Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank

F. Blake Morton[a,b*], Alexander Weiss[b,c], Hannah M. Buchanan-Smith[a,b], Phyllis C. Lee[a,b]

[a] Behaviour and Evolution Research Group, Psychology, School of Natural Sciences, University of Stirling, Stirling, U.K.

[b] Scottish Primate Research Group, U.K.

[c] School of Philosophy, Psychology and Language Sciences, Department of Psychology, University of Edinburgh, Edinburgh, U.K.

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***Correspondence:** F. B. Morton, Psychology, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, U.K.
E-mail address: morton.blake@gmail.com (F. B. Morton).

Social relationships vary in content, quality and patterning. Most researchers focus on whether and how nondispositional factors, including age, sex, kinship and rank, predict variance in the content, quality and patterning of relationships. However, within a species, these factors do not always predict partner choice. We examined whether similarity in any of five personality traits, Assertiveness, Openness, Neuroticism, Sociability and Attentiveness, independently contributed to variation in the affiliative and agonistic relationships of pairs of brown capuchin monkeys, *Sapajus apella*. Capuchins that were more similar in Neuroticism had higher affiliative relationship scores, while capuchins that were more similar in Sociability shared overall higher-quality relationships (i.e. the difference between the dyad's affiliative and agonistic scores). These effects were independent of age, sex, kinship and rank, suggesting that certain aspects of the psychology of these animals may contribute uniquely to the quality of their social relationships.

Keywords: *Cebus apella*, homophily, partner compatibility, sociability, social rank, temperament

Social relationships vary in content (e.g. sexual, parenting, affiliation or conflict), quality (e.g. the intensity of affiliation or aggression) and patterning (e.g. frequency and temporal stability) (Hinde, 1976). Studying how and why social relationships vary among interactants has implications for understanding theoretical and applied questions, such as gene flow (Morin et al., 1994; Pilot, Dahlheim, & Hoelzel, 2010), disease and information transfer (Allen, Weinrich, Hoppitt, & Rendell, 2013; Kuehl, Elzner, Moebius, Boesch, & Walsh, 2008; Zelner et al., 2012), health and wellbeing (Archie, Altmann, & Alberts, 2012; Kikusui, Winslow, & Mori, 2006), sexual selection (e.g. mate choice; DeVries, DeVries, Taymans, & Carter, 1995; Schülke, Bhagavatula, Vigilant, & Ostner, 2010), life history (Holt-Lunstad, Smith, & Layton, 2010; Seyfarth, Silk, & Cheney, 2012; Silk et al., 2010) and social decision making (e.g. cooperation versus conflict; Clutton-Brock & Huchard, 2013; Clutton-Brock, 2009).

Differences in nondispositional factors, including partners' age, sex, rank and kinship, are commonly used to explain why relationships vary (e.g. Clutton-Brock & Huchard, 2013; MacCormick et al., 2012; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001). This may be because such nondispositional factors reflect differences in partners' quality (e.g. health, fighting ability; Clutton-Brock & Huchard, 2013; Sapolsky, 2004), socioecological needs (e.g. food, sex, protection and/or parental investment; Clutton-Brock & Huchard, 2013; Isbell & Young, 2015; Trivers, 1972), physiology (e.g. stress and reproductive hormones; Sapolsky, 2004; Zimmerberg & Farley, 1993) and developmental trajectories (Hollén & Radford, 2009; Loretto, Fraser, & Bugnyar, 2012). Identifying nondispositional factors that contribute to social relationship variance has helped researchers understand why animals are selective in their choice of social partners. For instance, females usually seek higher-quality relationships (i.e. those that are more affiliative than agonistic) with males, particularly alpha group members, as this affords them better protection and access to high-quality food (Clutton-Brock & Huchard, 2013).

However, the explanatory power of nondispositional factors is not consistent across studies of social relationships. For example, in bottlenose dolphins, *Tursiops truncatus,* age and sex predict spatial affiliation in some populations (Lusseau & Newman, 2004), but not in others (Félix, 1997; Lusseau et al., 2006). In barnacle geese, *Branta leucopsis*, Kurvers et al. (2013) found that social rank was unrelated to social affiliation, whereas kinship had a significant effect. In brown (or 'tufted') capuchin monkeys, *Sapajus apella* (formerly *Cebus apella*; Alfaro, Silva, & Rylands, 2012), Tiddi, Aureli, Polizzi Di Sorrentino, Janson, and Schino (2011) reported that social tolerance was unrelated to kinship and rank, but weakly related to sex. Other factors may therefore contribute to social relationship variance beyond nondispositional factors.

