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Social bonds in female baboons: the interaction between personality, kinship and rank

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Previous analyses indicate that female baboons that form strong and stable social bonds reproduce more successfully than others, and that some elements of females' personalities are associated with the tendency to form close social bonds. Here we use a new method to confirm that females' personalities were stable over time, although not fixed, and that matrilineal kin had personalities that were no more alike than those of other individuals. Our results indicate that personality similarities enhance the strength of social bonds among some pairs of females but not others. Strong bonds between matrilineal sisters were correlated with similarity in their personalities and ages, but mothers and daughters formed uniformly strong bonds regardless of the similarities in their personalities or ages. Among nonkin, strong bonds were correlated with similarity in age and dominance rank, but not personality. Females adjusted the behaviours that contributed to their personality scores in response to unpredictable demographic events, like the death of a close relative. Results suggest that the personality traits of female baboons do not exist in isolation but are embedded in a network of rank and kin relations. Although a female baboon has little control over her dominance rank or the presence of kin, by varying the tenor of her social interactions she can take advantage of the opportunities, or overcome the constraints, imposed by demographic circumstances. For this reason, selection may have favoured particular personality traits that are relatively independent of rank and the presence of kin.

Individuals in a variety of species, including insects, birds and mammals, show consistent differences in behaviour across a variety of social and ecological contexts (reviewed in: Dingemanse & Wolf, 2010; Sih, Bell, & Johnson, 2004). Such differences, called 'behavioural syndromes' or 'personality types', are of particular interest when they are consistent over time, based on correlations among several functionally distinct behaviours (e.g. Cole & Quinn, 2012; Verbeeck, Boon, & Drent, 1996), not redundant with other measures like sex, age, dominance rank or the presence of kin (Seyfarth, Silk, & Cheney, 2012) and positively correlated with one or more measures of reproductive success (e.g. Dall, Houston, & McNamara, 2004; Dingemanse & Réal, 2005). When these conditions are met, the identification of animal personality types can improve our ability to explain the evolution of adaptive variations in behaviour.

Two or more animals may have similar personalities because of shared genes, shared ecological or social environments, or, most likely, some combination of these causal factors. Extensive research on humans has revealed moderate heritability of several personality dimensions (e.g. Bouchard & Loehlin, 2001) as well as significant environmental causation, even within the same family (e.g. Plomin & Daniels, 1987; reviewed in Larsen & Buss, 2008). van Oers, de Jong, van Noordwijk, Kempenaers, and Drent (2005) reach a roughly similar conclusion in their review of the many fewer studies of genetics and measures of personality in nonhuman species (see also Lea, Blumstein, Wey, & Martin, 2010). Little is known about the factors that influence personality in nonhuman primates. In a recent study of rhesus macaques, *Macaca mulatta*, Brent et al. (2013) found additive genetic variance for several measures of sociality while controlling for age, sex, dominance rank, and, in the case of females, family membership. Some of these measures were significantly correlated with measures of reproductive success and one was significantly correlated with genetic variation at two loci involved in serotonergic signalling (Brent et al., 2013).

Baboons (*Papio hamadryas* spp.) live throughout Africa in multimale, multifemale groups of 40–120 individuals. Females remain in the natal group throughout their lives, while males disperse to neighbouring groups at adulthood. Females form a linear

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dominance hierarchy that accurately predicts the direction of competitive interactions; daughters acquire ranks similar to those of their mothers, and ranks are generally stable for long periods (e.g. Altmann & Alberts, 2003; Cheney & Seyfarth, 2007). Close matrilineal kin (mothers and daughters, matrilineal sisters) often form strong, enduring social bonds characterized by frequent grooming, proximity and support in competitive alliances (Silk, Alberts, & Altmann, 2004; Wittig, Crockford, Seyfarth, & Cheney 2007). However, strong and stable bonds may also be formed between females in different matrilines (Silk et al., 2010a; Silk, Alberts, & Altmann, 2003; Silk, Altmann, & Alberts, 2006a, 2006b).

In two long-term studies conducted in Kenya (*P. h. cynocephalus*) and Botswana (*P. h. ursinus*), the best predictors of a female baboon's reproductive success were not her dominance rank, the presence or absence of kin, or the size of her matriline, but the strength and stability of her social bonds with other females. Reproductive success was measured by longevity and rates of offspring survival; bond strength was measured using two indices that quantified the strength and stability of a female's bonds with other females. One, the composite sociality index (CSI), was based on rates of approaches, grooming initiations and grooming durations within same-sex dyads, and reflected overall levels of sociality (Silk et al., 2003, 2010a). Another, the partner stability index (PSI), measured a female's retention of her top three female partners from one year to the next, and reflected the stability of close social bonds over time (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012). At both sites, the CSI was the best predictor of offspring survival (Silk et al., 2003, 2009). In Botswana, a composite measure of CSI and PSI was the best predictor of longevity (Silk et al., 2010b). High dominance rank also predicted greater longevity, but the effect of rank was both independent of and less strong than the effect of social bonds (Silk et al., 2010b).

