Variation in personality and fitness in wild female baboons

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Studies of personality in nonhuman primates have usually relied on assessments by humans and seldom considered the function of the resulting "trait" classifications. In contrast, we applied exploratory principal component analysis to seven behaviors among 45 wild female baboons over 7 y to determine whether the personality dimensions that emerged were associated with measures of reproductive success. We identified three relatively stable personality dimensions, each characterized by a distinct suite of behaviors that were not redundant with dominance rank or the availability of kin. Females scoring high on the "Nice" dimension were friendly to all females and often grunted to lower-ranking females to signal benign intent. "Aloof" females were aggressive, less friendly, and grunted primarily to higher-ranking females. "Loner" females were often alone, relatively unfriendly, and also grunted most often to higher-ranking females. Aloof and Loner females were rarely approached by others. Personality dimensions were correlated in different ways with three measures previously shown to be associated with fitness: stress levels and two behavioral indices reflecting the closeness of dyadic bonds formed by individuals. Females who scored high on Nice had high composite sociality indices (CSI) and stable partner preferences, whereas females who scored high on Aloof had lower CSI scores but significantly more stable partner preferences. Loner females had significantly lower CSI scores, less stable partner preferences, and significantly higher glucocorticoid levels. It remains to be determined which of the Nice or Aloof personality dimensions is more adaptive, or whether variation is maintained by contrasting effects on fitness.

It is now clear that individuals in many animal species vary in their degree of sociality, and that this variation is associated with fitness (e.g., refs. 1–5). Among baboons, females who establish close, enduring grooming relationships with others have greater longevity and offspring survival (6–8). Females also experience lower stress levels when their grooming networks are focused rather than diffuse (9). Interestingly, however, variation in the strength of social bonds is not well explained by obvious demographic attributes, like dominance rank or the availability of kin. Although females establish their closest bonds with kin, kin vary in the strength of their bonds, and some females without kin establish close bonds with others. It therefore seems likely that some individuals are more motivated or skilled than others at establishing and maintaining social bonds. In other words, variation in patterns of affiliation that are correlated with fitness may result in large part from variation in personality styles.

There is mounting evidence that personality traits in animals are biologically meaningful. Personality traits influence behaviors as diverse as dispersal, mate choice, nest defense, and helping behavior in insects, fish, birds, and mammals (e.g., refs. 10–16). However, little attention has been paid to variation in personality attributes that may be linked to the formation and maintenance of adaptive social bonds, particularly among nonhuman primates. Indeed, most studies of personality in nonhuman primates have relied wholly or in part on assessments by human observers and seldom considered the function of the resulting "trait" classifications (e.g., refs. 17–21). In contrast, we began with the behavior of the animals themselves and considered whether any functionally interesting personality dimensions emerged from these data.

We applied exploratory principal component analysis (PCA) to the behavior of wild female baboons over 7 y. To construct the components that were used to identify personality dimensions, we calculated annual rates for a number of behaviors not considered in previous analyses of sociality (22). These included: the frequency that females were alone; the rate at which they touched or embraced other females ("friendly"); the rate at which they were aggressive to other females (corrected for dominance rank); and the frequency with which they grunted when approaching higher- and lower-ranking females with or without infants. Among baboons, grunts serve as signals of benign intent and facilitate friendly interactions (23, 24). Although females are most likely to grunt when approaching mothers with young infants, they also grunt to females without infants. When females grunt to higher-ranking individuals, they are less likely to receive aggression. Conversely, when females grunt to lower-ranking individuals, those individuals are less likely to move away or show submissive behavior. We were especially interested in the frequency with which females grunted to lower-ranking individuals without infants because such vocalizations do not benefit the signaler in any obvious way. Instead, they appear to function primarily to alleviate the anxiety of the recipient.

We validated our approach in several ways. First, we examined whether females' behavior was consistent over time. Second, to determine whether PCA added anything new to our understanding of behavior, we examined the relation between a female's scores on each principal component and her age, matrilineal dominance rank, and the availability of kin. This issue of redundancy is important: if females' personalities were simply correlated with their rank and kinship, it would suggest that baboons' personalities are largely determined by demographic factors over which they have little control. In contrast, if personality differences were to some degree independent of these attributes, they might help to understand the evolution of individual differences in a society that is otherwise structured around kinship and rank.

