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

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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

Table 1
Behavioral definitions of adjectives used for questionnaire ratings. Definitions are obtained and/or modified from Wielebnowski (1999), Powell and Svoke (2008), and Shepherdson et al. (2013).

Vigilant	Pays attention to the surroundings and changes in surroundings
Active	Moves frequently (e.g. walks, climbs, paces a lot)
Aggressive to conspecifics	Frequently reacts hostile (e.g. attacks, growls) toward other pandas
Aggressive to people	Frequently reacts hostile and threatening toward people
Calm	Not easily disturbed by changes in the environment
Curious	Readily approaches and explores changes in the environment
Stereotypical	Shows stereotypic or unusual behaviors
Excitable	Overreacts to changes in the environment
Friendly to conspecifics	Social; initiates and seems to seek proximity of other pandas
Friendly to people	Initiates proximity; approaches enclosure bars readily and in a friendly manner
Fearful of conspecifics	Retreats and hides readily from other pandas
Fearful of people	Retreats readily from people
Anxious	Seems uneasy and worried about the environment or new events
Playful	Initiates and engages in play behavior (seemingly meaningless, but non-aggressive behavior) with objects and/or other pandas
Self-confident	Moves in a seemingly confident, well-coordinated, and relaxed manner
Clever	Learns quickly to associate certain events and appears to remember for a long time.
Innovative	Seems original and creative; solves problems
Solitary	Spends time alone; avoids company
Nervous	Shows restraint in movement and posture; easily agitated or alarmed
Vocal	Frequently and readily vocalizes
Bad tempered	Easily annoyed or made angry
Not Interested	Unresponsive to and seemingly unaware of significant events/situations
Shy	Reluctant to engage in social situations

or succeeded (i.e., copulation occurred with intromission) and whether cubs were produced.

2.4. Data analysis

2.4.1. Principal component analysis

Principal component analysis (PCA) is used in personality assessment to reduce variables into a substantially smaller set of uncorrelated variables that have simpler and more powerful explanatory value (Carter et al., 2013). We used PCA for data reduction purposes for both survey and novel object data. Eigen values, scree plots, and number of unique loadings on a variable were examined to determine which components were retained for interpretation. Four components of the PCA personality assessment obtained from caretaker surveys accounted for 53.3% of the observed variance: 1) Aggressive, 2) Playful-Clever, 3) Fearful, and 4) Excitable (Supplementary Material Table 1). Four components of the PCA personality assessment obtained from novel objects accounted for 60% of the observed variance: 1) Neophobic, 2) Active-Excitable, 3) Inactive-Communicative, and 4) Food Anticipatory (Supplementary Material Table 2). These components were given convenient descriptive labels without making assumptions regarding underlying motivation. PCA component scores were used to rank pandas into 'high' (H) or 'low' (L) based on the mean score of each component within a sex with 'high' being any value that fell above the mean and 'low' being any value below the mean.

2.4.2. Within-individual sources of variation and repeatability

We used a General Linear Mixed Model (GLMM) to evaluate the within-individual relationship between PCA scores and the following explanatory variables: age, weight (kg), test sequence, and gender,

Table 2
Behavioral definitions for novel object response study (sensu Swaisgood et al. (2001)).

Object Interaction	Any behaviors that involved direct interaction with the object such as manipulating, pawing, biting, carrying, and pushing
Latency to touch	
Total time	
Total visits	
Door & Human Directed Behaviors	Behavior and attention is directed toward the inner enclosure door toward food, caretaker, or bedroom area and away from the object.
Total time	
Total visits	
Total point samples human oriented	
Stereotypical Behaviors	Animal engages in unvarying and repetitive (three times or more) acts that have no obvious goal or function.
Total time	
Total different types	
Total point samples	
Total Active Behaviors (frequency)	Any behaviors that involve movement, including sustained locomotion in a non-stereotyped manner, searching for food, climbing, and responding to stimuli.
Chemical Communication	Any behaviors that involve scent marking, body rubbing, scent anointing, sniffing/olfactory investigation, flehmen, urinating, and defecating.
Total scent marks	
Total point samples	
Vocal Communication	Affiliative vocalizations include: bleats, chirps and sex squeal.
Total point samples affiliative	Aggressive vocalizations include: chomps, huffs, moans, snorts, barks, growls, and roars.
Total point samples aggressive	
Maintenance Behaviors	Resting included lying or sitting down, either awake or asleep.
Total point samples drinking	Alert, standing (can be bi-pedal), sitting or lying quietly, but remaining attentive, moving head from side to side and/or sniffing air, perhaps attending to external stimuli.
Total point samples resting	
Total point samples stationary alert	

with subject as a random factor. Only data for those individuals measured twice were included in this analysis ($N = 10$). All novel object repeat trials took place approximately one year after the original trial. We considered models containing all explanatory variables and all possible two-way interactions. We used the *glmulti* package in R that compares all candidate models and ranks them based on their Akaike information criterion (AIC) and Bayesian information criterion (BIC) (Calcagno and de Mazancourt, 2010). Models were considered to be significantly different from each other if ANOVAs resulted in $p \leq 0.05$.

Repeatabilities were calculated using the *rpt.aov* function in the *rptR* package (Nakagawa and Schielzeth, 2010). We used PCA scores as the response variable and panda identity as the group variable. Intraclass correlation coefficients (ICC) were also calculated using the *ICCest* function in the R package *ICC* (Wolak et al., 2012).