Because variation in the strength of social bonds was not significantly correlated with obvious demographic attributes like rank or the presence of kin, we used data from the same population of female baboons in Botswana to test whether variation in bond strength might be correlated with consistent individual differences in behaviour, or personalities (for recent reviews of personality studies in captive primates, see: Uher, 2011; Weiss, Adams, Widdig, & Gerald, 2011; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012). Because we wanted to test whether personality types were correlated with CSI and PSI scores, we based our analyses on seven behaviours that were both relatively independent of the behaviour of others and not used to construct CSI and PSI. These included forms of aggression, friendly behaviour and nonaggressive grunting to individuals in different contexts.

We found evidence of consistent individual differences in behavioural profiles over time (Seyfarth et al., 2012). The pattern of correlations among the different behaviours was best explained by three principal components. The loadings of behaviours onto these components allowed us to characterize females according to three personality dimensions, which we termed 'Aloof', 'Loner' and 'Nice'. Females scoring high on the Aloof dimension were relatively more aggressive, less friendly, and grunted almost exclusively to higher-ranking females. Other females seldom approached them. Females scoring high on the Loner dimension were often alone, relatively unfriendly, and also grunted primarily to higher-ranking females. These females also experienced higher glucocorticoid levels and were rarely approached by others. Females scoring high on the Nice dimension were very friendly, comparatively unaggressive, and grunted at high rates to all females, regardless of their rank. They were often approached by others (Seyfarth et al., 2012).

Individuals' scores on personality dimensions were generally uncorrelated with their rank or the presence of close female kin (but see below). We found no evidence that the dimension scores of close kin were more alike than those of less closely related individuals' (Seyfarth et al., 2012). This result, however, may have underestimated the degree of personality similarity within families because it analysed each dimension of personality separately. In this paper, we extend these analyses using a new method for comparing the personality types of two individuals using all three dimensions simultaneously.

There was some indication that females' personality types may indirectly influence their fitness by influencing the likelihood that they develop close social bonds with other females. We found that females with high scores on the Nice dimension had significantly stronger social bonds (i.e. higher CSI values) and tended to have more stable social bonds (i.e. higher PSI values) than other females. Females that scored high on the Aloof dimension had more stable social bonds than other females, while females that scored high on the Loner dimension had weaker social bonds than other females.

Individuals' personality traits, however, do not exist in isolation. They are embedded in a social network where a female's behaviour is affected by many variables, including not just her own personality and dominance rank, but also the presence or absence of preferred categories of partners and the personalities of potential partners. This poses an intriguing adaptive problem because, whereas a female baboon has little control over demographic attributes like her dominance rank or the presence of kin, she may have some ability to adjust her own behaviour; in other words, to shape her personality style. Here, we provide a more comprehensive analysis of how personality traits, dominance rank and the availability of close kin interact to affect the formation of strong, enduring and adaptive social bonds.

METHODS

Field Observations

Data were derived from a long-term study of wild chacma baboons (*P. h. ursinus*) in the Moremi Game Reserve, Botswana (Cheney & Seyfarth, 2007). The group had been observed since 1978. Maternal kinship was known for all individuals born in the group. For the purpose of this analysis, kin are defined as mothers, adult daughters and maternal sisters. Data on paternity were available for only a small number of adult females, limiting our ability to identify paternal half siblings. The primary causes of mortality were infanticide and predation (Cheney et al., 2004).

Adult female dominance ranks were calculated monthly based on the direction of approach–retreat interactions. Female ranks were calculated as the proportion of females dominated and could range from 0 to 1. For most of the study, the female dominance hierarchy remained stable.

Analyses were based on a total of 45 adult females (≥5 years of age) observed during the 7-year study period (2001–2007). Eleven females were present for the full 7-year period, seven females for 5 years, nine females for 4 years, six females for 3 years, 11 females for 2 years, and one female for 1 year ($N = 189$ female years). Individual females entered the data set when they reached 5 years of age and left the data set when they died, so each individual confronted a different array of potential partners every year. We therefore used each female-year as a separate data point (Seyfarth et al., 2012).

Ten-minute focal animal observations (Altmann, 1974) were conducted almost daily using a common protocol (Cheney & Seyfarth, 2007). All approaches, vocalizations and friendly and aggressive interactions were recorded on a continuous basis. We also noted all grooming interactions and their durations (Silk et al., 2010a).

For consistency with previous analyses (Seyfarth et al., 2012; Silk et al., 2012), we used females' average CSI with their top three partners when calculating bond strength.

Statistical Analysis

Statistical analyses were conducted using R statistical software (v.2.15; R Development Core Team, 2009). To test for a relation between ranks of scores on principal components (personality dimensions), dominance rank and the presence of kin, we used linear mixed models or generalized linear mixed models (lmer in R), entering female ID and year as random factors. To compare models, we used the anova function in R (Crawley, 2005). Only the results of statistically significant tests ($P < 0.05$) are presented.

