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Do “birds of a feather flock together” or do “opposites attract”? Behavioral responses and temperament predict success in pairings of rhesus monkeys in a laboratory setting

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Abstract

The growing recognition that social needs of primates in captivity must be addressed can present challenges to staff at primate facilities charged with implementing pair-housing solutions for animals. Unfortunately, there are few published papers that identify individual characteristics that might facilitate the social pairing process, and those that have looked at pre-pairing measures of behavior have produced mixed results. Using a database of $n=340$ isosexual pairing attempts, we report that measures associated with responses to a standardized infant assessment protocol (the BioBehavioral Assessment program) predict success in pairing attempts that occurred years later. Behavioral responses to a brief separation and relocation, to a human intruder challenge, as well as ratings of temperament, were obtained from rhesus monkeys at 3–4 months of age. Logistic regression was used to identify potential predictors of success when animals were paired up to 10 years after the behavioral assessments. Among females, success was higher when members of a pair were more similar (i.e., a smaller difference scores) in patterns of emotional responding (emotionality, nervous temperament) during the infant assessments. In contrast, among males, success was higher when the pair had lower mean values for Gentle and Nervous temperament scores; when the members were younger; when pairs had a greater weight difference; and when they came from the same rearing background. Together, our results suggest that broad measures reflecting patterns of emotionality in response to challenge, which can be assessed in infancy (but which remain relatively stable throughout life) can be usefully employed to increase the likelihood of success in pairing attempts.

Keywords

temperament; socialization; welfare; pairing; sex differences

INTRODUCTION

A variety of agencies that have oversight of animal research and related facilities in the United States have indicated strong support for social housing of nonhuman primates. For example, federal Animal Welfare regulations indicate that “Dealers, exhibitors, and research facilities must develop, document, and follow an appropriate plan for environment enhancement adequate to promote the psychological well-being of nonhuman primates” and that these plans must include “specific provisions to address the social needs of nonhuman primates of species known to exist in social groups in nature [USDA, 2013, subsection 3.81].” Similarly, the 8th Edition of the Guide for the Care and Use of Laboratory Animals [National Research Council, 2010], to which recipients of Public Health Service funds (e.g., NIH) must adhere, indicates that “Like all social animals, nonhuman primates should normally have social housing [National Research Council, 2010, p. 58].” And a position statement by the Association for Assessment and Accreditation of Laboratory Animal Care International (AAALAC, International), the principal organization that accredits animal facilities, has indicated that “social housing will be considered the default method of housing [AAALAC, 2015].” So complete is the consensus on social housing of nonhuman primates that the Office of Laboratory Animal Welfare [OLAW, 2015] has stated “There is universal agreement among oversight agencies that nonhuman primates should be socially housed.” Of course, exceptions are always allowed with proper justification, but it is clear that the regulatory and oversight environments continue to favor social housing for social species.

While the ideal housing situation may be to approximate as closely as possible the species-typical grouping patterns, this is sometimes not possible, especially in a laboratory situation. Meeting the social needs of animals in such environments is often achieved through pairing of animals, but this strategy often involves a number of decisions. Which animals are available for pairing? Should animals be housed together permanently or for only part of each day? Can experimental procedures continue to be performed on paired-housed animals? What is the best strategy for putting unfamiliar animals together? What are the metrics for success in a pairing program? Should animals be housed in same-sex or mixed-sex pairs? How long must newly-formed pairs be monitored for compatibility? Some of these issues will be addressed by others in this Special Issue [Hannibal et al., 2015; Truelove et al., 2015]. An excellent review on social pairing that addresses some of these (and many other) issues can also be found in DiVincenti & Wyatt [2011].

Given that “compatibility” is the *sine qua non* of a pairing program, a critical issue is whether knowing something about the enduring behavioral tendencies of an animal (often referred to as temperament or personality) can increase the chance of a successful pairing attempt. It is almost certainly the case that individuals who do pairing are using their knowledge and experience with the animals to make educated guesses that would increase the likelihood of success. In fact, DiVincenti and Wyatt [2011] note that, at their facility, engaging the researchers in the shift to social pairing proved valuable: “Because they know the personalities of their subjects, primary investigators and research technicians assist in selecting partners that have the highest chance of success [p. 861].” Yet there is very little actual data on this issue, and what little there is is often described only in published abstracts, not full reports. Unfortunately, the data that have been reported do not provide a