<H2>Personality and social relationships

Personality is an umbrella term used to describe individual differences in behaviour, affect and cognition that are consistent across time and contexts (Dingemanse & Réale, 2005; Gosling, 2008; Koski, 2014; Weiss & Adams, 2010). Measures of personality are associated with individual differences in social decision making (Aplin, Farine, Mann, & Sheldon, 2014; Krause, James, & Croft, 2010), performance on cognitive and learning tasks (Carere & Locurto, 2011; Morton, Lee, & Buchanan-Smith, 2013a; Sih & Del Giudice, 2012), risk taking (Dammhahn & Almeling, 2012), subjective wellbeing (Gartner & Weiss, 2013; King & Landau, 2003; Weiss et al., 2009; Weiss, King, & Perkins, 2006) and coping strategies (Coppens, de Boer, & Koolhaas, 2010; Martins et al., 2011). Personality traits are also heritable and reflect life history measures, including longevity and reproductive output (Biro & Stamps, 2008; Silk et al., 2010; van Oers, Drent, de Goede, & van Noordwijk, 2004; Weiss, Gartner, Gold, & Stoinski, 2013; Wolf, van Doorn, Leimar, & Weissing, 2007).

Despite the popular notion that ‘opposites attract’, individuals with similar personalities form stronger, more affiliative social bonds compared to other dyads. Such findings have been reported across a range of phylogenetically distant taxa, suggesting that similarities in personality may be a fundamental component of animal sociality. For example, pair bonding in eastern bluebirds, *Sialia sialis*, occurs more often between mates that are similar in aggressiveness (Harris & Siefferman, 2014). In rhesus macaques, *Macaca mulatta*, individuals are more affiliative with group members that are similar in Equability (e.g. calm/slow) and Adaptability (e.g. flexible/gentle) (Weinstein & Capitanio, 2008).

Personality similarities may signal partner quality (e.g. fighting ability or genetic compatibility). In great tits, *Parus major*, and in zebra finches, *Taeniopygia guttata*, similarity in exploration and aggression are positive indicators of future offspring quality (e.g. body mass; Both, Dingemanse, Drent, & Tinbergen, 2005; Schuett, Dall, & Royle, 2011). In guppies, *Poecilia reticulata*, sexual partners that are similar in boldness have higher parturition success than more dissimilar partners (Ariyomo & Watt, 2013).

Personality similarity may also reflect emotional or behavioural compatibility and predictability between potential social partners. In humans, perceived personality similarity promotes friendship intensity (e.g. Selfhout, Denissen, Branje, & Meeus, 2009) while couples in which both members have lower neuroticism (a measure of negative affect) report greater relationship satisfaction (e.g. Caughlin, Huston, & Houts, 2000; Heller, Watson, & Hies, 2004; Karney & Bradbury, 1997).

To date, most of what is known about associations between personality similarity and social relationship variance comes from studies of affiliative behaviour (e.g. Massen & Koski, 2014; Schuett et al., 2011; Seyfarth, Silk, & Cheney, 2014; Weinstein & Capitanio, 2008). Few data are available on the role that personality similarities play in agonistic relationships and overall social relationship quality (i.e. the intensity of affiliative versus agonistic behaviour between partners). Also, in many studies, nondispositional factors are usually not, or only partially, controlled for (e.g. Humbad, Donnellan, Iacono, McGue, & Burt, 2010; Massen & Koski, 2014; Schuett et al., 2011; Seyfarth et al., 2014; Weinstein & Capitanio, 2008; but see Seyfarth et al., 2014). Controlling for nondispositional factors is critical for several reasons. For instance, partner similarities in bold or aggressive personality traits may reflect attraction towards individuals that are similar in rank (e.g. Dahlbom, Lagman, Lundstedt-Enkel, Sundström, & Winberg, 2011). In addition, as these (and other) personality traits are heritable (Dochtermann, Schwab, Sih, & Dochtermann, 2015; Drent, van Oers, & van Noordwijk, 2003;

Sinn, Apiolaza, & Moltschaniwskyj, 2006), partner similarities in personality may be proxies for the degree of relatedness between pair members. Controlling for nondispositional factors therefore allows researchers to determine whether psychological factors other than those reflected by nondispositional factors contribute to variation in social relationships.

<H2>The present study

Studies of wild and captive brown capuchin monkeys often report mixed results with regard to the role of nondispositional factors in the social relationships of these animals. While Schino, Di Giuseppe, and Visalberghi (2009) and Tiddi, Aureli, and Schino (2012) found that brown capuchins preferentially give coalitionary support to kin, Ferreira, Izar, and Lee (2006) found no such preference within a different study population. Some studies report that brown capuchins groom ‘down’ the hierarchy (Parr, Matheson, Bernstein, & de waal, 1997), while others report no significant association between grooming and rank (Schino et al., 2009), or report that their population grooms ‘up’ the hierarchy (Tiddi et al., 2012). Therefore, personality may be an additional factor contributing to capuchin social relationships.

Brown capuchins, and the closely related white-faced capuchin, *Cebus capucinus*, exhibit pronounced individual differences in personality (Manson & Perry, 2013; Morton, Lee, Buchanan-Smith, et al., 2013b; Uher, Addessi, & Visalberghi, 2013). These differences are stable over time (Manson & Perry, 2013; Uher et al., 2013) and ratings of these traits are consistent across observers (Manson & Perry, 2013; Morton, Lee, Buchanan-Smith, et al., 2013b). Moreover, capuchin personality traits are associated with physiological measures (e.g. cortisol reactivity; Byrne & Suomi, 2002) and behavioural observations (Manson & Perry, 2013;

Morton, Lee, & Buchanan-Smith, 2013a; Morton, Lee, Buchanan-Smith, et al., 2013b; Uher et al., 2013).

