral responses to novel objects from May – August 2012 and 2013. We conducted four enrichment trials using four different novel objects, thereby reducing the effects of habituation to one novel object, which can be problematic when using novelty tests to measure personality (van Oers et al., 2005). These novel objects included: 1) 20 cm^3 ice blocks, 2) ice blocks with ½ apple and ½ carrot (fruitcicles), 3) tubs (75 cm × 60 cm × 60 cm) of water with two apple halves and one carrot, and 4) a rubber ball with a diameter of 75 cm. All trials were performed between 1330 and 1600. We recorded panda behavior for one hour after introduction of the novel object to the enclosure. Trials for individual subjects were separated by >24 h and were presented in randomized sequence to giant pandas. Each subject in the novel object study ($N = 18$) was presented once with each novel object (a total of 4 novel object trials) during the year. Ten individuals were presented with novel objects in both years to calculate within-individual sources of variation and repeatability (see below).

We used instantaneous point sampling at one-minute intervals to estimate the percentage of time spent in various activities, later grouped into major behavioral categories (Table 2). We also recorded total time and all frequencies of key behaviors (Table 2). Because we were interested in response to novelty in general and not to a specific object, we pooled data across novel object trials for an individual for each year of the study.

2.3. Mating procedure & reproductive performance

Specifics of the mating procedure are described in (Martin-Wintle et al., 2015). Response variables included whether a mating attempt failed