clear picture of the value of pre-pairing data for increasing success in pairings. For example, neither Crockett et al. [2005] nor Neu et al. [2007] reported that pre-pairing temperament/behavioral data predicted successful pairings. Others have reported different results, however. Though there were no control conditions, Lynch [1998] reported good success in pairing adult male *M. fascicularis* by pairing animals that had been classified as “dominant” (“a monkey that seems to be assertive or will come up to the front of the cage [p. 4]”) or “submissive” (“one that seems to be shy or stays to the back of the cage [p. 4]”). (We suggest that the terms “dominant” and “submissive” are misnomers in this context, in that these are dyad-level terms, and cannot be applied correctly to individually-housed animals; based on the definitions given by Lynch [1998], better terms may be “bold” and “shy,” respectively.) McMillan et al. [2003] reported on adult female rhesus monkeys that had been paired successfully once with one partner and unsuccessfully once with a different partner. Temperament scores were more similar for the subject and her successful partner, than between the subject and her unsuccessful partner. Finally, Baker [2010] focused on individual differences in aggression directed at humans. Female rhesus monkeys that were more aggressive toward people were more likely to form successful pairs than were females that were less aggressive. Among males, it was the difference in temperament of pair-mates that was influential: successful pairs were more likely to have males whose fearful responses to observers were similar to each other (i.e., a small difference score), compared to members of unsuccessful pairs.

The limited literature reviewed above points to two questions: what are the traits that might be most influential in contributing to success (boldness/inhibition, emotionality, sociability), and what particular combination works best – should individuals be similar in their trait profile (“birds of a feather flock together”) or should individuals differ from each other (“opposites attract”)? While the data from nonhuman primate studies are limited, there is considerable information in Psychology on the broad topics of interpersonal attraction and relationship quality. Much of this literature, however, is focused on romantic partner attraction and marital relationships, and may be of limited value for two reasons. First, “marital” relationships (a better term might be relationships that involve a pair bond) are typically attachment relationships, which have different qualities than do relationships characterized as “friendships” [e.g., Bartels & Zeki, 2000]; one might expect that the criteria involved in evaluating a potential romantic partner would be different from the criteria used to establish a friendship. In the most commonly used laboratory species of nonhuman primates (which are generally polygynous), adult heterosexual pairs, even after considerable time living together, do not display pair bonds [Mason, 1975]. Second, social pairings of laboratory-housed monkeys are usually done within-sex to avoid pregnancy; the dynamics between a heterosexual pair and an isosexual pair are likely to be different.

The previous caveats notwithstanding, some research with humans seems pertinent. One theoretical model, called the Interpersonal Circumplex, identifies two orthogonal dimensions that form the basis of interpersonal style, namely warmth/affiliation and dominance (also referred to as assertiveness or control) [Wiggins, 1979]. This influential model suggests that complementarity on the two dimensions facilitates satisfying social relations. Here, “complementarity” refers to two individuals having reciprocal styles on the dominance dimension (i.e., dominance invites submission), and similar styles on the warmth dimension

(i.e., warmth invites warmth). Kiesler [1996, discussed by Ansell et al., 2008] discusses additional considerations indicating that complementarity is likely to be greatest when individuals are peers, of the same gender, interact in an unstructured setting, and when the situation is such that what one person does has an influence on the other individual. These considerations have led to studies of same-sex relationships in the context of college roommates, a context which, we would argue, approximates the situation of same-sex pair-housed laboratory animals more closely than does either a pair bond situation, or more contrived laboratory studies of human dyadic interaction. One such study of randomly assigned, same-sex, college dormitory roommates, for example, found that, despite the fact that female pairs overall exhibited greater complementarity than did male pairs, the degree of complementarity predicted dyadic cohesion for both male roommate and female roommate pairs [Ansell et al., 2008].

The Ansell et al. [2008] study suggested that relationship quality in young adults was affected by complementarity – similarity in warmth, and reciprocity in assertiveness/dominance. Other human studies, focused on different domains and subject populations, have found more equivocal results. For example, in studying friendships in preschool-aged children, Gleason et al., [2005] found that similarity in temperament (activity level, impulsivity, and soothability) did not predict friendship status. In contrast, friendships in college-age students were characterized by positive (though small) correlations (i.e., similarity) in personality characteristics – the correlation in Extraversion scores was 0.26, for example [Berry, Willingham, Thayer 2000], suggesting that “birds of a feather” may indeed flock together..

Finally, a handful of nonhuman primate studies have examined friendships (or positive social interaction) in social group (i.e., not pair-housing) settings. Capitanio [2004] reported higher frequencies of approach in three-member adult male groups whose mean levels of Sociability were high. Weinstein and Capitanio [2008] studied yearling rhesus monkeys that were living in large outdoor enclosures, and found that these animals preferentially associated with animals that were similar to themselves on the characteristics of adaptability (flexible, gentle) and equability (calm, not active). And among captive chimpanzee groups, similarity in Sociability and Boldness characterized friendships [Massen & Koski, 2014].