Third, we examined the relation between individuals' scores on personality dimensions and their scores on three other measures previously shown to be associated with fitness (6–9): their stress levels and two behavioral indices of the strength of dyadic bonds, the Composite Sociality Index (CSI) and the Partner Stability Index (PSI). The CSI is based on rates of approaches, grooming initiations, and grooming durations within dyads, and reflects overall levels of sociality (22). The PSI measures a female's retention of her top three partners from one year to the next, and reflects the stability of partners over time (25).

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Finally, by examining the rate at which females were approached by others, we tested whether personality dimensions were also recognized by the baboons themselves.

Results

Consistency Across Years. Females were generally consistent in their behavior across years (Table S1). For example, females who ranked high on rates of friendly behavior in one year typically ranked high on rates of this behavior across most of the years they were studied, yielding a significant coefficient of concordance. We conducted 16 tests using seven behavioral measures taken from females sampled for 4–7 y. All but two tests yielded a statistically significant positive correlation; two others revealed a positive trend.

Exploratory PCA. To search for correlations among behaviors, we performed exploratory PCA on the entire dataset, using an orthogonal, varimax rotation and taking each female year as an independent value. Starting with two components, we increased the number of components until the change in the fit of the model to the original correlation matrix (the change in the value of "fit" returned by the "principal" function in R) began to decrease. Based on these results, we selected a model with three principal components. Each component was uncorrelated with the others (correlation coefficients ranged from −0.016 to 0.021). This model accounted for 51% of the overall variance in the correlation matrix (n = 189, df = 3, χ^2 = 166.4, $P < 0.001$). We then examined the loadings of each behavior onto each component (Table 1). Loadings are correlations between behavioral variables and principal components; loadings >0.32 and loadings that differentiated the three components were of particular interest (26).

Individuals who scored high on component 1 (for ease of discussion, "Aloof") were more aggressive than others. These individuals grunted at high rates when they approached higher-ranking females who had infants but rarely grunted to others, particularly if they were lower-ranking and did not have infants.

Individuals who scored high on component 2 ("Loner") were often alone and grunted most frequently when approaching higher-ranking females without infants.

Individuals who scored high on component 3 ("Nice") were much more friendly than others and grunted when approaching all females, regardless of their ranks and whether or not they had infants. These individuals were seldom alone.

Stability of Personality Dimensions. Human personality research suggests that behavior is the result of an interaction between the person and the situation (27). Although an individual's behavior may be relatively consistent over time, psychologists also find variability across different social contexts and time periods (28). Consistency (or its absence) may be a personality trait in its own right.

Table 1. Loadings of behaviors onto three principal components

Behavior	Component 1: Aloof	Component 2: Loner	Component 3: Nice
Alone	0.14	**0.67**	**−0.32**
Aggression	**0.64**	0.04	−0.06
Friendly	0.03	−0.17	**0.76**
Grunting			
HR no inf	−0.03	**0.71**	0.19
HR inf	**0.71**	0.17	0.30
LR no inf	**−0.55**	**0.34**	**0.37**
LR inf	−0.00	0.10	**0.51**

Loadings > 0.32 are in boldface (26). HR inf, higher-ranking with infant; HR no inf, higher-ranking with no infant; LR inf, lower-ranking with infant; LR no inf, lower-ranking with no infant.

Baboons' scores on personality dimensions, like their behavior (Table S1), were generally stable over time. As before, we used component scores to determine ranks and the Kendall coefficient of concordance to measure consistency in the rank order of individuals across years (Table S2). Rankings were significantly correlated from one year to the next.

Over the duration of the study there were 144 cases in which a female was observed during consecutive years. For Aloof and Nice, the correlation between a female's score in year t and her score in year t+1 was significantly positive (Aloof: β = 0.223, SE = 0.091, t = 2.446, P = 0.027; Nice: β = 0.243, SE = 0.081, t = 3.010, P = 0.002). For Loner it was not (β = −0.001, SE = 0.079, t = −0.015, $P > 0.10$).