2.4.3. Assortative mating and reproductive success

Mate dyads were considered to be statistically independent, as the same male and female were never paired together more than once in our data set. We conducted three fundamental analyses. (1) *All personality combinations.* Mate dyads were characterized by their personality trait ranks into one of the following four group combinations: 1) female low, male low (L_L), 2) female low, male high (L_H), 3) female high, male low (H_L), and 4) female high, male high (H_H). (2) *Mate dyad similarity*. Mate dyads were grouped into either similar (L-L or H-H) or dissimilar (L-H or H-L) pairs. We predicted that if pairs' overall similarity in personality contributed to mate compatibility, then pairs with similar personality across multiple traits would have enhanced reproductive performance. (3) *Mate dyad relative personalities*. Because ‘low’ and ‘high’ was determined from scores above the mean (‘high’) or below the mean (‘low’) *within* sexes, these categories did not necessarily give a relative score for the pair (i.e., whether a male was lower or higher than a female on a given PCA component). Therefore, we also categorized pairings based on the male's PCA score relative (higher, lower) to the female's score.

To investigate direction and strength of relationships between personality traits and reproductive performance we conducted unpaired ANOVAs or Kruskal-Wallis tests. If significant differences were found, Tukey HSD tests were used for post hoc analyses. Statistical significance (α) was set at $p < 0.05$ for all tests, but we also followed marginally significant tests ($p < 0.08$) with post hoc tests. Where assumptions of normality and homogeneity of variance were not met we used nonparametric statistics. Analyses were performed in R Studio (Version 0.98.981; R Studio Inc. 2009–2013; R Version 3.0.2) for Mac OS X.

3. Results

3.1. Within-individual sources of variation and repeatability

Best models for all PCA components obtained from novel object tests and repeatability analysis are reported in Supplementary Table 3 and the accompanying text. There was significant support for the presence of consistent individual variation in response to novel objects based on the individual PCA components. The Neophobic PCA component showed very low repeatability and the other three PCA components showed moderately strong repeatabilities.

3.2. Mate dyad personality combinations

Specific personality trait combinations as evaluated by caretaker surveys were associated with higher reproductive success than others (Tables 3 & 4). Tukey HD post hoc tests indicated that Low-Aggressive females paired with High-Aggressive males (L_H) had more successful intromissions and had a higher probability of producing cubs than other personality combinations except for H_H combinations (Fig. 1a). Mate dyad combinations with regard to Fearfulness influenced intromission success but not cub production (Table 3), with dyads composed of Low-Fearful males and females (L_L) and dyads composed of High-Fearful females mated with Low-Fearful males (H_L) showing higher intromission successes than dyads where both male and female were rated High-Fearful (Fig. 1b; Table 4). Additionally, L_L mate dyads had significantly more intromissions than H_H but not H_L or L_H Fearful combinations. Tukey HD post hoc tests indicated that Low-Excitable females paired with High-Excitable males had significantly more intromission successes than H_H dyads (Fig. 1c; Table 4).

Personality combinations within the PCA component scores as determined by novel object tests showed no significant difference in intromission success or cub production between groups on any of the personality characteristics measured, however, this may have been due to small sample sizes in certain combinations of groups (Tables 5 & 6).

3.3. Mate dyad similarity in personality

The analysis presented above evaluated whether specific combinations of personality traits influenced reproductive outcomes. Here we tested the hypothesis that similarity in personality traits influences reproductive outcomes. To achieve this, we categorized pairings as either similar (L_L, H_H) or dissimilar (H_L, L_H) with regard to each of the personality traits.

Table 3
Relationship between reproductive success and caretaker-derived personality types. Statistical analyses of reproductive performance for mate dyads of giant pandas and their relationship to personality scores obtained from caretaker survey component (PCA) for Aggressive, Playful-Clever, Fearful, and Excitable. ‘Combinations of personalities’ reports the significance of the general ANOVA or Kruskall-Wallis test (parametric versus nonparametric data distributions) for differences between all pairing types (L_L, L_H, H_L, H_H). ‘Personality similarity’ reports the significant difference between pairs that were similar in personality (grouped L_L or H_H) and those that were dissimilar in personality (grouped L_H, H_L). ‘Relative personalities’ reports the significant difference among pairs composed of males ranked higher than the female versus pairs composed of males ranked lower. Bold numbers indicate significant difference between PCA personality groups at $p < 0.05$, italics represent marginally significant differences between PCA personality groups at $p < 0.08$.

Variable	PCA Component			
	Aggressive	Playful-Clever	Fearful	Excitable
Combinations of personalities				
Intromission	*2.47 (0.06)*[a]	0.90 (0.83)[a]	**11.66 (0.009)**[b]	**7.51 (0.05)**[b]
Cub production	**3.75 (0.05)**[a]	2.92 (0.40)[a]	2.06 (0.13)[a]	0.63 (0.60)[a]
Similarity in personalities				
Intromission success	1.83 (0.18)[c]	0.14 (0.71)[c]	1.22 (0.27)[c]	**6.79 (0.009)**[c]
Cub production	0.55 (0.46)[c]	0.36 (0.55)[c]	0.02 (0.88)[c]	1.08 (0.30)[c]
Relative personalities				
Intromission	**5.13 (0.02)**[c]	0.83 (0.77)[c]	1.66 (0.20)[c]	0.03 (0.86)[c]
Cub production	**3.95 (0.05)**[c]	0.07 (0.80)[c]	1.91 (0.17)[c]	0.18 (0.67)[c]

[a] ANOVA; $F_{3,26}$ (p value).
[b] Kruskall-Wallis; χ^2 (p value).
[c] Chi-squared tests; χ^2 (p value).