Together, these and other studies suggest that the probability of achieving a successful social pairing attempt might be increased by consideration of the animals’ temperaments. In the present report, we describe a retrospective analysis examining this issue. Indoor-housed animals were identified that had experienced successful or unsuccessful pairing attempts. We studied all pairs in which both members had participated in the California National Primate Research Center’s BioBehavioral Assessment (BBA) program as infants. While we did not have measures of the animals’ sociability, inasmuch as the BBA program examines behavior in a nonsocial context, we did examine patterns of behavioral responsiveness and temperament, and whether complementarity on measures was associated with greater success. While the BBA program generates a variety of outcome measures that might be relevant to pairing success (e.g., serotonin transporter genotype, cortisol concentrations), behavior managers at most facilities don’t have access to such information; consequently,

our goal in the present analysis was to identify behavioral correlates of success that might be easily measured by individuals at other facilities who are charged with performing pairings.

METHODS

Subjects

Subjects were rhesus monkeys (*Macaca mulatta*) that were members of 340 isosexual pairing attempts (169 female pairs, 171 male pairs) that occurred between March 2007 and June 2012. Each pairing attempt was unique – the same two animals were not paired more than once – although any given animal could be in the database more than once (range = 1–5, mode = 1). A total of 493 unique animals (255 females, 238 males) populated the pairing database that we used. The subjects were born into one of four rearing environments at CNPRC [described in detail in Gottlieb, Capitanio, McCowan, 2013]: outdoor half-acre field corrals, each containing up to 200 animals of all ages and both sexes (n=362); outdoor corncrubs, each of which was ~400 square feet and contained 15–30 animals (n=57); indoor nursery, in which animals were separated at birth and raised individually until 4–5 weeks of age, at which point they were paired (n=58; we note that this pairing event is not included in the data we analyze below); and our indoor-mother-reared colony, in which an infant was reared with its biological or foster mother and at most, one additional mother and infant pair (n=16). Animals were a mean of 5.5 years of age (range = 1.2 – 11.1 years) at the time of pairing for the present study. Twenty of the n=255 females had an infant present during the pairing attempt. The dataset used for this analysis comprised all pairing attempts in which both members of the pair had been assessed in CNPRC's BBA program (see next section).

The present study was performed in accordance with all applicable guidelines, including those described in the *Guide for the Care and Use of Laboratory Animals*, the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates, and all applicable laws of the United States. All procedures were approved by the Institutional Animal Care and Use Committee at the University of California, Davis, which is an AAALAC-accredited facility.

BioBehavioral Assessment program

At a mean age of 107.2 days (range = 89 – 130), each animal participated in the BBA program, described in detail in Golub et al. [2009]. Briefly, infants were separated from their mothers and transported to a testing room by 0900 h, for a 25-h period during which they were administered several behavioral tests (blood samples were also taken on four occasions, but are not considered here). Data from three assessments were used for the present analysis. These data sets were chosen because each derives from relatively simple procedures that could be employed at other facilities.

Behavioral responsiveness—Beginning at 0915, each animal was observed in its individual holding cage for a five minute period, using a pre-determined random order. Frequency and duration behaviors reflecting activity and emotional responsiveness were recorded using focal animal sampling. An identical set of observations were performed at 0700 on the next day. Exploratory and confirmatory factor analyses revealed a two-factor

structure, and scales were constructed for Day 1 Activity (comprising locomotion, time spent not hanging from the side of the cage, environmental exploration, and whether the animal ate, drank, or crouched during the observation) and Day 1 Emotionality (comprising rates of cooing and barking, and whether the animal scratched, displayed threats, or lipsmacked). Similar scales, using the same behaviors, were constructed for the Day 2 observations. In general, the Day 1 data reflect the animals' initial responses to relocation and separation, and the Day 2 data reflect how well the animals have adapted to the testing situation. Behavior definitions and details of the factor analyses and scale construction can be found in Golub et al. [2009].

Human intruder—Beginning at approximately 1400 h, each individual was relocated from its holding cage to a test cage in an adjacent room for a human intruder test [Gottlieb & Capitanio, 2013]. Four one-min trials were conducted. During the first trial, the experimenter positioned herself ~1 m in front of the cage and presented her left profile to the animal. At the end of the minute, the experimenter moved to ~0.3 m from the cage, while still maintaining a profile position. After holding that position for a minute, the experimenter moved back to the 1 m position and made direct eye contact with the animal. One minute later, the experimenter returned to the 0.3 m position while maintaining direct eye contact for an additional minute. Frequency and duration data were coded for each trial. Data from all four trials were combined and subjected to exploratory and confirmatory factor analyses, and four factors were found: Activity (active, cage shake, environment explore), Emotionality (convulsive jerk, grimace, self-clasp, coo), Aggression (threat, bark, other vocalizations), and Displacement (tooth grind, yawn). Human intruder data were included in the present analysis because they reflect data collected under potentially challenging circumstances that indoor-housed animals might experience several times per day: unfamiliar humans staring at, or walking by, them. Behavior definitions and details of the factor analyses and scale construction can be found in Gottlieb & Capitanio [2013].