To determine whether personality styles clustered in any meaningful way, we ranked each female in each year according to her scores on each of the three dimensions, then searched for clusters using the "partitioning around medoids" function, a form of k-means cluster analysis (29). The average silhouette width (30) revealed that data were best described by k = 3 clusters, so each female-year was assigned to one of three clusters based on its distance to the nearest medoid. Cluster 1 (n = 51 female years) was characterized by the highest values on Nice and the lowest values on Loner. Cluster 2 (n = 56) was characterized by the lowest values on Nice, and cluster 3 (n = 83) was characterized by the highest values on both Loner and Aloof. Although many individuals could be assigned with some confidence to a particular cluster, there was also considerable overlap: no cluster was isolated and clusters graded into one another (Fig. 1).

Although roughly half of all personality styles changed from one year to the next, most females' cluster assignments, like their component scores, were consistent across time. Of the 33 females observed for 3 y or more, 27 (82%) remained in the same cluster in over 50% of the years they were observed. The general consistency of personality styles may be comparable to the "profile stability" found in human personality studies (28, 31).

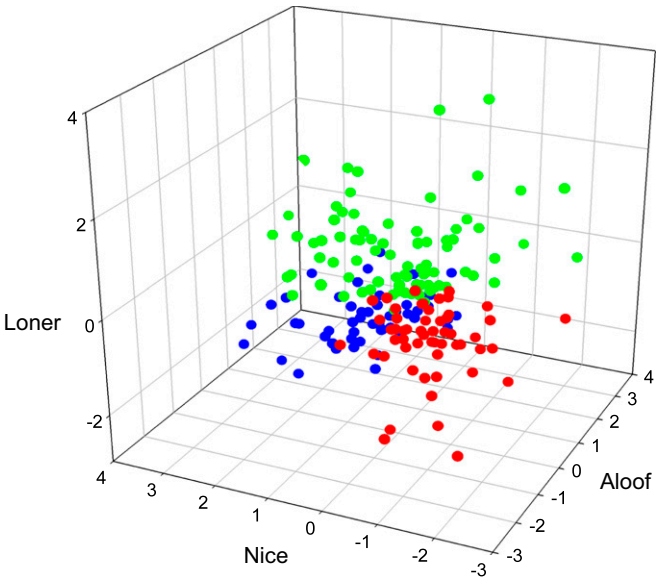

Fig. 1. The distribution of scores on three principal components or personality dimensions. Each point represents scores on Aloof, Loner, and Nice components (n = 45 females observed for 1–7 y, for a total of 189 female-years). Colors depict the assignment of a female to a particular personality cluster in that year. The choice of three clusters and cluster assignments were made using the partitioning around medoids program.

Explanatory Value of the Components. ***Potential covariates. Dominance rank.*** To test whether individuals' personality dimensions simply reflected their dominance rank, we used a linear mixed model with dominance rank as the sole predictor and component score as the dependent measure. Scores on Aloof and Nice were unrelated to dominance rank (Table 2). However, low-ranking females had significantly higher Loner scores than did high-ranking females ($n = 189$, $\beta = -0.769$, SE = 0.297, $t = -2.755$, $P = 0.002$) (Table 2).

Among the behaviors that were strongly loaded onto Loner, only "alone" was significantly correlated with dominance rank: high-ranking females were less likely to be alone than were low-ranking females ($\beta = -0.848$, SE = 0.233, $t = -3.635$, $P = 0.001$). The loading of this variable was not just an artifact of dominance rank, however, because a model that used both Loner score and dominance rank to predict the frequency of being alone was significantly better than a model that used dominance rank alone (anova model comparison, $\chi^2 = 111.9$, $df = 1$, $P < 0.001$). Thus, females who scored high on the Loner component were more likely to be alone than would have been expected based solely on their rank (Fig. 2).

Kin. The availability of kin did not significantly influence females' personality styles: 86%, 75%, and 74% of the females assigned to clusters 1, 2, and 3, respectively, had kin present in the group during that year. Scores on Aloof and Nice were unrelated to the availability of kin (Aloof: $\beta = 0.151$, SE = 0.198, $t = 0.763$, $P > 0.10$; Nice: $\beta = 0.210$, SE = 0.207, $t = 1.016$, $P > 0.10$). However, females' scores on Loner were significantly less extreme when they had kin present in the group ($\beta = -0.404$, SE = 0.190, $t = -2.13$, $P = 0.014$) (Table 2). (See *SI Text* for data on additional covariates and similarities among kin).