Table 4
Relationship between reproductive success and caretaker surveys. Values and measures of reproductive success for mate dyads of giant pandas grouped by personality similarity and dissimilarity based on caretaker survey principal component (PCA) scores for Aggressive, Playful-Clever, Fearful, and Excitable. Superscripts indicate differences between groups based on *t*-tests or Mann-Whitney *U* tests at $p < 0.05$. Matching superscript letters indicate no difference between groups with differing letters indicating a significant difference. Female rankings are designated first and male rankings second.

Variable	Mate dyad group			
	L_L	L_H	H_L	H_H
Aggressive PCA component score				
Total mate pairings	7	11	6	6
Total successful intromissions	2^{b}	9^{a}	2^{b}	$4^{a,b}$
Cubs produced	1^{b}	7^{a}	1^{b}	$3^{a,b}$
Cubs maternally reared	0	7	1	3
Female[1]	−0.31 ± 0.31	−0.59 ± 0.60	0.19 ± 0.13	0.67 ± 0.48
Male[1]	−1.2 ± 0.19	0.48 ± 0.62	−1.10 ± 0.24	0.75 ± 0.84
Playful-Clever PCA component score				
Total mate pairings	7	9	6	8
Total successful intromissions	3^{a}	5^{a}	4^{a}	5^{a}
Cubs produced	2^{a}	4^{a}	1^{a}	5^{a}
Cubs maternally reared	2	4	0	5
Female[1]	−0.45 ± 0.38	−0.55 ± 0.41	0.97 ± 0.59	0.98 ± 0.50
Male[1]	−0.40 ± 0.34	0.99 ± 0.52	−0.26 ± 0.09	0.94 ± 0.55
Fearful PCA component score				
Total mate pairings	4	6	9	11
Total successful intromissions	4^{a}	$2^{a,b}$	8^{a}	3^{b}
Cubs produced	3^{a}	1^{a}	5^{a}	3^{a}
Cubs maternally reared	3	1	5	2
Female[1]	−0.54 ± 0.23	−0.74 ± 0.41	1.31 ± 0.56	1.01 ± 0.60
Male[1]	−1.03 ± 0.20	−0.23 ± 0.20	−1.03 ± 0.20	−0.26 ± 0.02
Excitable PCA component score				
Total mate pairings	8	7	4	12
Total successful intromissions	3^{b}	7^{a}	$2^{a,b}$	5^{b}
Cubs produced	3^{b}	$4^{,b}$	$1^{a,b}$	4^{b}
Cubs maternally reared	3	4	1	3
Female[1]	−1.04 ± 0.60	−1.01 ± 0.54	0.73 ± 0.29	0.58 ± 0.27
Male[1]	−0.58 ± 0.61	0.57 ± 0.38	−0.62 ± 0.41	0.47 ± 0.15

[1] Means ± standard deviation of the component scores for each sex within the group.

Of the personality traits evaluated with caretaker surveys, similarity influenced reproductive outcomes only for Excitability, with pairs that were dissimilar more likely to achieve successful intromission than those with similar personalities (Tables 3 & 4; Fig. 2a). Our analysis for novel object tests indicated that pairs that were similar for the trait Neophobic (Fig. 2b) and dissimilar for the trait Food Anticipatory (Fig. 2c) were more likely to have intromission success and produce cubs (Tables 5 & 6).

3.4. Mate dyad relative personality scores

Here we tested the hypothesis that similarity for personality traits *relative to the opposite sex partner* influences reproductive outcomes. In these analyses we categorized pairs according to whether the male's score was higher or lower than the female's score. Among those personality traits evaluated by caretaker surveys, only Aggressiveness influenced reproductive outcomes. Males that were more Aggressive than their female partner were more likely to achieve intromission and produce cubs than pairs where the male was less aggressive than the female (Fig. 3a; Tables 3 & 4). Chi-square tests performed on PCA components obtained from pooled novel object tests revealed that dyads composed of males that were higher on the Inactive-Communicative PCA component scores than females had significantly more intromission success and cub production than dyads composed of males with lower scores than females (Fig. 3b; Tables 5 & 6).