To test the stability of individuals' scores on all three personality dimensions simultaneously, we treated each female in each year as occupying a point in three-dimensional 'personality space', as illustrated in Seyfarth et al. (2012). To measure the extent to which an individual was consistent in her personality scores over time, we calculated the Euclidean distance between all possible pairs of points. If two points, p and q, in three-dimensional space have the Cartesian coordinates $p = x_1, y_1, z_1$ and $q = x_2, y_2, z_2$, then the Euclidean distance between them, d_{pq}, is calculated as

$$d_{pq} = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2}$$

RESULTS

Stability in Personality Dimensions

To test whether the same female observed over multiple years was more alike in her personality style than different females observed in the same year, we compared the Euclidean distances (see Methods) for the same female observed in all possible 2-year combinations ($N = 385$ 'self-dyads') with the Euclidean distances for all close kin dyads (mother–daughter and sister–sister) observed in the same year ($N = 133$) and all other dyads observed in the same year ($N = 2315$).

The 2833 Euclidean distances generated were normally distributed, with a mean and standard deviation of 123.82 ± 48.15. To test whether differences in the identity and relatedness of individuals were correlated with differences in Euclidean distance, we used a likelihood ratio test to compare a full model using self and kin and other designations as predictors against a null model that included only the random effects (Crawley, 2005, p. 109). A linear mixed model with Euclidean distance as the dependent measure, the three designations as predictors and the identity (or identities) of the individual(s) in the dyad as random factors ($\beta \pm SE = 7.932 \pm 1.290$, $t = 6.15$, $P = 0.0001$) fit the data better than a null model that included only the random factors (anova model comparison in R: $\chi^2_1 = 37.33$, $P = 0.0005$).

Based on this result, we examined the pairwise differences between the dyad classes, again using a linear mixed model with individual ID(s) as random factors (Fig. 1). Euclidean distances for self-dyads were significantly smaller (that is, personalities were more alike) when compared with close kin ($\beta \pm SE = 16.088 \pm 4.608$, $t = 3.491$, $P = 0.004$) and with others ($\beta \pm SE = 8.245 \pm 1.324$, $t = 6.229$, $P = 0.0001$). These results suggest that individuals were generally consistent in their personality dimensions over time.

We found no evidence that individuals' personalities became more or less stable as they grew older. However, the presence of kin did affect the stability of an individual's personality: individuals with one or two female kin present in the group had smaller changes in Euclidean distances from one year to the next than did individuals with no kin present in one or both of those years ($\beta \pm SE = 6.474 \pm 3.887$, $t = -1.67$, $P = 0.038$). The presence of kin was associated with more stable personalities because it decreased the magnitude of year-to-year changes on the Nice personality dimension ($\beta \pm SE = 9.79 \pm 3.19$, $t = -3.07$, $P = 0.0008$). In contrast, the presence of kin had no effect on the stability of scores on the other dimensions of personality.

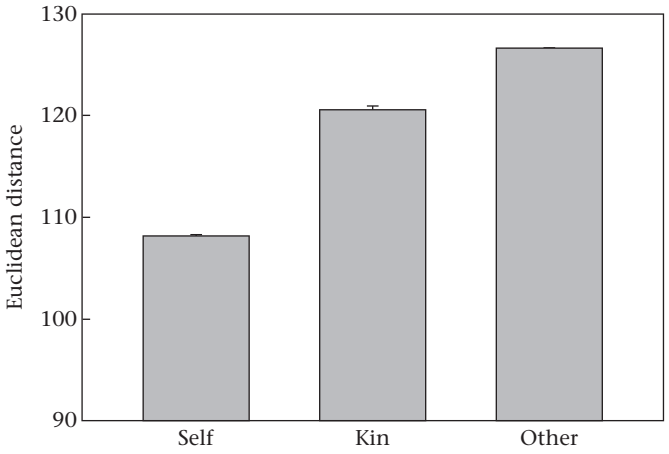

Figure 1. Mean (+SE) Euclidean distances for 385 female baboon (*Papio hamadryas ursinus*) self-dyads (defined as the same individual tested in different years, using all individuals observed for 2 years or more), 133 close kin dyads (defined as mother–daughter or sister–sister dyads observed in the same year) and 2315 nonkin dyads (defined as all other female dyads observed in the same year). Euclidean distance is defined in the text.

Individuals whose personalities were more stable from year to year did not have significantly higher scores on either the CSI or the PSI. When kin were present, individuals were not necessarily nicer, but their scores on the Nice dimension were more stable, making their personalities overall more stable.