Temperament—Just prior to the infant's reunion with its mother (or pair-mate), the technician who performed the testing rated the overall temperament of each animal during the 25-hr test period using a listing of 16 adjectives and a 1–7 Likert-type scale, with 1 reflecting a total absence of the behavior and 7 reflecting an extremely large amount of the behavior. Exploratory and confirmatory factor analyses suggested a four-factor structure to the data: Vigilant (vigilant, not depressed, not tense, not timid), Gentle (gentle, calm, flexible, curious), Confident (confident, bold, active, curious, playful), and Nervous (nervous, fearful, timid, not calm, not confident). (Note, the adjectives preceded by “not” indicate the item was reverse-scored; for example, a high score on the Vigilant scale indicated that animals tended to have high scores on the individual vigilant item, and low scores on the depressed, tense, and timid items.) Temperament ratings were included because they are easy to conduct by individuals at other facilities. Trait definitions and details of the factor analyses and scale construction can be found in Golub et al. [2009].

Social pairing

Animals to be paired were moved to adjacent cages that had been fitted with a sliding partition (referred to as a pairing door) that opens to allow access to the adjacent cage. The

move occurred at least 24 hours before the pairing attempt, which began by opening the pairing door about two inches to first permit the individuals to see each other. If the animals were nervous or mildly aggressive, a metal grate would be inserted for a period of time ranging from one day to two weeks (grates were always used for males over 10kg). When the pair demonstrated affiliative behavior, as evidenced by display of lipsmacking, presenting for groom or sex, grunting, proximity, or recruiting behavior (i.e., against a third animal located in another cage in the room) the door was opened and full contact was permitted. Pairs were monitored for a variable length of time over one or more sessions (mean=93.5 min, range= 5–600 min; animals that were monitored for the lower durations were typically yearlings and/or animals that had been housed together previously [e.g., in a field corral]; animals monitored for the longer times were primarily novel pairs) before they were considered successful or not successful. “Success” was defined as pair members that seek each other’s company (i.e., being in the same cage and showing grooming, play, or proximity), have consistent dominant/subordinate roles as indicated by social signaling (grimace, lipsmack, threat), and do not appear fearful of each other outside of feeding time; once animals showed these behaviors for at least 3 –5 days, they were considered successful. If successful, animals were either paired permanently or for 5–6 hours per day (continuous or intermittent pairing, respectively), based largely on experimental protocol; however, if the animals displayed aggression during feeding, they were paired on an intermittent basis (i.e., after morning feeding, and ending before the afternoon feeding), and were still considered a successful pair. (Pairs were not kept permanently in protected contact using the metal grate.) In the present sample, 121 pairings were unsuccessful, and 219 were successful; success was related to sex of subjects: 56.7% of male pairings were successful, compared to 72.2% of female pairings (Chi-square(1)=8.867, $P=.003$). Success was not related to the identities of the technicians who performed the pairings ($P=.668$).

Data analysis

Logistic regression was used to predict the binary measure of pairing success. Although measures of pairing success were complete for all animals, a subset of the animals had incomplete data for the predictor variables that were to be tested (specifically, four of the 255 females were missing data for some BBA measures; no males had missing data). Multiple imputation was therefore applied to the observed data, with 30 imputed data sets generated following recommendations in Graham, Olchowski, and Gilreath [2007] to perform a high number of imputations. Multiple imputation is considered to be a valid method for addressing missing data under the assumption that data are missing at random. Thus, multiple imputation is less restrictive with regard to the assumption about missing data, compared to restricting a data analysis to only those cases with complete data [Little & Rubin, 2002], which is valid only if data are missing completely at random. Using only complete cases also results in a reduced sample and consequently reduces statistical power.

As described earlier, for these data, individual animals were involved in up to five pairings with different animals. To account for instances in which an animal appeared in more than one pairing, an animal effect was included in the model. Separate analyses were performed for males and females, and for each analysis, we included as covariates 1) whether animals were reared indoors (0: nursery, indoor-mother reared) or outdoors (1: corncrubs, field

corrals), 2) a variable indicating whether animals experienced the same (1: both reared outdoors, or both reared indoors) or different (0) rearing conditions, 3) age (in days) at testing during the BBA, 4) weight at the time of pairing, 5) the difference in weight at the time of pairing, 6) age (in years) at the time of pairing, and 7) the difference in age at the time of pairing. All difference scores were calculated as absolute values. For females, we also included as a covariate the presence or absence of an infant. Finally, to test the hypothesis that age might interact with rearing history in affecting pairing success, we performed a preliminary analysis with an interaction term for age by rearing, and found a significant ($P=0.0467$) effect for males only, and so this effect was retained in our statistical modeling.

Because of the large number of measures, we ran three analyses for each sex, one for each data set (behavioral responsiveness, human intruder, temperament). Covariates were entered for each analysis, as well as dyad-level measures for the BBA data – we calculated the mean value of the measures for each pair (which enabled us to assess the overall level of behavioral functioning of the pair: were the animals together high or low in emotionality, for example), as well as the absolute value of the difference score for each pair (which enabled us to test the hypothesis about similarity or complementarity affecting success). Inclusion of both means and difference scores also enabled us to examine the effect of one of these while the other was statistically controlled. Below, we report the parameter estimates and their significance ($\alpha=.05$) for these separate analyses. For each sex, a final model was run that included only covariates plus significant variables from the individual analyses.