4. Discussion

We have shown that personality trait matching is an important determinant of reproductive outcomes in the iconic giant panda and, by extension, may be important for many other conservation-dependent species where this possibility has not been tested. Giant pandas mated assortatively with regard to several personality traits—including Aggressiveness, Excitability, Neophobic, Inactive-Communicative, and Food Anticipatory—tested in two contexts, novel object presentations and caretaker surveys. We found specific combinations of personality traits that resulted in higher intromission or greater cub production. Trait dissimilarity (for Excitability and Food Anticipatory) and trait similarity (for Fearfulness) were associated with better reproductive outcomes. Pairs were more likely to mate and produce cubs if the male was more Aggressive than the female and when both animals within a pair were Low-Fearful. The latter finding is consistent with previous research demonstrating that "bold" female pandas were judged to be less aggressive toward male partners in caretaker surveys (Powell et al., 2008), although our measures of personality traits do not map directly to those used by these investigators. That panda personalities have fitness consequences in mate compatibility contexts underscores that this inter-individual variation is not statistical noise, but adaptive (sensu (Dall et al., 2004). These findings have clear implications for conservation managers, who can adopt simple personality testing methods or evaluative surveys to characterize individual personality traits and use this to guide future breeding management decisions. The fact that personality traits are stable through time means that managers may need to make these assessments infrequently (perhaps only once), making management of assortative mating based on personality traits an efficient and effective management tool. Future research should further address the stability of personality across breeding and non-breeding seasons, although as a practical tool our findings indicate that non-breeding season personality assessments are predictive of reproductive performance.

Caretaker surveys and novel object tests yielded complementary non-redundant information useful for determining how to form pairs with regard to personality traits. One method (novel object testing followed by Discriminant Function Analysis) uses a quantitative integration of observed behaviors into an intercorrelated composite variable with no a priori assumptions regarding which behaviors "go

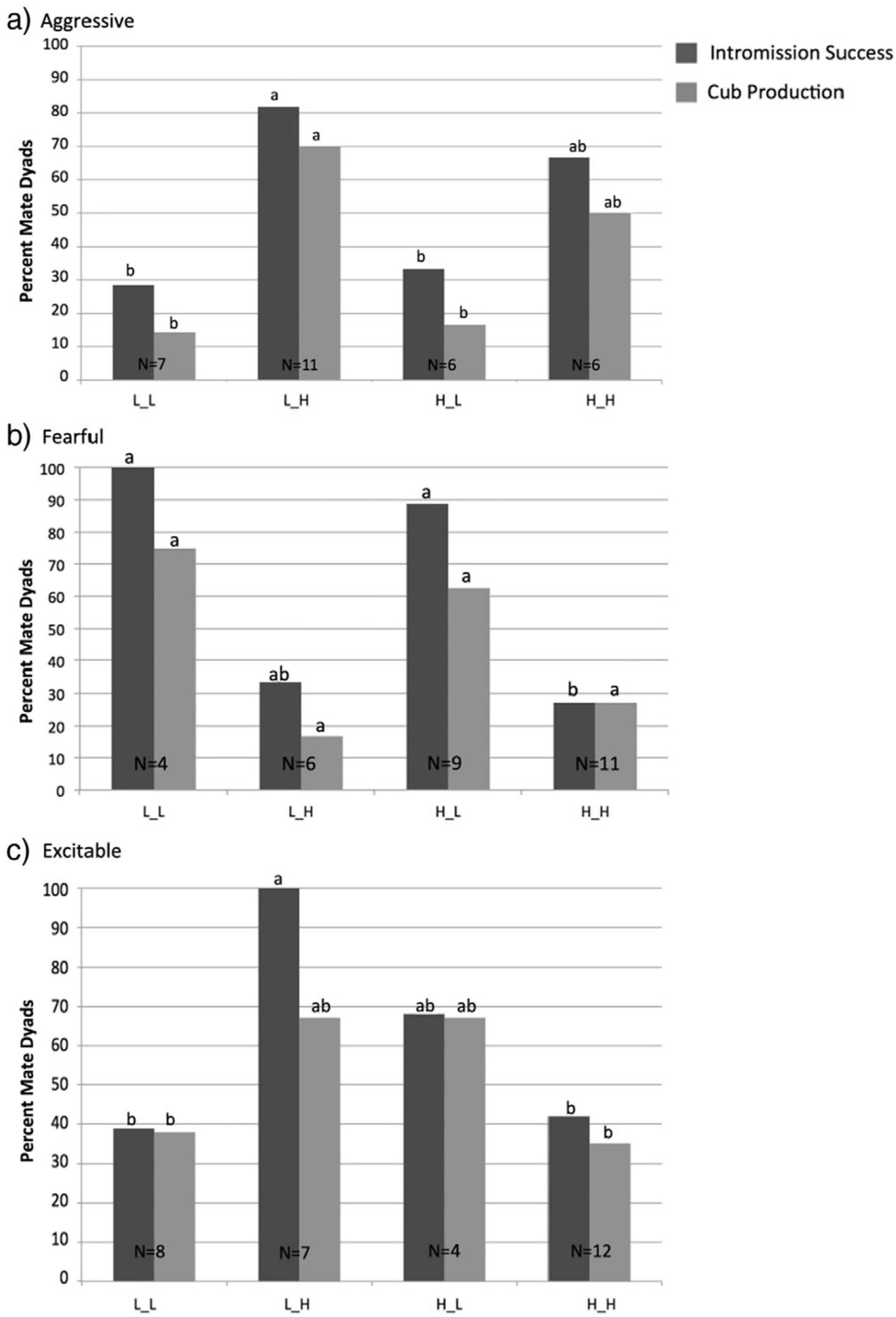

Fig. 1. Mate dyad reproductive success for combinations of personality tests based on caretaker surveys. The percent of mate dyads resulting in successful intromission and cub production for mate pairings of females and males for the (a) Aggressive, (b) Fearful, and (c) Excitable component scores. L_L indicates mate pairs that were both ranked low on personality component scores, L_H indicates females that were ranked low and males that were ranked high, H_L indicates females that were ranked high and males that were ranked low, and H_H indicates females and males that were both ranked high. N represents the number of mate dyads. Different letters indicate a significant difference between groups of $p \leq 0.05$ via Tukey HD post hoc tests following significant ($p \leq 0.08$) ANOVAs.