Personality Similarity among Kin versus Nonkin

To test whether kin dyads were more alike than nonkin dyads, we compared the Euclidean distances for mother–daughter and sister–sister dyads with those for other dyads. There was no significant difference in the Euclidean distances for kin and nonkin (Fig. 1). Within the kin class, the difference between mother–daughter and sister–sister dyads was not statistically significant.

Effects of Age and Rank Differences on Personality Similarity

Maternal kin occupy adjacent ranks, so kinship and rank distance are confounded. Thus, to test whether rank differences were linked to personality similarity, we limited the analysis to nonkin dyads in which both individuals were observed in the same year ($N = 2315$). Among nonkin dyads, the mean $\pm$ SD difference in partners' dominance ranks was 0.371 ± 0.236, and Euclidean distance was significantly smaller when the partners were closer in dominance rank ($\beta \pm SE = 14.35 \pm 4.21$, $t = 3.40$, $P = 0.001$).

We examined the effects of age differences on related and unrelated dyads. Among nonkin dyads ($N = 2315$), the mean $\pm$ SD difference in partners' ages was 4.94 ± 3.90 years; among kin dyads ($N = 133$), the mean difference was 6.19 ± 3.11. In both cases, Euclidean distance was unrelated to the partners' difference in age.

Effect of Personality Similarity on the Formation of Close Social Bonds

As in earlier analyses (Silk et al., 2006a, 2006b, 2010a), dyads were defined as 'strongly bonded' if one of the individuals involved

had the other as one of her top three partners, as measured by CSI. To explore whether similarity in personality influenced the formation of strong social bonds we examined the 2448 dyads in which both individuals were observed in the same year.

The single most important predictor of strong bond formation was the individuals' kin relationship: 48 of 133 close kin dyads (36.1%) were strongly bonded, compared with 215 of 2315 nonkin dyads (9.3%). For close kin dyads, the mean ± SD *z* score of their CSI was 2.147 ± 2.955, and for nonkin dyads, it was −0.123 ± 0.526. Given this result, and the imbalance in sample size between close kin and nonkin dyads, we conducted further analyses on these two groups separately.

We conducted two analyses to test the effects of personality similarity on the formation of social bonds. First, we used a linear mixed model in which each dyad's *z*-transformed CSI score was the dependent measure. Predictors were the partners' Euclidean distance, the difference in their dominance ranks, the difference in their ages and the sums and differences of their scores on the Aloof, Loner and Nice dimensions. The identities of the two individuals were entered as random factors. In this analysis we considered only the dyad's CSI score and ignored whether or not the individuals were strongly bonded as defined above. Second, we used a model in which dyad quality (strongly bonded or not, a binary variable) was the dependent measure. Predictors and random factors were the same. Because the dependent measure in this analysis was binary, we used a generalized linear mixed model with a binomial error structure.

Among all kin dyads (Table 1), the best predictor of a dyad's CSI score was the sum of the individuals' scores on the Loner dimension: individuals with lower scores on the Loner dimension had higher CSIs ($P = 0.028$). The best predictors of a dyad's status (strongly bonded or not) were several measures of personality similarity. A strong bond was significantly more likely when the sum of the individuals' Loner scores was low ($P = 0.049$) and when the individuals were more alike in personality: that is, when their Euclidean distance was smaller ($P = 0.028$). This relationship was found in all three personality dimensions: strongly bonded dyads were more alike than other kin dyads on the Aloof ($P = 0.034$), Loner ($P = 0.043$) and Nice dimensions ($P = 0.008$).

Table 1
Results of a generalized linear mixed model testing which variables best predicted scores on the composite sociality index (CSI) in closely related female baboons (mother–daughter and sister–sister dyads, $N = 133$) and which kin dyads were closely bonded (see text for definition)

Dependent measure	Predictor	β±SE	Statistics
CSI score	Euclidean distance	0.008±0.008	t=1.001, P=0.278
	Difference in rank	−2.255±1.097	t=−2.056, P=0.055
	Difference in age	0.039±0.028	t=−1.399, P=0.593
	Sum Aloof scores	−0.001±0.001	t=−0.636, P=0.710
	Sum Loner scores	−0.001±0.001	t=−0.448, P=0.028*
	Sum Nice scores	0.002±0.001	t=−1.981, P=0.278
	Difference in Aloof score	−0.005±0.005	t=−0.997, P=0.281
	Difference in Loner score	−0.005±0.005	t=−1.012, P=0.201
	Difference in Nice score	−0.004±0.005	t=−0.858, P=0.332
Closely bonded?	Euclidean distance	0.048±0.021	z=−2.202, P=0.028*
	Difference in rank	−5.419±3.192	z=−1.697, P=0.090
	Difference in age	0.034±0.072	z=−0.482, P=0.630
	Sum Aloof scores	0.001±0.003	z=0.641, P=0.521
	Sum Loner scores	−0.006±0.003	z=−1.971, P=0.049*
	Sum Nice scores	0.001±0.003	z=0.339, P=0.735
	Difference in Aloof score	−0.031±0.014	z=−2.121, P=0.034*
	Difference in Loner score	−0.026±0.013	z=−2.018, P=0.044*
	Difference in Nice score	−0.039±0.015	z=−2.632, P=0.008**

The identities of the individuals involved were entered as random factors.
*$P < 0.05$; **$P < 0.01$.