RESULTS

Females

Similarity in measures reflecting emotionality was associated with greater success. The difference score for Day 1 Emotionality was significant (estimate $=-0.7961$, $t(169)=-2.68$, $P=0.0081$); because the parameter estimate was negative, the smaller the difference between pair-mates on this measure, the greater the likelihood of a successful outcome. A smaller difference score on the Nervous temperament measure was also associated with greater success (estimate $=-0.6487$, $t(165)=-2.38$, $P=0.0187$). Finally, in the analysis of the human intruder data, an effect was found for the difference score for Emotionality (estimate $=-1.7814$, $t(165)=-2.28$, $P=0.0227$); as with the other measures, the estimate was negative, indicating greater success for individuals whose emotional responses during the human intruder were more similar. No other measures (including among the covariates) were significant predictors of pairing success.

In the final model that included the Day 1 Emotionality, the Nervous temperament, and the human intruder Emotionality measures (along with the covariates), all three measures remained significant predictors of pairing success – pairs that had smaller difference scores (i.e., were more similar) for Day 1 Emotionality ($P=0.0270$), Nervous temperament ($P=0.0329$), and Emotionality during the human intruder test ($P=0.0063$) were more likely to be successful. Covariates did not predict pairing outcomes. See Table I.

Males

In contrast to the females, dyad-level BBA predictors of success for male pairings were not scores reflecting similarity, but rather were scores reflecting mean values of temperament measures. Specifically, success was more likely among pairs whose mean levels of Gentle (estimate = -1.2864 , $t(171) = -2.20$, $P = 0.0291$), and Nervous temperament (estimate = -1.5191 , $t(171) = -2.85$, $P = 0.0049$) were low. Age at pairing was significant (estimate = -4.5682 , $t(171) = -2.10$, $P = 0.0372$), indicating that pairing success was more likely with younger animals. While weight was not significant, the difference in weight between pair-mates was highly significant (estimate = 0.5480 , $t(171) = 3.22$, $P = 0.0015$); success was more likely among pair-mates whose weights were more dissimilar. Finally, all of the rearing measures were significant. Likelihood of pairing success was lower for outdoor-reared animals (estimate = -26.7028 , $t(171) = -2.08$, $P = 0.0388$), but this effect was moderated by age: a significant age x rearing variable (estimate = 4.4860 , $t(171) = 2.06$, $P = 0.0413$) suggested that males that were reared outdoors and paired at older ages were more likely to be successful. Finally, similarity in rearing history (i.e., both reared indoors or both reared outdoors) was also a significant predictor of success (estimate = 10.8866 , $t(171) = 2.19$, $P = 0.0299$).

As with the females, we constructed a final model that included only the significant BBA measures (means for Nervous and Gentle temperament) plus all covariates. Table II indicates that all of the effects found in the prior analysis remained significant. The likelihood of a pairing being successful was increased for pairs with lower mean scores for Gentle temperament ($P = 0.0038$) and for Nervous temperament ($P = 0.0055$), as well as for animals that were younger ($P = 0.0431$), had been reared indoors ($P = 0.0478$), and were members of pairs that had large weight differences ($P = 0.0012$) and similarity in rearing history ($P = 0.0394$). Finally, although indoor-rearing was associated with greater pairing success compared to outdoor-reared animals overall, we found that, among animals reared outdoors, those that were paired at later ages were also likely to achieve successful pairings ($P = 0.02457$).

DISCUSSION

Our results indicate that measures of biobehavioral organization (reflected in behavioral responses to separation and relocation, behavioral responses to a human intruder challenge, and temperament ratings), obtained in infancy, predicted successful outcomes of pairing attempts up to a decade later. Importantly, our analyses show that, at least for isosexual pairings, predictors of success for males and females differed considerably.

Success in female pairings

For females, the three biobehavioral predictors of success in pairing attempts were associated with emotionality, and the chances of successful pairings were increased by females' similarity in these measures. The first measure was Day 1 Emotionality, which is a measure of behavioral responsiveness taken from focal animal observations on the monkeys, beginning at approximately 15 min (Day 1) after the relocation and separation from their mothers/pair-mates, and comprised behaviors associated with vocalizing (coos, barks), affective responding (lip smacks, threats), and anxious behavior (scratch). (We note that the parallel Day 2 measures, which are more reflective of adaptation during the BBA testing,

were not significant predictors.) The second measure was Nervous temperament, which comprises the individual traits of nervous, fearful, timid, and not calm or confident. Elsewhere, we have argued that Nervous temperament is similar to Neuroticism in humans [Capitanio et al., 2011] – animals high in Nervous temperament tend to display more negative, and less positive, behavior in a human intruder test, for example. The third measure was Emotionality recorded during the human intruder test, which comprised behaviors such as coo and grimace. For all three measures, the smaller the difference between potential pair-mates, the greater was the likelihood of success. Note that the individual analyses for responsiveness, temperament, and human intruder measures also included mean values for these measures (i.e., the means for each dyad for Day 1 Emotionality, Nervous temperament, and human intruder Emotionality were included in their respective separate analyses), none of which were significant predictors of success. In practical terms, these results suggest that regardless of the degree of emotionality that animals display (i.e., whether they are low, intermediate, or high), the important parameter is matching females' degree of emotional responding.