together", while the other (caretaker surveys) relies on human observers that cognitively integrate a number of behavioral responses to assign personality type. Our study benefited from incorporating both approaches, which together provide greater insights into the role of personality in reproduction. For example, we were not able to evaluate aggressiveness with our novel objects test (although we are currently exploring this possibility with mirror tests) and thus caretaker surveys provided non-redundant information that proved valuable for mating recommendations. While making direct comparisons among findings derived from the two different methods we employed is challenging due to methodological differences, it is also interesting to note that Neophobia, as measured by novel object testing, and Fearfulness, as measured by caretaker surveys, both yielded findings indicating that pairing individuals with similar scores for these measures leads to better reproductive performance. Further, although the current momentum in the scientific literature on personality is toward reduction of measured variables and forming composite functional categories for traits (e.g., Réale et al., 2007), our research conducted on a rich variety of behavioral measures related to personality underscores the potential importance of examining more variables, particularly in a conservation

Table 5
Relationship between reproductive success and personality types as determined by novel object tests. Statistical analyses of reproductive performance for mate dyads of giant pandas and their relationship to personality scores obtained from novel object component (PCA) for Neophobic, Active-Excitable, Inactive-Communicative, and Food Anticipatory. 'Combinations of personalities' reports the significance of the general ANOVA or Kruskall-Wallis testing for differences between all pairing types (L_L, L_H, H_L, H_H) the significance of specific pairings are not reported further. 'Personality similarity' reports the significance in the difference of pairs that were similar in personality (grouped L_L or H_H) to those that were dissimilar in personality (grouped L_H, H_L). 'Relative personalities' reports the significance of pairs composed of males ranked higher than the female versus pairs composed of males ranked lower. Bold numbers indicate significant difference between PCA personality groups at $p < 0.05$, italics represent marginally significant differences between PCA personality groups at $p < 0.08$.

Variable	PCA component			
	Neophobic	Active-Excitable	Inactive-Communicative	Food Anticipatory
Combinations of personalities				
Intromission	0.70 (0.87)[a]	0.15 (0.70)[a]	0.01 (0.93)[a]	0.70 (0.41)[a]
Cub production	0.03 (0.87)[a]	0.39 (0.76)[a]	1.15 (0.30)[a]	0.03 (0.87)[a]
Similarity in personalities				
Intromission success	**12.52 (0.003)**[b]	0.10 (0.76)[b]	0.16 (0.69)[b]	**12.52 (0.003)**[b]
Cub production	**6.02 (0.03)**[b]	0.51 (0.49)[b]	0.05 (0.83)[b]	**6.02 (0.03)**[b]
Relative personalities				
Intromission	1.78 (0.20)[b]	1.82 (0.18)[b]	**4.89 (0.04)**[b]	0.63 (0.44)[b]
Cub production	0.12 (0.73)[b]	*3.69 (0.07)*[b]	**5.19 (0.04)**[b]	0.19 (0.67)[b]

[a] ANOVA; $F_{3,15}$ (p value).
[b] Chi-squared tests; χ^2 (p value).

management context which places value on exposition of useful management tools rather than eco-evolutionary insights. Simplifying personality trait variables may lead to an impoverished understanding of the behavioral portfolio that gives rise to the evolutionary basis for personality. By performing post hoc Discriminant Function Analysis or other variable reduction methods, these factors can be simplified without the loss of valuable knowledge.

Specific findings from our study inform conservation breeding management for giant pandas and have relevance for other species maintained in breeding programs. Aggressiveness is a personality trait highlighted by our findings, and commonly considered and debated in discussions of breeding management (Lindburg and Fitch-Snyder, 1994), including giant pandas (Swaisgood et al., 2006). In the present study, Low-Aggression females paired with High-Aggression males had higher mating and cub production than other pairings, especially those where the male was rated low for Aggressiveness. Managers often try to minimize aggression during breeding, but these findings point to the need to allow the expression of at least a certain amount of aggression. In fact, our results suggest that management strategies may be required to increase aggressiveness in some males whose aggressiveness scores fall too low on the continuum. Aggression and male-male competition are a natural part of mating among wild giant pandas (Nie et al., 2012; Schaller et al., 1985) and are critical for securing access to mates. It is perhaps not surprising therefore that male aggression appears to have favorable influences on mating success and forms the basis for assortative mating patterns.

While aggressiveness appears beneficial for males but not females, fearfulness is not a desirable personality trait in either males or females.

Table 6
Reproductive success of personality combinations based on pooled novel object tests. Values and measures of reproductive success for mate dyads of giant pandas grouped by personality similarity and dissimilarity based on novel object test principal component (PCA) scores for Neophobic, Active-Excitable, Inactive-Communicative, and Food Anticipatory. Female rankings are designated first and male rankings second.