Predictive value. Glucocorticoid levels. Across all individuals there was a positive correlation between dominance rank and stress, as measured by glucocorticoid (GC) levels, with lower-ranking females exhibiting higher GC levels than higher-ranking females ($n = 99$, $\beta = -0.356$, SE = 0.221, $t = -1.611$, $P = 0.049$). Females' scores on Aloof and Nice were unrelated to GC levels. In contrast, GC levels were significantly correlated with scores on Loner ($n = 99$, $\beta = 0.172$, SE = 0.057, $t = 3.01$, $P = 0.003$) (Table 2). These higher GC levels were not simply an artifact of dominance rank, however, because a model that used rank + Loner score to predict GC levels was significantly better than a model that used rank alone (anova model comparison, $\chi^2 = 7.479$, $df = 1$, $P < 0.001$). Thus, females who scored high on Loner had higher GC levels than would have been predicted based on their rank alone (Fig. 3).

Table 2. Potential covariates and predictive value of personality component scores

Potential covariates and predictive values	Aloof	Loner	Nice
Potential covariates			
Dominance rank	−0.001	−0.769**	−0.228
Presence of kin	0.151	−0.404*	0.210
Predictive value			
GC	−0.057	0.172**	0.079
CSI	0.051	−0.129*	0.145*
PSI	0.165**	−0.029	0.111(*)
Rate of being approached	−0.121*	−0.123(*)	0.093

Potential covariates: Data show β-coefficients derived from separate linear mixed models in which rank or kin was the predictor and component score on Aloof, Loner, or Nice was the dependent measure. Predictive value: Data show β-coefficients derived from separate linear mixed models in which component score on Aloof, Loner, or Nice was the predictor and baseline GC levels, CSI, PSI, or the rate of being approached was the dependent measure. Data were drawn from all individuals over all years with individual identity and year entered as random factors. For definitions see *Methods*. $^{**}P < 0.01$, $^{*}P < 0.05$, (*) $P = 0.07$.

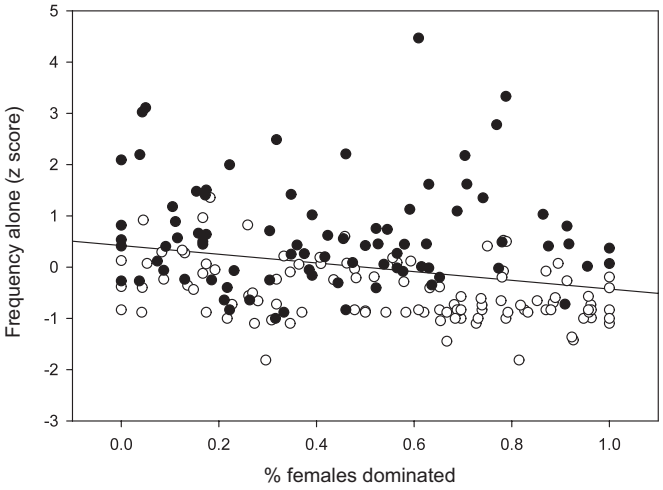

Fig. 2. The relation between dominance rank (percent females dominated), *z*-scores for mean annual frequency of being alone, and females' scores on the Loner component. Black circles show females whose Loner scores in a given year were above the overall mean, open circles show females below the mean. Low-ranking females were more likely to be alone than high-ranking females, and females who scored above the mean on the Loner component were more likely to be alone than expected based solely on their rank.

CSI. To test whether personality dimensions helped to explain differences in CSI, we used a linear mixed model with each component score as the sole predictor and CSI as the dependent measure. Scores on Nice were significantly positively correlated with CSI ($\beta = 0.145$, SE = 0.069, $t = 2.112$, $P = 0.024$), whereas scores on Loner were significantly negatively correlated with CSI ($\beta = -0.129$, SE = 0.064, $t = -2.00$, $P = 0.013$) (Table 2). Scores on Aloof were unrelated to scores on CSI ($n = 189$, $\beta = 0.051$, SE = 0.064, $t = 0.783$, $P > 0.10$).