In the present study, we investigated associations between personality similarities and the affiliative and agonistic components of brown capuchin social relationships. We predicted that, controlling for age, sex, kinship and rank, subjects with similar personalities would share higher-quality social relationships, defined here as relationships that were more affiliative than agonistic.

<H1>Methods

<H2>Study site and subjects

Eighteen brown capuchin monkeys (*Sapajus* sp.) were studied at the Living Links to Human Evolution Research Centre (LL), located within the Royal Zoological Society of Scotland (RZSS), Edinburgh Zoo, U.K. (Macdonald & Whiten, 2011). Subjects were from two breeding groups. At the time of study, the ‘East’ group contained four adult males, three adult females, one juvenile male and five infants (following age–sex categories in Fragaszy, Visalberghi, & Fedigan, 2004). The ‘West’ group contained four adult males, three adult females, two juvenile males, one juvenile female and five infants. Infants dependent on their mothers (i.e. those less than a year old) were not included as study subjects. Subjects’ ages ranged from 2 to 40 years for males (mean ± SD = 10.79 ± 8.55 years, *N* = 11) and 3 to 14 years for females (mean ± SD = 8.86 ± 3.63 years, *N* = 7). All group members were captive born except an adult male from East group, who was hand-reared, and the original wild-caught alpha male of West group; both individuals came to LL as established members of their groups.

Both breeding groups were housed separately in identically designed 189 m^3 indoor enclosures with natural light and near-permanent access to a 900 m^2 outdoor enclosure containing trees and other vegetation, providing ample opportunity to engage in natural behaviours. All monkeys received commercial TrioMunch pellets supplemented with fresh fruits and vegetables three times daily and were given cooked chicken and hardboiled eggs once a week. Water was available ad libitum at all times. Further details of housing and husbandry are provided in Leonardi, Buchanan-Smith, Dufour, MacDonald, and Whiten (2010).

<H2>Ethical note

This study was entirely observational except for one aspect of data collection involving puzzle feeders, which were placed within the monkeys' outdoor enclosures (see 'Behavioural sampling'). Subjects could interact freely with the puzzle feeders, which were made entirely of nonhazardous material. The feeders provided a source of food snacks (raisins) and enrichment to subjects. This study was approved by Edinburgh Zoo and the ethics committee of the Psychology Department at the University of Stirling, and complied with the ASAB/ABS (2012) Guidelines.

<H2>Personality

Details on data collection and analyses of our subjects' personalities are provided in Morton, Lee, Buchanan-Smith, et al. (2013b). Briefly, subjects in the present study were part of a study of 127 brown capuchin monkeys housed at seven sites who were rated by 3.24 ± 1.61 knowledgeable informants on the 54 traits contained in the Hominoid Personality Questionnaire (Weiss et al., 2009). Capuchins at Living Links were rated in August 2010. Principal components analysis of mean ratings across all sites and observers for the 54 reliable traits revealed five personality dimensions: Assertiveness, Openness, Attentiveness, Neuroticism and Sociability (Table 1). These personality dimensions showed good inter-rater reliabilities and were associated with relevant behaviours recorded up to a year later (Table 1; Morton, Lee, & Buchanan-Smith, 2013a; Morton, Lee, Buchanan-Smith, et al., 2013b), thereby demonstrating the validity and temporal stability of subjects' personality scores. Data used to assess social relationship quality come from the same time period as the behaviours used to validate our personality scores (see 'Behavioural sampling').

In the present study, personality similarities between partners were calculated for each personality dimension by subtracting one partner's personality *z*-score on that dimension from the other partner's *z*-score on that dimension, and taking the absolute value. To make the results more interpretable, this value was then transformed into a *z*-score.

<H2>Behavioural sampling

We recorded 54 h of focal observations between May and August of 2011, totalling 3 h per individual. Data were collected 1 year after subjects' personalities were assessed. Behaviours (Table 2) were recorded daily per focal monkey for 10 min. Monkeys were sampled evenly between 0900 and 1730 hours. Incidences of aggression, coalitions, scrounging and food sharing were recorded continuously; all other behaviours were recorded at 1 min intervals using point sampling (Martin & Bateson, 2007). In each point sample, group members within two body lengths from the focal were recorded. The total number of sampling points was the same for all subjects.