Variable	Mate dyad group			
	L_L	L_H	H_L	H_H
Neophobic PCA component score				
Total mate pairings	6	8	3	1
Total successful intromissions	5	1	1	1
Cubs produced	3	0	1	1
Cubs maternally reared	3	–	1	1
Female[a]	2.93 ± 13.73	0.69 ± 13.72	73.32 ± 26.68	–
Male[a]	11.07 ± 11.18	58.59 ± 20.76	7.34±	–
Active-Excitable PCA component score				
Total mate pairings	9	3	3	3
Total successful intromissions	4	0	3	1
Cubs produced	3	–	1	1
Cubs maternally reared	3	–	1	1
Female[a]	10.80 ± 3.13	12.06 ± 3.84	28.96 ± 3.70	27.48 ± 3.76
Male[a]	17.51 ± 6.25	29.16 ± 3.66	15.01 ± 7.83	24.25 ± 2.29
Inactive-Communicative PCA component score				
Total mate pairings	4	3	5	6
Total successful intromissions	1	3	1	3
Cubs produced	0	2	0	3
Cubs maternally reared	–	2	–	3
Female[a]	1.68 ± 3.93	0.32 ± 3.97	13.67 ± 4.23	10.94 ± 3.84
Male[a]	-2.70 ± 6.87	12.75 ± 1.70	0.44 ± 0.01	11.08 ± 1.89
Food Anticipatory PCA component score				
Total mate pairings	6	8	3	1
Total successful intromissions	5	1	1	1
Cubs produced	3	0	1	1
Cubs maternally reared	3	–	1	1
Female[a]	3.42 ± 8.56	4.30 ± 8.65	57.16 ± 15.97	–
Male[a]	14.47 ± 7.01	53.20 ± 14.77	11.45 ± 9.52	–

[a] Means ± standard deviation of component scores for each sex within the group.