Mother–daughter and sister–sister dyads differed in the factors associated with strong bond formation (Table 2). Among mothers and daughters, no personality measures predicted CSI scores or dyad status (closely bonded or not). By contrast, sisters had significantly higher CSI scores if they were similar in age ($P = 0.004$) and were significantly more likely to be strongly bonded if they had a lower summed Loner score ($P = 0.009$) and were more alike on all measures of personality (Aloof: $P = 0.044$; Loner: $P = 0.044$; Nice: $P = 0.022$; Euclidean distance: $P = 0.042$). In other words, mother–daughter dyads were very likely to have high CSI scores and be strongly bonded regardless of their ages or personality dimensions, whereas sisters were more likely to have high CSI scores and be strongly bonded when they were similar in age and personality.

Among nonkin dyads (Table 3), similarity in personality had little effect on the strength of social bonds. Instead, the best predictors of a dyad's CSI score were the differences in their ages (individuals closer in age had higher CSIs: $P = 0.004$), the differences in their dominance ranks (individuals of similar rank had higher CSIs: $P = 0.001$) and the sum of their Aloof scores (dyads with a lower summed score had higher CSIs: $P = 0.018$). The best predictor of whether a dyad was strongly bonded or not was the difference in the individuals' dominance ranks. Closely ranked individuals were more likely than others to be strongly bonded ($P = 0.048$).

To quantify the relative importance of these variables across different dyad classes, we calculated the effect size (Cohen's *d*;

Table 2
Results of generalized linear mixed models testing baboon mother–daughter ($N = 51$) and sister–sister ($N = 82$) dyads separately

Dyad	Predictor	β±SE	Statistics
Mother–Daughter			
CSI score	Euclidean distance	0.005±0.005	t=0.417, P=0.685
	Difference in rank	−2.079±6.134	t=−0.339, P=0.733
	Difference in age	−0.013±0.075	t=−0.174, P=0.864
	Sum Aloof scores	−0.001±0.002	t=−0.298, P=0.765
	Sum Loner scores	−0.002±0.002	t=−1.178, P=0.250
	Sum Nice scores	0.005±0.002	t=1.966, P=0.059
	Difference in Aloof score	−0.004±0.009	t=−0.477, P=0.636
	Difference in Loner score	−0.004±0.008	t=−0.494, P=0.614
	Difference in Nice score	0.002±0.009	t=0.189, P=0.855
Closely bonded?	Euclidean distance	0.032±0.030	z=1.066, P=0.286
	Difference in rank	13.147±13.595	z=0.967, P=0.334
	Difference in age	0.030±0.168	z=0.178, P=0.858
	Sum Aloof scores	0.003±0.005	z=0.566, P=0.572
	Sum Loner scores	0.002±0.005	z=0.368, P=0.713
	Sum Nice scores	−0.004±0.005	z=−0.717, P=0.474
	Difference in Aloof score	−0.025±0.022	z=−1.157, P=0.247
	Difference in Loner score	−0.014±0.019	z=−0.760, P=0.447
	Difference in Nice score	−0.029±0.021	z=−1.377, P=0.169
Sister–Sister			
CSI score	Euclidean distance	1.085±13.516	t=0.247, P=0.442
	Difference in rank	−14.75±20.921	t=−0.628, P=0.356
	Difference in age	−23.55±4.622	t=−3.255, P=0.004**
	Sum Aloof scores	11.427±17.882	t=0.075, P=0.492
	Sum Loner scores	15.767±0.222	t=0.711, P=0.960
	Sum Nice scores	17.510±22.142	t=0.823, P=0.726
	Difference in Aloof score	−22.27±7.082	t=−0.181, P=0.462
	Difference in Loner score	−6.708±7.768	t=−0.344, P=0.160
	Difference in Nice score	−30.64±6.658	t=−0.276, P=0.359
Closely bonded?	Euclidean distance	0.071±0.035	z=2.034, P=0.042*
	Difference in rank	−5.481±3.841	z=−1.427, P=0.154
	Difference in age	−0.162±0.125	z=−1.300, P=0.194
	Sum Aloof scores	0.003±0.004	z=0.623, P=0.533
	Sum Loner scores	−0.012±0.005	z=−2.623, P=0.009**
	Sum Nice scores	0.001±0.005	z=0.276, P=0.783
	Difference in Aloof score	−0.044±0.022	z=−2.014, P=0.044*
	Difference in Loner score	−0.043±0.022	z=−2.017, P=0.044*
	Difference in Nice score	−0.057±0.025	z=−2.285, P=0.022*

CSI: composite sociality index. The identities of the individuals involved were entered as random factors.
*$P < 0.05$; **$P < 0.01$.