Between 15 May 2011 and 8 June 2011 five puzzle feeders were introduced to the outdoor enclosures of the East and West groups. All group members could freely interact with the feeders. Each feeder was made out of a cylindrical piece of white piping (length: 76.2 cm; diameter: 5.08 cm), with approximately 8–10 holes drilled into it (Appendix Fig. A1). Each hole was 2.5 cm in diameter. Feeders were attached vertically to trees, 2–10 m apart. For each feeder, the bottom of the pipe was left open while the top of the pipe was closed. Ten paper packets, each containing five raisins, were placed in the top portion of each feeder, and wooden sticks were inserted into the holes of the pipes to prevent the packets from falling out from the bottom. This prevented subjects from accessing the paper packets in the top portion of the pipe, but allowed the packets to drop freely from the pipe once all the wooden sticks had been removed.

Feeders were introduced 4 days a week for approximately 30 min each day or until all of the puzzle feeders had been solved. During sessions, we recorded all instances in which a monkey approached another monkey at a feeding site, noting whether the receiving monkey responded to their approach by avoiding or staying at the feeder within the first 10 s of being approached. East group underwent eight sessions and West group underwent 10 sessions. These data were used to calculate avoid–stay symmetries in calculations of relationship quality.

<H2>Data reduction and computing social relationship quality

Measures of relationship quality were calculated per subject interacting with all other available partners, resulting in a total of 73 dyads. Following previous studies of social relationship quality (e.g. Fraser, Schino, & Aureli, 2008; Koski, de Vries, van de Kraats, & Sterck, 2012; Majolo, Ventura, & Schino, 2010; McFarland & Majolo, 2011; Rebecchini, Schaffner, & Aureli, 2011), 10 behavioural measures (Table 3) were calculated as events per monkey dyad and subjected to a principal components analysis (PCA) with varimax and promax rotation. A scree plot and parallel analysis were used to determine the number of components to extract from the PCA (Horn 1965; Zwick & Velicer, 1986). Components were considered robust if they contained absolute loadings that were greater than or equal to |0.7| and/or were greater than |0.4| on four or more items (Guadagnoli & Velicer, 1988). For each component, we computed unit-weighted scores (Gorsuch, 1983) and converted these into *z*-scores.

Overall mean numbers of social dyadic interactions are provided in Appendix Table A1; the values are low because they reflect behaviour per dyad, not per individual, and therefore contain zeros for noninteracting dyads. These values are within the range of values reported by other studies using similar methods (e.g. Majolo et al., 2010; McFarland & Majolo, 2011; Rebecchini et al., 2011). We used means instead of medians because there would otherwise be zeros for some contexts.

<H2>Nondispositional factors

Age (in years) was determined for the time period when data on subjects' social relationships were collected. Win/loss outcomes from agonistic interactions were used to calculate David's scores, a continuous measure of rank, for each subject (Gammell & Vries, 2003). Then, for each of these nondispositional factors, similarity was calculated for each dyad by subtracting one partner's value from the other partner's value, and taking the absolute value. These values were then transformed into *z*-scores.

In addition to age and rank similarity, we recorded for each dyad whether they were the same or opposite sex. We also recorded their genetic relatedness based on pedigrees and expressed this using Wright's coefficient of relatedness: r = 0.5 for parent–offspring and full sibling pairs, r = 0.375 for three-quarter siblings (inbreeding), r = 0.25 for grandparent–grandchild relations, r = 0.25 for aunt/uncle–nephew/niece relations, r = 0.125 for half siblings and $r = 0.125$ for first cousins. Thus, in all cases except for relatedness, lower values indicate higher degrees of similarity between the members of a dyad.

<H2>Statistical analyses

We assessed the affiliative and agonistic components of capuchins' social relationships by entering the behavioural calculations listed in Table 3 into a PCA using SPSS 19 (IBM Corp., Chicago, IL, U.S.A.). For this analysis we determined the number of components to extract using both the scree plot and a parallel analysis (Field, 2009; Horn 1965).

For our tests of associations between partner similarities in nondispositional factors and personality and relationship quality, we used robust analyses to reduce the impact of potential outliers. Furthermore, because each subject would be represented in multiple dyads, and observations were therefore not independent, we used bootstrapping to generate 95% confidence intervals in these analyses. All of the association tests were conducted using R version 3.1.2 (R Core Team, 2014).

We used Spearman rank order correlations to examine bivariate associations between relationship scores and similarity in age, kinship, rank and the five personality dimensions. For these analyses we used the boot function (Canty & Ripley, 2012) to generate confidence intervals using the bias-corrected and accelerated bootstrap (Davison & Hinkley, 1997; Efron, 1987).

To test whether similarity in sex was associated with each of the three relationship scores we used the FRBhotellingMM function (Van Aelst & Willems, 2009) to conduct robust Hotelling tests using the MM-estimator. To test whether the effects of personality similarity contributed to each of the three relationship scores over and above the contribution of nondispositional factors, we used the FRBmultiregMM function (Van Aelst & Willems, 2009) to conduct three robust multiple regressions using the MM-estimator. The 95% confidence intervals for these analyses were generated using the bias-corrected and accelerated bootstrap (Davison & Hinkley, 1997; Efron, 1987).