We were somewhat surprised that the covariates did not predict success in female pairings, particularly the presence or absence of an infant. We are aware of no studies that have specifically examined this variable in the context of pairing, but based on the overall attractiveness of infants to other females, we expected that infant presence might facilitate success. Similarly, age and weight of the females were also not influential, which is in contrast to results that others have reported, in which greater success was achieved with younger animals [Truelove et al., 2015; though see discussion of results for males, below]. Finally, whether the animals were reared indoors or outdoors was not, by itself, influential in pairing success. We do know that there are substantial behavioral (and some physiological) differences between indoor (mother-reared or nursery-reared) versus outdoor (field-cage or corncrib) reared animals [Capitanio et al., 2006]. There is, however, considerable overlap in the distributions of BBA measures between animals from the different rearing conditions. What our results suggest is that, at least for females, it is the behavioral consequences of those rearing conditions, and not the rearing conditions, per se, that are the important measures. This is important, in that staff who are involved in establishing pairs may not have detailed information on the rearing histories of their subjects. They do know, however, (and can assess) whether the animal is high or low in emotionality.

Success in male pairings

The results for males differed from those for females in three important ways. First, the significant BBA predictors were those from the temperament assessments only. Second, whereas for females the difference scores were most predictive of success, for males, it was the mean values that were most predictive. And third, physical and rearing measures were highly significant predictors of pairing success. We discuss each in turn.

In contrast to the results for females, specific behavioral measures, from the responsiveness and human intruder assessments, were not predictive of later pairing success for males; rather, the important predictors were from the temperament ratings, which reflect the observer's assessment of the animal's overall functioning during the entire 25-hr assessment

period. As with females, Nervous temperament was an important predictor. The second significant predictor for males, however, was the Gentle temperament factor, which comprises ratings on the individual traits of gentle, calm, flexible, and curious. While it might seem counterintuitive that animals with less Gentle temperaments would be associated with greater success, we have reported elsewhere [Gottlieb, Capitanio, & McCowan, 2013] that animals that were low on this factor were more likely to display motor stereotypy when housed indoors. Our interpretation was that being low on Gentle temperament may be an indicator of having a more active coping style, which could get expressed as pacing behavior (the principal measure of motor stereotypy in that study). Animals that are active copers (low scores on Gentle), and whose levels of neuroticism (Nervous temperament) are low, may work to find a prosocial solution to an encounter with an unfamiliar conspecific that occurs within a limited physical environment. In future work, it would be useful to collect quantitative data on the specific behaviors involved in successful vs. unsuccessful pairing attempts to confirm this suggestion.

The second major difference between the results for the males and the females was that, for males, it was the mean, and not the difference, scores that were associated with successful outcome. This result suggests there may be males that may not be able to be successfully paired with other males. To achieve a lowest mean value of Nervous temperament (for example), both individuals should have low scores for the measure. Our results suggest that such a pairing may have a high probability of success. When one individual has a high Nervous score and the other has a low score, or when both individuals have intermediate scores, the probability of success could be reduced. But when both individuals have high scores, our results suggest that such pairings are far less likely to be successful – in practical terms, if one has a highly Nervous animal, pairing it with one that is very low on this trait may be the best possibility for that animal. It's important to reiterate that the individual analyses that we performed included the difference scores for the measures; this means that, for individuals with an intermittent mean score for Nervous temperament, for example, it did not matter whether the mean was achieved by having one high and one low Nervous animal, or by both animals being intermediate in Nervous temperament – the magnitude of the difference was not important, just the absolute level (mean) of the trait for the two animals. Again, it would be interesting to have behavioral data that could illuminate whether there are different strategies by which one high and one low Nervous animal achieve a successful pairing compared to two intermediate-Nervous animals.