Table 3
Results of a generalized linear mixed model testing only nonkin female baboon dyads ($N = 2315$)

Dependent measure	Predictor	β±SE	Statistics
CSI score	Euclidean distance	−0.001±0.001	t=0.076, P=0.944
	Difference in rank	−0.665±0.089	t=−7.464, P=0.001**
	Difference in age	−0.019±0.005	t=−3.656, P=0.0004**
	Sum Aloof scores	−0.001±0.001	t=−0.636, P=0.018*
	Sum Loner scores	−0.001±0.001	t=−0.741, P=0.453
	Sum Nice scores	0.001±0.001	t=0.323, P=0.702
	Difference in Aloof score	−0.001±0.001	t=−0.055, P=0.871
	Difference in Loner score	−0.001±0.001	t=0.011, P=0.920
	Difference in Nice score	−0.001±0.001	t=−0.042, P=0.900
Closely bonded?	Euclidean distance	0.006±0.007	z=0.892, P=0.373
	Difference in rank	−1.396±0.351	z=−3.972, P=0.048*
	Difference in age	−0.027±0.021	z=−1.290, P=0.197
	Sum Aloof scores	−0.001±0.001	z=−1.363, P=0.173
	Sum Loner scores	−0.001±0.001	z=−1.423, P=0.155
	Sum Nice scores	−0.001±0.001	z=−0.722, P=0.470
	Difference in Aloof score	−0.004±0.004	z=−1.030, P=0.303
	Difference in Loner score	−0.002±0.004	z=−0.522, P=0.602
	Difference in Nice score	−0.004±0.004	z=−1.009, P=0.313

CSI: composite sociality index. The identities of the individuals involved were entered as random factors.
*$P < 0.05$; **$P < 0.01$.

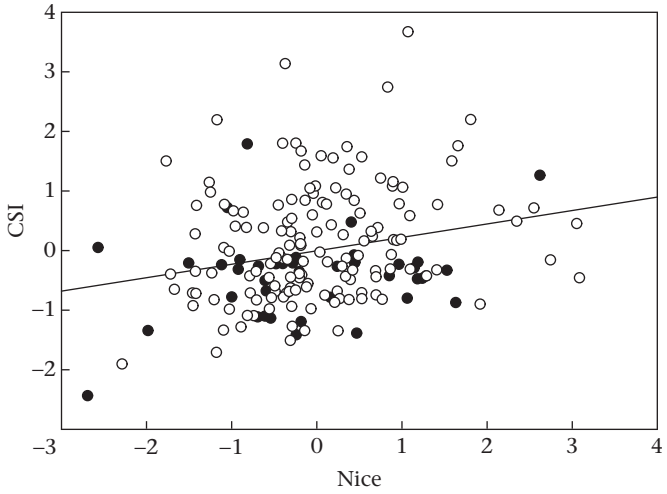

Figure 2. Distribution of z scores on the 'Nice' personality dimension and the composite sociality index (CSI) for female baboons who did (open circles) or did not (closed circles) have kin (a mother, daughter or sister) present in the group at the time. The line represents the least-squares regression line for all points. When no kin were present, individuals had lower CSI scores than would have been predicted from their score on the Nice dimension.

Cohen, 1988) for all significant predictors of strong bond formation. Among all dyads, kinship status ($d = 0.865$) had a large effect size. Among mother–daughter dyads, measures of age, personality and dominance rank had no effect on strong bond formation. Among sister–sister dyads, the individuals' summed Loner scores ($d = 0.539$) and the difference in their Nice scores ($d = 0.256$) had moderate effects, while the difference in their Euclidean distance ($d = 0.181$) and the difference in their Loner ($d = 0.115$) and Aloof ($d = 0.079$) scores had smaller effects. Among nonkin dyads, the individuals' difference in dominance rank ($d = 0.257$) had a moderate effect.

Indirect Effects of the Presence of Kin

Previous work suggested that the presence of kin influences individuals' personality scores and may thus influence bond formation. Individuals' scores on the Loner dimension were significantly lower (that is, less extreme) when they had kin present in the group than when they did not (Seyfarth et al., 2012). To explore this relationship further, we tested whether the presence of kin had a mitigating effect not only on an individual's Loner score but also on the strength of the bonds she formed with others. When close kin were present, the correlation between Loner score and CSI was nonsignificant; when kin were absent, the correlation was significantly negative ($\beta \pm SE = -0.169 \pm 0.056$, $t = -2.998$, $P = 0.002$). As a result, the loss of a close relative, particularly if it was the subject's only close kin, may have not only increased glucocorticoid levels (Engh et al., 2006) but also produced more enduring changes in the subject's personality and social relationships.