<H1>Results

<H2>Principal Components Analysis

Both the scree plot (Appendix Fig. A2) and parallel analysis (Appendix Table A2) suggested that two components should be retained. These two components explained 55.0% of the variance and were weakly correlated (r = -0.072). A comparison between the varimax- and promax-rotated solutions revealed little difference in structure (Table 4, Appendix Table A3). Thus, interpretation of the components was based on the varimax-rotated solution.

Component 1 was characterized by moderate to high loadings on behaviours related to social affiliation (e.g. proximity, grooming) and was therefore labelled ‘Affiliative’. Component 2 was characterized by high loadings on conflict and conflict symmetry and was therefore labelled ‘Agonistic’.

Monkey dyads with higher scores on components 1 and 2 thus engaged in more affiliative and agonistic behaviours, respectively. Therefore, for remaining analyses, relationship quality was defined as the difference between the affiliative score and agonistic score for each dyad, whereby ‘higher-quality’ relationships were those that were more affiliative than agonistic.

<H2>Social relationships and similarities in personality and nondispositional factors

Dyads similar in Sociability had significantly higher affiliative scores (Table 5). Dyads similar in age, rank and Openness had significantly lower agonistic scores. In terms of relationship quality, dyads similar in rank, Openness and Sociability had higher-quality relationships than did other dyads. Kinship, sex and the other three personality traits were not significantly related to affiliative scores, agonistic scores or overall relationship quality.

The results of the robust Hotelling tests revealed that same-sex dyads did not differ significantly from opposite-sex dyads in their affiliative scores (4979 bootstrap samples, T^2_{R} = 1.65, $P = 0.26$), in their agonistic scores (4549 bootstrap samples, T^2_{R} = 3.29, $P = 0.19$), or in their overall relationship quality (4959 bootstrap samples, T^2_{R} = 0.49, $P = 0.55$).

The results of the multiple regression analysis are presented in Table 6. The sole predictor of affiliative scores was Neuroticism: monkeys that were more similar in Neuroticism were more affiliative. None of the personality traits or nondispositional factors were independently related to agonistic scores. The sole predictor of overall relationship quality was Sociability: higher relationship quality was associated with dyads who were more similar in Sociability.

<H1>Discussion

When nondispositional factors were not controlled for, similarities in Openness and Sociability were positively related to subjects' affiliative scores and overall relationship quality. When we controlled for nondispositional factors, the unique effects of similarities in Neuroticism and Sociability were independently related to higher affiliative scores and overall relationship quality, respectively. Our findings therefore support the hypothesis that capuchin dyads with similar personalities, regardless of whether both partners scored high, low or somewhere in between on these traits, share higher-quality social relationships, and that for some traits these effects are independent of nondispositional factors.

At the individual level, previous studies have shown that Openness is negatively associated with the amount of time that brown capuchins behave aggressively towards others (Morton, Lee, Buchanan-Smith, et al., 2013b), and that less aggressive capuchins typically avoid more aggressive individuals (Janson, 1990). Thus capuchins more similar in Openness may share higher-quality relationships because they are more socially compatible. Since capuchins that scored high on Openness were also more playful and curious (Morton, Lee, Buchanan-Smith, et al., 2013b), these capuchins might also have been attracted to one another due to their general playfulness and interest in each other's activities. Individual differences in Openness are inversely related to differences in age and social rank (Morton 2014), which may explain why this personality trait did not contribute to dyadic differences in relationship quality independent of nondispositional factors.

Previous work has shown that individual differences in capuchin Sociability are positively related to the amount of time subjects spend in close proximity to others in general (Morton, Lee, Buchanan-Smith, et al., 2013b). Across a range of taxa, individuals that score highly on traits related to neuroticism (e.g. shyness, reactivity) show greater levels of stress and emotional instability (Gunthert, Cohen, & Armeli, 1999; Millot et al., 2014; Raoult, Brown, Zuberi, & Williamson, 2012). Among our study subjects, individuals that score highly on Neuroticism typically show greater signs of agitation (e.g. greater movement within their main enclosures and poorer attention span during cognitive testing; Morton, Lee, & Buchanan-Smith, 2013a; Morton, Lee, Buchanan-Smith, et al., 2013b; Morton 2014). Thus, individuals that are similar in Sociability and Neuroticism may establish higher-quality social relationships with one another because they are more emotionally and/or socially compatible.

The association between social relationship quality and similarity in Openness, Sociability and Neuroticism is not unique to capuchins. In chimpanzees, *Pan troglodytes*, similarities in Sociability are positively related to the amount of time partners spend in close proximity to each other (Massen & Koski, 2014). In humans, similarities in Openness, Extraversion and Neuroticism, which are analogous to capuchin Openness, Sociability and Neuroticism, respectively (Morton, Lee, Buchanan-Smith, et al., 2013b), are associated with lower levels of aggression and higher rates of affiliation in relationships (Barlett & Anderson, 2012; Dijkstra & Barelds, 2007; Jones, Miller, & Lynam, 2011). Such striking overlap between phylogenetically distant species (Steiper & Young, 2006) suggests that the importance of these personality traits to relationship quality has a long evolutionary history.

