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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).