Our previous analysis also showed that individuals' scores on the Nice dimension were significantly positively correlated with their CSI scores (Seyfarth et al., 2012). To explore this relationship in more detail, we examined the residuals around this regression line and found that, when kin were absent, females had lower CSIs than expected for a given score on Nice, whereas when kin were present, females had higher CSIs for a given score on Nice (Fig. 2). The difference was significant (Student's t test: $t_{99} = -2.239$, $P = 0.027$). Thus, the presence of kin appeared to augment the positive effect that an individual's Nice score had on her CSI, suggesting that an individual who lost one of her close kin would have to increase her Nice score (that is, engage in more friendly behaviour, less aggression and more grunting) in order to maintain the same CSI.

To test this hypothesis, we examined the relation between the change in a female's Nice score and the change in her CSI score from the year before to the year after the death of a close adult relative. For mothers who lost a daughter and for daughters who lost a mother, there was a significantly negative correlation between the changes in these two measures, as females who experienced the greatest decrease in their CSI score showed the greatest increase in their Nice score (Spearman rank correlation: $r_S = -0.678$, $N = 12$, $P < 0.02$). For females who lost a sister, the correlation was also negative, but not significantly so.

Third, previous analysis revealed that individuals' scores on Aloof were significantly positively correlated with their PSI scores (Seyfarth et al., 2012). To examine this relationship in more detail, we examined the data separately for individuals who did or did not have kin present in the group. When kin were present, this relationship remained significant ($\beta \pm SE = -0.246 \pm 0.070$, $t = 3.50$, $P = 0.0004$). However, when kin were absent, it disappeared. Thus, the presence of kin strengthened the effect of the Aloof element on the stability of social bonds.

DISCUSSION

Personality traits of adult female baboons remained relatively stable over time: Euclidean distances between personality scores from one year to the next were significantly smaller within females than between females. Although personality traits were generally stable, however, they were not fixed. Females adjusted the behaviours that contributed to their personality scores in response to demographic events, like the death of a close relative.

Supporting previous results and using a new method to measure personality similarity, we found no evidence that females' personalities were more alike within than between matrilineal families. Differences in personality among matrilineal kin could not be related to differences in females' dominance ranks because kin held very similar ranks. By contrast, among unrelated females, similarity in personality was significantly more likely when the individuals held similar dominance ranks. This difference between kin and

nonkin is intriguing because it suggests that the similarities in dominance rank within matrilineal families did not cause individuals to adopt similar personalities, but across matrilines, individuals whose ranks were more alike somehow developed similar personality types.

Three interacting factors were correlated with the formation of strong, enduring social bonds: matrilineal kinship, dominance rank and personality. Matrilineal kinship was the single most important factor: mother–daughter and sister–sister dyads were roughly four times more likely to be strongly bonded than were dyads composed of less closely related individuals. Within the kin class, however, there were striking differences between mother–daughter and sister dyads. Mothers and daughters formed the strongest bonds and did so regardless of rank, age or personality. Sisters formed the next-strongest bonds, but these bonds were significantly stronger when sisters were alike in age and personality. This generalization applied to each personality dimension separately and to personality overall: sisters were more likely to be closely bonded when they had similar scores on the Aloof, Loner and Nice dimensions and when they were separated by smaller Euclidean distances, a measure of personality similarity that combined all three dimensions.

By contrast, the formation of close bonds among nonkin was largely unrelated to personality and depended almost entirely on the individuals' ages and dominance ranks: individuals of similar age and rank were more likely than others to form a strong bond. These results resemble those found in white-faced capuchin monkeys, *Cebus capucinus*. Perry, Manson, Muniz, Gros-Louis, and Vigilant (2008) found that adult females were strongly attracted to those of similar rank when group size was small and matrilineal kin were few in number, but they increasingly restricted their interactions to kin as group size increased and matrilineal kin became more numerous.

We cannot yet determine why matrilineal sisters who were similar in age and personality were more closely bonded than other sisters. Because they were similar in age, they may have been full siblings (Altmann, 1979), which may have influenced their behavioural traits. Our limited data on paternity, however, did not allow us to test this hypothesis. Arguing against the view that personality similarity was a function of genetic relatedness, we found that maternal kin were no more alike in personality than were nonkin. Siblings closer in age may have been attracted to one another because they were at similar stages of development, and bonds formed early in life may have persisted into adulthood. Closely bonded sisters may have been more alike in personality because individuals actively sought out and interacted with sisters who were most like them, or because once two individuals began to interact regularly their personalities became more alike. Frequent interaction, however, does not necessarily cause a convergence in personality: the high rates of interaction between mothers and daughters were uncorrelated with similarity in personality, and personality similarity was not a correlate of strong bond formation among nonkin. Indeed, one could just as easily argue that an individual might benefit from bonds formed with others who have different personalities from her own. The causes, development and evolution of close bond formation remain open, unresolved issues.