In addition to personality, individuals that were similar in age and rank were less aggressive towards one another, and monkeys that were similar in rank shared higher-quality relationships. The effect of age similarity on agonistic scores may be related to the fact that capuchin rank is associated with age in this sample (Lefevre et al., 2014; Morton 2014). These findings are also consistent with previous work in other capuchin populations: higher-ranking individuals (particularly the alpha male) tend to direct aggression towards younger, lower-ranking individuals, which in turn may impact the overall quality of their social relationships (Fragaszy et al., 2004; Janson, 1990).

<H2>Future Directions

One remaining question concerns the mechanism(s) that bring about associations between personality similarities and relationship quality in capuchin dyads. One possibility is that capuchins seek social partners with similar personalities. A second possibility is that partners' personalities converge over time as a result of conditioning or sharing social experiences. To determine whether our findings are the result of 'attraction' and/or 'convergence' will require a longitudinal study in which personality and social relationship quality are measured at multiple time points.

Further research is also needed to determine why similarities in Sociability and Neuroticism were related to social relationship quality independent of nondispositional factors. Considering the kinds of behaviours associated with these personality traits (e.g. a propensity for social affiliation and agitation, respectively; Morton, Lee, Buchanan-Smith, et al., 2013b), one intriguing possibility is that individual differences in Sociability and Neuroticism reflect differences in the emotional and/or sociocognitive traits that capuchins use to make social decisions that are not simply reflected by nondispositional factors.

Irrespective of whether nondispositional factors were controlled for, similarity in Assertiveness and Attentiveness were not associated with differences in partners' affiliative scores, agonistic scores or overall relationship quality despite previous work showing that both traits correlate with individual differences in subjects' affiliative and agonistic behaviour (Morton, Lee, Buchanan-Smith, et al., 2013b). It is unlikely that these results are due to changes in the stability of subjects' scores on Assertiveness and Attentiveness. Previous studies of capuchins have found good evidence for rank order stability of personality measures (Manson & Perry, 2013; Uher et al., 2013), and, as previously noted, our subjects' scores on Assertiveness and Attentiveness predicted relevant behaviours up to a year later, including behaviours used to assess relationship quality in the current study. Similarities in specific personality traits (i.e. Sociability, Openness, Neuroticism), rather than personality similarities in general, may therefore play a greater role in defining the quality of capuchin social relationships. Alternatively, the relatively small number of dyads might have resulted in statistical power being too low to detect effects from particular personality traits. Although we guarded against Type I errors by means of robust analyses and bootstrapping procedures, further work with larger samples is needed to determine whether these findings generalize to other capuchin populations.

Kinship and sex were not related to relationship quality. Previous work has reported mixed results with regard to the role that kinship and sex play within capuchin societies (Ferreira et al., 2006; Tiddi et al., 2011, 2012; Welker, Höhmann, & Schäfer-Witt, 1990). It may be that these nondispositional factors impact relationship quality only under certain socioecological conditions, such as differences in group composition or the number of matrilines within groups (Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008). Alternatively, as noted before, the small number of dyads within our study may have precluded our ability to detect significant effects from these variables. Finally, given our concerns about statistical power, we did not examine interaction effects in our analyses. Therefore a fruitful avenue for future research would be to determine whether, for example, kin and nonkin dyads differ with regard to what personality traits contribute to their relationship quality.

Seyfarth et al. (2014) studied wild baboons, *Papio ursinus*, and reported that similarities in personality were positively associated with partners' affiliative relationship quality. As in our study, these effects were independent of age, sex, kinship and rank. To our knowledge, similar analyses (i.e. those that adequately control for all possible effects from nondispositional factors) are notably lacking in other studies. Also, as previously noted, few studies on any species have tested for independent effects of personality on both the affiliative and agonistic components of social relationship quality for their subjects. Further data on a range of primate and nonprimate taxa are therefore needed in order to fill these gaps in the literature. An integrated comparative approach will allow researchers to better understand the adaptive function and evolutionary history of personality–relationship associations.

<H2>Conclusions

Similarities in personality (Openness, Sociability, Neuroticism) were significantly related to the affiliative and agonistic components of capuchins' social relationships. More importantly, some of these effects (Sociability/Neuroticism) were independent of nondispositional factors. Such findings suggest that certain aspects of personality (e.g. emotional and/or social compatibility) may contribute to the quality of capuchins' social relationships beyond what is reflected by age, sex, kinship and rank.

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Appendix

Table 1. Highest item loadings and examples of positive correlations with behavioural codings for capuchin personality dimensions

	Personality dimensions				
	Assertiveness	Openness	Neuroticism	Sociability	Attentiveness
Highest loadings	+ Aggressive + Bullying – Submissive	+ Inventive + Innovative + Inquisitive	– Cool – Stable + Excitable	+ Sociability + Affectionate – Solitary	– Disorganized – Unperceptive – Thoughtless
Examples of positive correlations with behaviour	Rates of aggression[b]	Task participation and learning performance[a]	Social avoidance and lack of focus on tasks[b,c]	Time spent in close proximity to others[b]	Longer attention span during cognitive testing[b]

+ and – refer to the direction of trait loadings. For example, '+ Excitable' means that subjects high in Neuroticism are excitable and '- Solitary' indicates that subjects high on Sociability are not solitary.