The third principal difference between the results for males and females was the extent to which physical and rearing factors were important predictors of success for males. Here, our results confirm those of others [Truelove et al., 2015] that younger animals are more likely to be successful in pairing attempts. The difference in age was not influential, however; rather weight differential between the two animals was a highly significant predictor of success – the greater the weight discrepancy, the greater the likelihood of success [Doyle et al., 2008; though see Maguire-Herring et al., 2013 and West et al., 2009 for contrasting results]. It's likely that for males, a larger weight differential may prevent any contest for dominance status; with rank easily and quickly established, affiliation may be displayed more quickly as well. Finally, rearing history was an important predictor of success for males. Somewhat surprisingly, indoor-reared animals were more likely to demonstrate

successful pairings. This may be because of indoor-reared animals' greater general familiarity with the experience of being indoors, having experienced that environment in early life (we note that it is possible that some indoor-reared animals may have gone on to spend time outdoors before being brought back inside for project assignments). The effect of rearing is more complicated however, in that the effect of rearing was moderated by age, and was affected by the rearing history of the partner as well. Our results showed that there was a subset of outdoor-reared animals that were also likely to show success in pairing attempts – animals that were paired at an older age. At our facility, males are generally brought indoors for specific, project-related purposes or around the time of sexual maturity (A. Cameron, personal communication). In general, animals that are “older and outdoor-reared” have likely lived for a longer period of time in the rich social environment of our field cages or corncrubs before their relocation indoors. Elsewhere, we have demonstrated that having lived a higher proportion of one's life outdoors protects against the development of motor stereotypy and of self-biting following a move to indoor housing (Gottlieb, Capitanio, McCowan, 2013; Vandeleest, McCowan, Capitanio, 2011); the present results suggest this may also facilitate success in social pairing, at least for males. Finally, we found that pairing success was also facilitated by pair-members' having had the same early rearing experiences: animals that were both indoor-reared or were both outdoor-reared were more likely to form successful pairs than were animals of mixed-rearing backgrounds. It's possible that similarity in rearing experience is associated with similarity in how familiar the animals are with the routines of indoor living. Animals that are discrepant in this regard might face a special challenge: their attempts to establish an affiliative relationship with each other are taking place against a backdrop of the less-experienced of the two males trying also to adapt to indoor living.

Conclusions and limitations

Together, our results show some similarities and dissimilarities with previous reports. The study described by McMillan et al. [2003; see also Coleman, 2012] indicated that similarity among adult female rhesus monkeys on the trait of behavioral inhibition resulted in more affiliative behavior. Our data also suggest that similarity (i.e., a small difference score) in behaviors reflecting patterns of emotionality are associated with greater likelihood of success. In contrast, Baker [2010] suggested that male pairs that were successful were more likely to have similar patterns of fearfulness toward observers. In our analysis, similarity in responding was more evident for females than for males, with the exception that the lowest mean value for Nervous or Gentle temperament would be obtained when both individuals show a similar pattern of behavior toward the human. Interestingly, our analysis of female pairings did show results that are somewhat consistent with results found by Ansell et al. [2008] for college roommates: the degree of complementarity (one measure of which was similarity in warmth) was associated with greater dyadic cohesion.

The differences between our study and others that have been reported may be due to a number of factors. First, our study employed a definition of “success” that might be somewhat idiosyncratic to our institution, involving active affiliation, in addition to clear dominance/subordinate roles. It is our experience that other institutions may have a higher tolerance for aggressive behavior than is the case at our facility. Moreover, we suspect that

our facility utilizes intermittent pairing more than other facilities. While the use of intermittent pairing is sometimes done to facilitate investigators' experimental protocols, some animals are given intermittent pairing if they display aggression during feeding during the initial pairing attempts. It's possible that at other facilities such animals might be continuously paired (especially at facilities with a higher tolerance for aggression), or perhaps not paired at all. Thus, facility-specific norms, which might result in samples at different facilities that have different characteristics, might affect which predictors predict success. We also note that some of the other studies cited above [e.g., Lynch, 1998] studied species other than rhesus monkeys, which have a reputation for being highly aggressive and "despotic." Thus, the dynamics involved in achieving compatibility could very well be different based on overall species characteristics.

One might consider as a limitation the fact that our behavioral measures were made in infancy. We note, however, that the broad characteristics that we have identified (patterns of emotionality, nervous temperament, activity level) are relatively stable throughout life [Kalin & Shelton, 1998; Shiner & Caspi, 2012]. This suggests that trying to quantify similar measures in individually-housed animals, especially if such measures are obtained under somewhat challenging conditions as in the BBA program, just prior to pairing attempts, may be very feasible at other institutions; our data suggest the types of behavioral phenomena one might focus on. Finally, we recognize that other factors might be influential in contributing to pairing success. As we described earlier, the database for the BioBehavioral Assessment program contains a number of potentially relevant variables, such as rearing history, genotype, degree of Chinese ancestry, and measures of physiological responsiveness that we could have included in our analyses. Our goal with the present analysis, however, was to identify easily observable behavioral factors that could be measured by staff at other facilities who may be presented with very limited information about the animals to be paired, such as the animals' rearing histories, or serotonin transporter genotype.