The qualitative difference in bond formation between mother–daughter and sister–sister dyads highlights, once again, the unique nature of the mother–offspring bond and its persistence into adulthood. The importance of similarity in age replicates analysis in Silk et al. (2006a) on Amboseli baboons and Silk et al. (2010a) on baboons in the present study. In both cases, the authors suggested that individuals of a similar age might often be paternal half sisters. The importance of similarity in dominance rank also replicates prior research (Silk et al., 2006b, 2010a). Evidence that rank, and not personality, is a primary determinant of strong bond formation among nonkin is consistent with models proposing that individuals often compete for the opportunity to interact with high-ranking individuals, and that middle- and low-ranking animals may compromise by interacting with others of similar rank regardless of any other factors (e.g. Schino & Aureli, 2009; Seyfarth, 1977).

To summarize, our results suggest that, when 'like bonds with like', the result is a higher CSI, and this in turn is linked to fitness benefits. For sisters, whose dominance rank differences were small, 'like' meant 'being of similar age and personality', for nonkin, whose rank differences were much greater, 'like' meant 'being of similar age and dominance rank'.

Finally, the presence of kin had three important indirect effects on the link between personality and measures related to fitness. First, the presence of kin mitigated the deleterious effect that a high score on the Loner dimension had on a female's CSI. Ordinarily, females with high Loner scores were less likely than others to form close bonds, had lower CSI scores, and hence had lower fitness. When kin were present, however, this relationship disappeared and the impact of being a Loner decreased.

Second, the presence of kin enhanced the beneficial effect that a high score on Nice had on the CSI. When kin were present, females with high Nice scores had even higher CSIs than they would have had in the absence of kin. Since a female's overall CSI depended on her interactions with both kin and nonkin (Silk et al., 2010a), the data suggest that the presence of kin was correlated with a general increase in sociability towards others regardless of whether they were close relatives. When a close relative died, a female's Nice score tended to increase, raising the possibility that she was attempting to compensate for the loss of a close partner by establishing new bonds with others (Engh et al., 2006). In a previous analysis, females who scored high on Nice tended to increase their number of grooming partners in the 3 months following the death of a close relative, whereas females who scored high on Loner decreased their number of partners (Seyfarth & Cheney, 2013).

Third, the presence of kin enhanced the beneficial effect that a high score on Aloof had on the PSI. When kin were present, females with high Aloof scores had even higher PSI scores than they would have had in the absence of kin. Because a female's PSI was affected by her interactions with both kin and nonkin (Silk et al., 2012), results suggest that the presence of kin was correlated with a general increase in the consistency and stability of a female's close partners, regardless of whether or not they were close relatives, again suggesting an attribute of personality.

At this point in our analysis, we can draw three conclusions about female baboon personalities that may be relevant to studies of animal personality in general. First, personality traits do not exist in isolation. They are, instead, embedded in a social network where an individual's behaviour is affected by the interaction between her own personality, her dominance rank, the presence or absence of close kin and the personalities of other females with whom she interacts (among other variables; see also Brent et al., 2013). Second, although the personalities of female baboons are generally uncorrelated with dominance rank and kinship (Seyfarth et al., 2012), they are affected by rank and kinship in various ways. Third, although a female baboon has little control over her dominance rank or the presence or absence of kin, she does have some control over her personality. For example, when a female loses a close companion to predation, she cannot change her rank, nor can she change the family to which she belongs, but she can change the quality of the social interactions that contribute to her personality traits and influence the likelihood of forming strong social bonds.

Taken together, these results suggest that, by varying her personality, a female can take advantage of the opportunities, or overcome the constraints, imposed by her family membership, dominance rank and unpredictable demographic events. A female

with kin can afford to be alone more often and be less friendly to others without lowering her CSI; conversely, a female without kin, or a female who loses a close relative to predation, must spend less time alone and engage in more friendly behaviour if she is to maintain the same CSI. A female with kin can form her strongest bonds with the family members whose personalities are most like hers; a female without kin, particularly a low-ranking female, must form her strongest bonds with those whose dominance ranks and ages are most like hers, regardless of their personalities. If reproductive success is correlated with CSI (Silk et al., 2009), then female fitness may be affected by the interaction between personality (Nice is better, Loner is worse) and demographic circumstances (the presence of close kin).

If this explanation is correct, it may clarify why personality dimensions were correlated with the CSI in previous studies (Seyfarth et al., 2012) but rank and kinship were not (Silk et al., 2003, 2009, 2010a). Because rank and kinship are fixed whereas personality is not, personality provides a degree of freedom by which a female can adjust her behaviour in an attempt to increase her CSI. If she is successful, and selection should favour females who are motivated to do so, the behaviours that contribute to her personality will change in ways that augment her CSI, and CSI and personality will become positively correlated. By contrast, rank and kinship will not change, so these variables will continue to have an inconsistent, unpredictable relation to the CSI. Female baboons have different personalities because, in their attempt to maximize fitness, they confront different constraints and opportunities.

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