[a] Morton, Lee, Buchanan-Smith, et al. (2013a).

[b] Morton, Lee, Buchanan-Smith, et al. (2013b).

[c] Morton (2014).

Table 2. Behaviours recorded during focal sampling

Behaviour	Definition
Aggression	Open-mouth threats, vocal threats, lunging, chasing, hitting and/or biting
Coalitionary support	Another individual intervenes during a conflict between two parties, directing aggression towards only one of the combatants
Feeding	Searching for or ingesting food
Food sharing	One individual allows another individual to take pieces of its food (from hands or mouth)
Grooming	Picking through the hair of another individual
Scrounging	Exploiting food found by others; successful begging or stealing food from others
Solitary	No monkey within two body lengths of the focal animal

Table 3. Definitions and calculations of social behaviours entered into principal components analysis

Social behaviour	Definition	Calculation
Avoid/Stay symmetry	Symmetry in number of times a monkey avoided/stayed at monopolizable food source as they were approached by other member of the dyad	(no. times A approaches B) / [(no. times A approaches B) + (no. times B approaches A)]
Coalitions	Number of aggressive events in which one member of the dyad supports the other	[(no. times A supports B) + (no. times B supports A)]
Aggression	Number of aggressive events within dyad	[(no. times A attacks B) + (no. times B attacks A)]
Aggression symmetry	Symmetry in conflict within dyad	(no. times A attacks B) / [(no. times A attacks B) + (no. times B attacks A)]
Food sharing	Number of food-sharing events within dyad	[(no. times A gives to B) + (no. times B gives to A)]
Food sharing Symmetry	Symmetry in food sharing within dyad	(no. times A gives to B / [(no. times A gives to B) + (no. times B gives to A)]
Grooming	Number of focal minutes spent grooming each other	[(no. minutes A grooms B) + (no. minutes B grooms A)]
Grooming symmetry	Symmetry in grooming within dyad	(no. minutes A grooms B) / [(no. minutes A grooms B) + (no. minutes B grooms A)]
Social foraging	Number of focal minutes spent in close proximity (≤2 body lengths) to each other while at least one member of dyad is engaged in foraging	[(% of time A within proximity of B) + (% of time B within proximity of A)]
Spatial proximity	Number of focal minutes spent in close proximity (≤2 body lengths) to each other	[(% of time A within proximity of B) + (% of time B within proximity of A)]

Proximity calculations do not include time spent grooming or time spent social foraging (both of which were analysed as separate variables).

Table 4. Varimax-rotated structure of PCA for behavioural measures calculated per monkey dyad

	Varimax rotation		
Behaviour index	PC1	PC2	*h*^{2}
Social foraging	**0.846**	-0.026	0.321
Spatial proximity	**0.803**	-0.112	0.293
Grooming	**0.772**	-0.077	0.438
Coalitions	**0.771**	-0.033	0.658
Food sharing	**0.651**	-0.120	0.602
Food sharing symmetry	**0.532**	0.272	0.716
Conflict	-0.053	**0.875**	0.357
Conflict symmetry	0.049	**0.865**	0.751

Salient loadings (>|0.4|) for each behaviour in boldface; PC=principal component.

Table 5. Spearman correlations (r_S) between similarities in age, kinship, rank and personality traits and affiliative/agonistic scores and overall relationship quality (i.e. difference between affiliative and agonistic scores)

	Affiliative		Agonistic		Quality	
	r_S	95% CI	r_S	95% CI	r_S	95% CI
Age	0.17	[-0.05 to 0.38]	**0.45**	**[0.22 to 0.61]**	**-0.26**	**[-0.46 to -0.01]**
Kinship	0.04	[-0.22 to 0.27]	-0.19	[-0.40 to 0.03]	0.15	[-0.09 to 0.37]
Rank	-0.11	[-0.32 to 0.10]	**0.33**	**[0.09 to 0.54]**	**-0.37**	**[-0.57 to -0.14]**
Assertiveness	0.00	[-0.26 to 0.25]	0.16	[-0.08 to 0.37]	-0.12	[-0.33 to 0.11]
Openness	-0.10	[-0.32 to 0.15]	**0.29**	**[0.07 to 0.50]**	**-0.42**	**[-0.61 to -0.20]**
Neuroticism	-0.18	[-0.40 to 0.07]	0.09	[-0.15 to 0.32]	-0.12	[-0.36 to 0.13]
Sociability	**-0.39**	**[-0.58 to -0.14]**	0.10	[-0.14 to 0.33]	**-0.33**	**[-0.52 to -0.11]**
Attentiveness	0.05	[-0.22 to 0.29]	0.12	[-0.10 to 0.33]	-0.14	[-0.37 to 0.09]

95% CI = bootstrapped 95% confidence intervals. *df* = 63. ‘Quality’ = difference between affiliative and agonistic component scores per dyad. Spearman correlations with confidence limits that did not include 0 are presented in boldface. Confidence intervals and *P* values generated by fast and robust bootstraps with 5000 samples in all analyses.