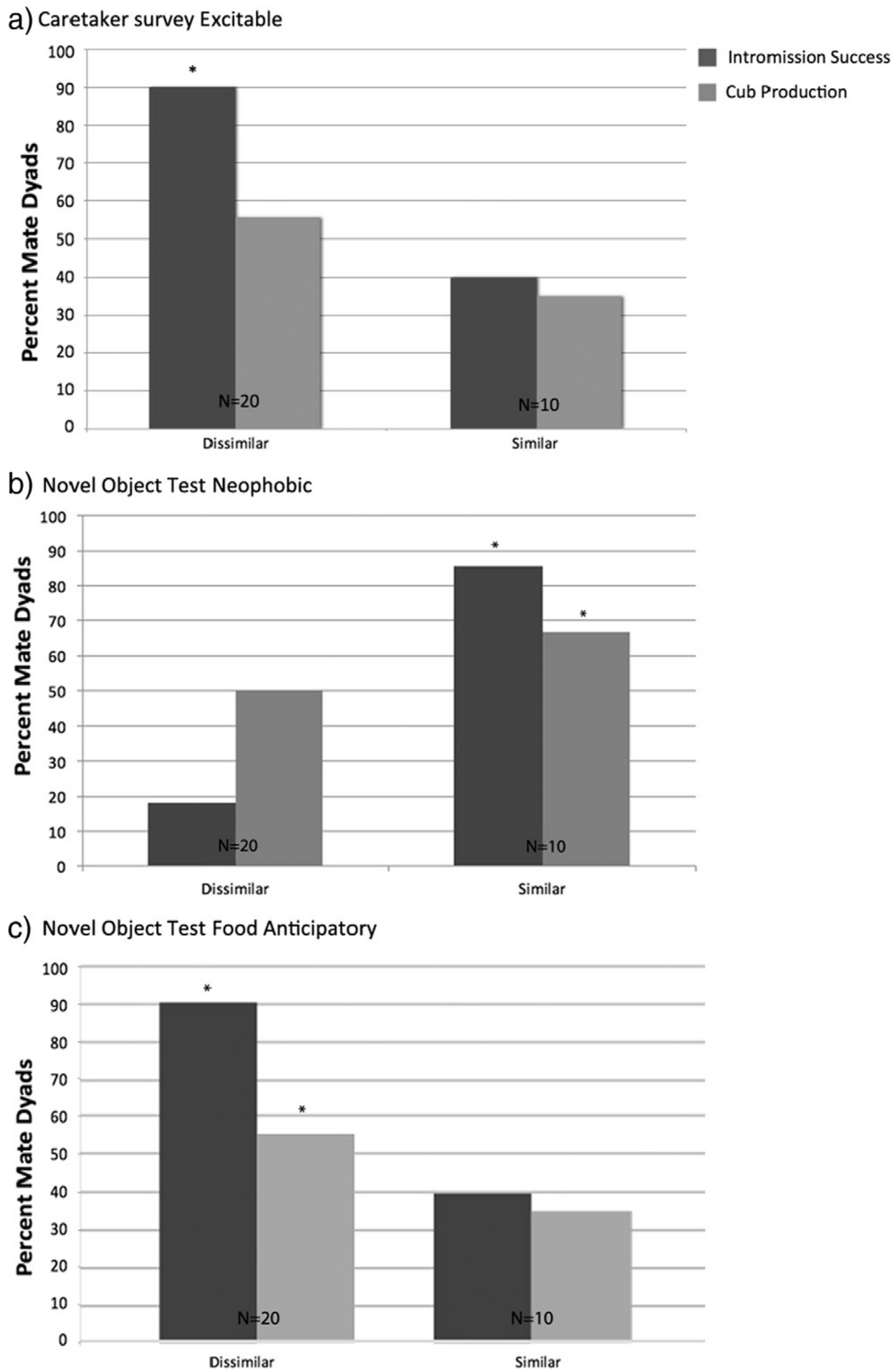

Fig. 2. Mate dyad reproductive success based on similarity of personality between mate pairs. The percent of mate dyads resulting in successful intromission and cub production grouped by mate pairings based on personality component scores for (a) Excitable based on caretaker surveys, (b) Neophobic, and (c) Food Anticipatory based on novel object tests. Different subsets of individuals were used for analyses based on caretaker surveys and novel object tests. N represents the number of mate dyads. * indicates $p \leq 0.05$ via a Chi-squared test.

High Fearfulness appears to be an obstacle to successful mating, particularly for males (Fig. 1b). Similarly, Powell et al. (2008) have shown that 'Shy'(a trait that corresponds well with our Neophobic component) giant panda females displayed less sexual behavior toward males than bold females. These findings are similar to studies in other species, such as cheetahs, where non-breeders were more tense-fearful than breeders (Wielebnowski, 1999). Management strategies could be developed to counter factors that promote fearfulness (such as environmental or social stressors, negative reinforcement by caretakers, abusive behavior by tourists) and compromise reproduction (Carlstead and Shepherdson, 1994) and/or develop methods that would accommodate these personality types during mating (such as decreased human presence during mating introductions).

Similarly, Excitability and tendency to perform stereotypies were associated with poor reproductive performance, but this finding only applies to females. In fact, the best trait combinations pair an Excitable male with a female that scores low on Excitability and stereotypy. A possible explanation is both Excitability and stereotypy are associated with

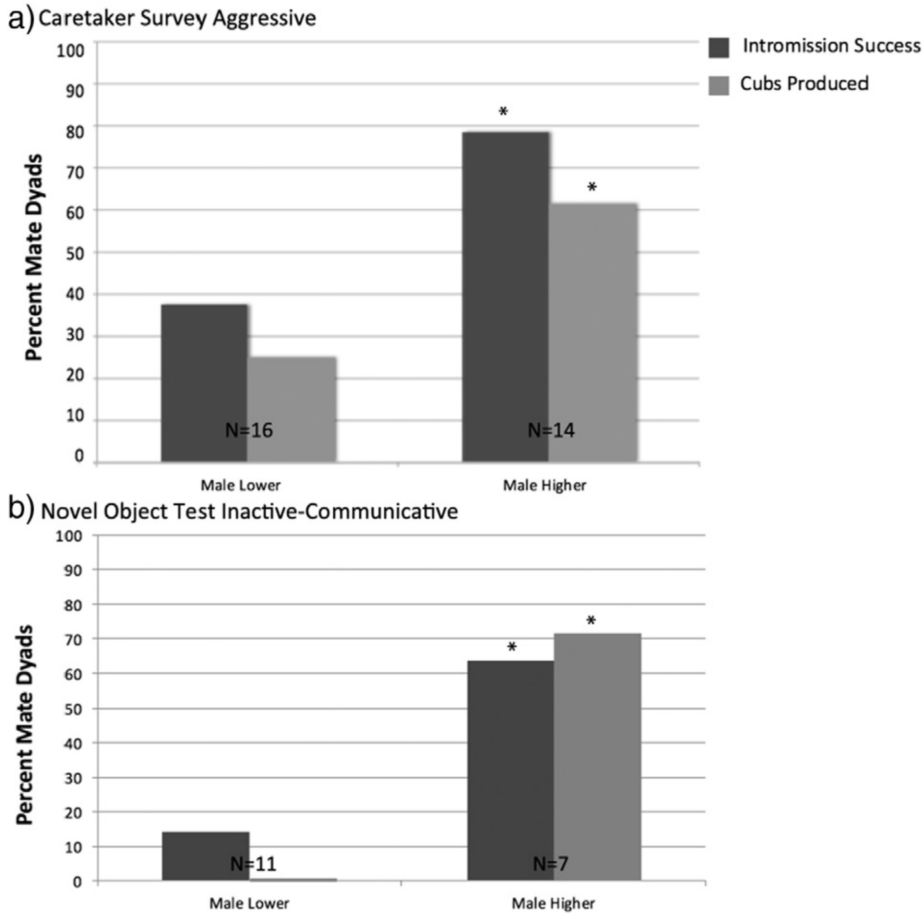

Fig. 3. Mate dyad reproductive success based on relative personality of a mate dyad. The percent of mate dyads resulting in successful intromission and cub production for mate pairings composed of females mated to males ranked lower and higher than them on (a) caretaker survey Aggressive component scores, and (b) pooled novel object test Inactive-Communicative component scores. Different subsets of individuals were used for analyses based on caretaker surveys and novel object tests. N represents the number of mate dyads. * indicates $p \leq 0.05$ via a Chi-squared test.

high levels of sexual motivation in males (e.g., frustrated ethological needs (Hughes and Duncan, 1988)) although expressed in this less desirable outlet. Regardless of the motivational underpinnings, panda managers should attempt to place their least Excitable females with more Excitable males to increase reproductive success.