In conclusion, our data suggest that success (as we have defined it) in isosexual pairings of rhesus monkeys is dependent on behavioral factors. Importantly, which factors are important differs for males and females. At the dyad level, "birds of a feather" do seem to flock together for females, inasmuch as similarity between partners in emotionality, regardless of whether both animals are high, low, or somewhere in-between, seems to lead to success. The story for males is more complicated. Because for males the mean values, and not the difference scores, were significant dyad-level predictors, male "birds of a feather" also seem to flock together, but only at the lower end of the distribution for the relevant behavioral factors. If one member of a pair is high on one particular measure (e.g., Nervous temperament), the best chance for a successful pairing might be achieved by hoping that "opposites attract," that is, by providing a potential partner that is low on the same measure, in order to lower the overall mean value for the dyad. Collection of quantified behavioral data during the pairing process would be very helpful for understanding how measures such as those identified in this analysis influence moment-to-moment behavior during the early stages of pairing.

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Table 1

Predictors of pairing success for females.

Parameter Estimates						
Parameter	Estimate	Standard Error	DF	t Value	Pr > t	95% Confidence Limits
<i>b0</i>	5.2529	2.9893	165	1.76	0.0807	-0.6494 11.1552
<i>DIEmoDiff</i>	-0.4661	0.2088	165	-2.23	0.0270	-0.8785 -0.05378
<i>NervDiff</i>	-0.5342	0.2483	165	-2.15	0.0329	-1.0244 -0.04400
<i>HIEmoDiff</i>	-0.8136	0.2939	165	-2.77	0.0063	-1.3939 -0.2332
<i>OutdoorRear</i>	-0.2927	0.4400	165	-0.67	0.5067	-1.1614 0.5759
<i>Infant</i>	-0.06753	0.4425	165	-0.15	0.8789	-0.9412 0.8061
<i>Weight</i>	-0.06671	0.09893	165	-0.67	0.5011	-0.2620 0.1286
<i>BBAAge</i>	-0.4398	4.6359	165	-0.09	0.9245	-9.5931 8.7135
<i>PairingAge</i>	-0.09402	0.06629	165	-1.42	0.1580	-0.2249 0.03687
<i>DiffAge</i>	0.2396	0.1574	165	1.52	0.1298	-0.07113 0.5503
<i>DiffWeight</i>	0.1948	0.2105	165	0.93	0.3561	-0.2208 0.6104
<i>DiffRear</i>	-0.5197	0.7019	165	-0.74	0.4601	-1.9057 0.8662

The following covariates were included: OutdoorRear = outdoor rearing [0=no, 1=yes], Infant = presence [1] or absence [0] of infant, Weight at time of pairing, Age in days at BBA testing, Age in years at pairing, and difference scores for Age at pairing and Weight at pairing. RearDiff was coded for pair-members that had different rearing conditions [0] or the same rearing conditions [1]. For the BBA measures, the suffix ".Diff" refers to the absolute value of the difference scores between pairmates. DIEmo refers to Day 1 Emotionality from the behavioral responsiveness assessment, Nerv reflects the Nervous temperament score, and HIEmo refers to the Emotionality score from the human intruder test.

Table II

Predictors of pairing success for males.

Parameter	Parameter Estimates					
	Estimate	Standard Error	DF	t Value	Pr > t	95% Confidence Limits
<i>bo</i>	-7.0267	4.1316	171	-1.70	0.0908	-15.1823 1.1289
<i>GentlMean</i>	-1.3061	0.4446	171	-2.94	0.0038	-2.1838 -0.4284
<i>NervMean</i>	-1.3134	0.4668	171	-2.81	0.0055	-2.2348 -0.3919
<i>OutdoorRear</i>	-22.7819	11.4294	171	-1.99	0.0478	-45.3427 -0.2211
<i>Weight</i>	-0.1021	0.08554	171	-1.19	0.2344	-0.2709 0.06677
<i>BBAAge</i>	3.8008	4.9838	171	0.76	0.4467	-6.0369 13.6385
<i>PairingAge</i>	-3.9701	1.9480	171	-2.04	0.0431	-7.8153 -0.1250
<i>DiffAge</i>	-0.2693	0.2214	171	-1.22	0.2256	-0.7064 0.1678
<i>DiffWeight</i>	0.5405	0.1636	171	3.30	0.0012	0.2175 0.8635
<i>DiffRear</i>	9.1512	4.4075	171	2.08	0.0394	0.4511 17.8514
<i>AgexRear</i>	3.8698	1.9480	171	1.99	0.0486	0.02457 7.7150

The following covariates were included: OutdoorRear = outdoor rearing [0=no, 1=yes], Weight at time of pairing, Age in days at BBA testing, Age in years at pairing, and difference scores for Age at pairing and Weight at pairing. RearDiff was coded for pair-members that had different rearing conditions [0] or the same rearing conditions [1]. AgexRear refers to an interaction of age at pairing by OutdoorRear. For the BBA measures, the suffix “Mean” reflects a mean of the pairmates’ values. Gentl and Nerv reflect the Gentle and Nervous temperament scores, respectively.