Table 6. Independent effects of nondispositional factors and personality variables on affiliative scores, agonistic scores and overall relationship quality (i.e. difference between affiliative and agonistic scores)

	Affiliative				Agonistic				Quality			
Effect	*b*	SE	95% CI	*P*	*b*	SE	95% CI	*P*	*b*	SE	95% CI	*P*
Intercept	-0.39	0.13	[-0.63 to -0.14]	0.005	-0.43	0.32	[-1.07 to 0.17]	0.18	-0.03	0.22	[-0.45 to 0.40]	0.89
Sex	0.14	0.11	[-0.08 to 0.34]	0.21	0.08	0.22	[-0.32 to 0.55]	0.69	0.09	0.17	[-0.26 to 0.40]	0.64
Age	0.01	0.01	[0.00 to 0.03]	0.12	0.01	0.01	[-0.01 to 0.03]	0.55	0	0.01	[-0.02 to 0.02]	0.95
Rank	-0.01	0.05	[-0.11 to 0.10]	0.9	0.12	0.09	[-0.06 to 0.28]	0.16	-0.18	0.1	[-0.37 to 0.02]	0.07
Kinship	-0.09	0.37	[-0.80 to 0.62]	0.82	-0.23	0.39	[-0.94 to 0.61]	0.55	-0.19	0.49	[-1.20 to 0.73]	0.67
Assertiveness	-0.11	0.07	[-0.24 to 0.02]	0.086	0.01	0.07	[-0.14 to 0.14]	0.84	-0.06	0.07	[-0.21 to 0.08]	0.35
Openness	-0.04	0.08	[-0.20 to 0.12]	0.68	0.01	0.06	[-0.11 to 0.13]	0.86	-0.15	0.1	[-0.35 to 0.06]	0.15
Neuroticism	**-0.19**	**0.07**	**[-0.35 to -0.08]**	**0.002**	0.09	0.23	[-0.38 to 0.50]	0.71	-0.04	0.08	[-0.21 to 0.12]	0.57
Sociability	-0.12	0.06	[-0.24 to 0.01]	0.066	-0.01	0.06	[-0.13 to 0.10]	0.8	**-0.17**	**0.07**	**[-0.31 to -0.05]**	**0.007**
Attentiveness	0.14	0.08	[-0.03 to 0.27]	0.1	-0.01	0.07	[-0.15 to 0.12]	0.83	-0.02	0.08	[-0.21 to 0.12]	0.65

Significant results ($P < 0.05$) in boldface. *df* in all cases = 63. Standard errors (SE), 95% confidence intervals (95% CI), and *P* values generated by fast and robust bootstraps with 5000 samples in all three analyses.

Table A1. Mean ± SE social behaviour per monkey dyad

Social behaviour	Mean ± SE per dyad
Avoid/Stay symmetry	-7.32 ± 1.3
Coalitions	0.21 ± 0.07
Conflict	1.01 ± 0.18
Conflict symmetry	0.49 ± 0.19
Food sharing	0.44 ± 0.11
Food sharing symmetry	0.001 ± 0.1
Grooming	1.82 ± 0.41
Grooming symmetry	0.03 ± 0.35
Spatial proximity	12.16 ± 1.63
Social foraging	4.74 ± 0.64

N = 73. Negative values indicate that one monkey within the dyad stayed more than retreated when approached by the other monkey.

Table A2. Results of Horn's (1965) parallel analysis for component retention

Component	Adjusted eigenvalues
1	**2.920683**
2	**1.202033**
3	0.858408
4	0.708558
5	0.549795
6	0.568731
7	0.533918
8	0.527448
9	0.549315
10	0.568179

1000 iterations, using the 95th percentile estimate; adjusted eigenvalues >1.0 indicate dimensions to retain; two components retained (boldface). Unadjusted eigenvalues are those used for the scree test (Appendix Fig. A2).

Table A3. Promax-rotated structure of PCA for behavioural measures calculated per monkey dyad

	Promax rotation		
Behaviour Index	PC1	PC2	h^2
Social foraging	**0.847**	0.010	0.321
Spatial proximity	**0.802**	-0.078	0.293
Grooming	**0.771**	-0.044	0.438
Coalitions	**0.771**	0.000	0.658
Food sharing	**0.649**	-0.092	0.602
Food sharing symmetry	**0.541**	0.295	0.716
Conflict	-0.027	**0.875**	0.357
Conflict symmetry	0.075	**0.869**	0.751

Salient loadings (>|0.4|) for each behaviour in boldface; PC=principal component.

Figure A1. Diagram illustrating the design of each puzzle feeder introduced to the outdoor enclosure of East and West groups.

Figure A2. Scree test for component retention. Black circles indicate components that were retained; white circles indicate components that were discarded.