The personality traits associated with being Inactive-Communicative and having a tendency to communicate using scent also bore strong influence on reproductive outcomes. Chemical communication plays a large role in governing giant panda reproductive behavior (Swaisgood et al., 2004; Swaisgood et al., 2000), so it is perhaps unsurprising that this variable should be included in a principal component explaining variation in reproductive success. While there were not specific combinations of personality traits related to Inactive-Communicative that indicated higher reproductive success, pairs where the males were ranked higher relative to the female had higher copulation rates and cub production than pairs that were dissimilar. These findings indicate that managers should place males that rate high on this trait with females that rate lower than the male. Ariyomo and Watt (2013) also found evidence for associative mating in guppies, *Poecilia reticulate*, where similarity for the boldness trait was associated with higher reproductive success.

These findings for the effects of personality on mate compatibility and reproductive outcomes are all the more interesting because we found them in a seasonal polygnyous mammal with no paternal care. In fact, ours is the first study to document associative mating based on personality traits in a species with a uniparental care system. Mate preference for a partner that will provide reliable parental care is thought to be a primary selective force driving the evolution of personality-based associative mating (Schuett et al., 2010) making our findings more remarkable. The most plausible functional significance for our findings include: 1) personality is an indicator of mate quality, and is heritable, conferring genetic benefits to offspring; 2) personality is an indicator of genetic compatibility (e.g., for the major histocompatibility complex, MHC); or 3) compatible personality types simply have an easier time coordinating courtship and copulation successfully. Another novel aspect of our research is that we tested for and found personality traits in females that influenced associative mating patterns—typically

Table 7
Breeding manager recommendations. Based on significant findings, the following mate combinations are recommended/discouraged as guidance for managers.

	Care Taker Survey Evaluation	Novel Object Evaluations
Try to pair	• Low-Aggressive ♀ with High-Aggressive ♂ • Low-Fearful or High-Fearful ♀ with Low-Fearful ♂[a] • Low-Excitable ♀ with High-Excitable ♂ • Pairs that have similar scores for Fearfulness • Males that are more Aggressive than ♀	• Pairs that have similar scores for Neophobia • Pairs that have similar scores for Food Anticipatory • ♂ has higher scores for Inactive-Communicative than ♀
Do not pair	• Low-Aggressive ♀ with Low-Aggressive ♂ • Low-Fearful or High-Fearful ♀ with High-Fearful ♂[a]	• ♂ has lower scores for Inactive-Communicative than ♀

[a] Indicates a potential need for management strategy that reduces fearfulness in males.

neglected in the literature on personality and sexual selection (Schuett et al., 2010). This finding raises the possibility that mate compatibility and/or preference in male polygynous mammals is more important than previously believed (see also Martin-Wintle et al. (2015)). Future research should address the genetic basis of personality (e.g. Weiss et al. (2000)) in pandas, whether personality traits remain stable inside and outside the breeding season, explore the possibility that changed selective regimes in captivity are favoring certain personality types (i.e., domestication (McDougall et al., 2006), and determine the role of personalities in wild or reintroduced pandas.

5. Conclusions

Our study is the first to show that certain combinations of personalities can predict successful breeding in a conservation breeding program. Mate choice is considered with increasing frequency in conservation breeding programs (Martin-Wintle et al., 2015; Wedekind, 2002), yet personality is rarely considered. Conservation breeding programs are playing an increasing role in species recovery (Conde et al., 2011), yet have not reached their full potential for a variety of reasons (Fa et al., 2014). Species loss is problematic not only for legislative and philosophical reasons, but also for the critical contributions species make to ecosystem resiliency and services (Gascon et al., 2015). Conservation breeding and reintroduction are tools available for preventing species loss, but they need to become more effective through improved application of behavioral and biological knowledge. A cornerstone of conservation breeding is maintenance of genetic diversity through selection of mates based on mean kinship (Ballou and Lacy, 1995), yet genetic management without considering behavioral management often fails (Martin-Wintle et al., 2015; Swaisgood and Schulte, 2010; Wedekind, 2002). Our study illustrates the value of considering personality traits when breeding giant pandas and underscores the observation that genetic management alone is not likely to deliver the high reproductive rates needed to make conservation breeding sustainable and cost-effective, and supply candidates with a diversity of behaviors needed for reintroduction to the wild. Breeding failures arising from poor behavioral compatibility between mates may lead to the very genetic erosion that genetic management is meant to address. Further, if assortative mating functions to bring compatible genotypes together, then efforts to promote assortative mating based on personality traits may increase the genetic viability of offspring.

To be useful for conservation breeding, results such as ours must be distilled into an easy-to-follow management plan not too dissimilar from the way studbooks are used to manage mean kinship. To that end, we have created a table detailing the specific combinations of personalities most likely to yield successful breeding for giant pandas (Table 7). To implement this plan, managers are encouraged to conduct simple personality evaluations using caretaker surveys, novel object tests, or both. These results are then overlaid with the recommendations in Table 7 to determine the most compatible pairs for attempted matings. It is our hope that when combined with genetic management, this tool will enhance breeding success and improve conservation breeding programs for a number of species dependent on ex situ conservation efforts for recovery.

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Appendix A. Supplementary data

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