Over all females, CSI scores were positively, but not significantly, correlated with dominance rank ($\beta = 0.461$, SE = 0.305, $t = 1.512$, $P = 0.084$) and significantly positively correlated with the availability of kin ($\beta = 0.490$, SE = 0.190, $t = 2.577$, $P = 0.003$)

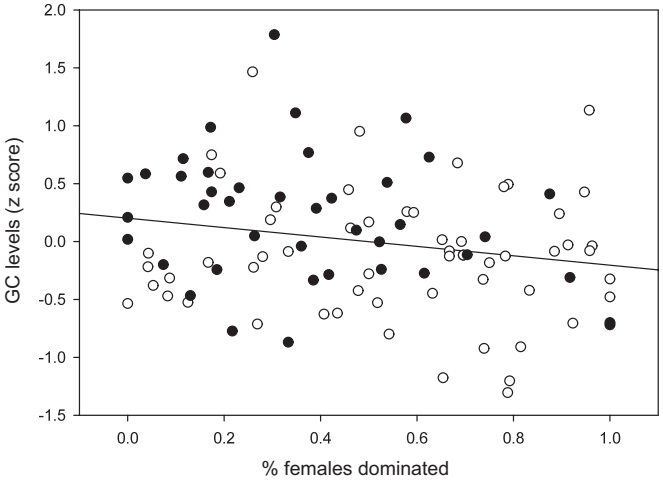

Fig. 3. The relation between dominance rank, *z*-scores for mean annual GC levels, and scores on the Loner component. Legend as in Fig. 2. Low-ranking females had higher GC levels, and females who scored above the mean on the Loner component had higher GC levels than expected based solely on their rank.

(22). However, when we compared the models based on rank or the availability of kin alone with a model based on the additive predictors rank + kin + Loner + Nice, the latter model was significantly better than both the model based on rank + kin (anova model comparison $\chi^2 = 7.44$, $df = 2$, $P = 0.02$) and the models based on kin or rank alone (rank: $P < 0.01$; kin: $P < 0.05$).

In sum, personality component scores differed clearly in their relation to CSI. Nice was significantly positively correlated with CSI, Loner was significantly negatively correlated with CSI, and Aloof fell between these extremes. These differences were not simply because of differences in rank or the availability of kin. Instead, personality dimensions accounted for variance in CSI scores beyond that explained by rank and kinship.

PSI. To test whether personality scores helped to explain differences in PSI, we used a linear mixed model with component score as the sole predictor and PSI score as the dependent measure. Scores on Aloof were significantly positively correlated with PSI ($\beta = 0.165$, SE = 0.062, $t = 2.664$, $P = 0.006$), and scores on Nice were close to significant ($\beta = 0.111$, SE = 0.065, $t = 1.709$, $P = 0.071$). Scores on Loner were unrelated to PSI (Loner: $\beta = -0.029$, SE = 0.063, $t = -0.458$, $P > 0.10$) (Table 2).

Over all females, the PSI was unrelated to dominance rank ($\beta = 0.247$, SE = 0.240, $t = 1.028$, $P > 0.10$) or the availability of kin ($\beta = 0.187$, SE = 0.164, $t = 1.142$, $P > 0.10$).

In sum, personality component scores differed clearly in their relation to the PSI. Females scoring high on Aloof and Nice had more stable bonds than others. Personality dimensions accounted for variance in the PSI beyond that explained by rank and kinship.

Baboons' recognition of other animals' personalities. The rate at which females were approached by others suggested that the baboons themselves were sensitive to differences in each other's personalities. Overall, high-ranking females were approached at significantly lower rates than low-ranking females ($\beta = -1.174$, SE = 0.272, $t = -4.313$, $P < 0.001$). Rates of being approached, however, were also correlated with individuals' component scores. Females scoring high on Aloof were less likely to be approached ($\beta = -0.121$, SE = 0.700, $t = -1.737$, $P = 0.039$), as were (to a lesser extent) females scoring high on Loner ($\beta = -0.123$, SE = 0.700, $t = -1.757$, $P = 0.076$). Scores on Nice showed no such relation ($\beta = 0.927$, SE = 0.074, $t = 1.247$, $P > 0.10$). These differences were not solely a result of dominance rank, because a model based on dominance rank + Aloof score was significantly better than a model based on dominance rank alone ($\chi^2 = 4.17$, $df = 1$, $P < 0.041$), as was a model based on dominance rank + Loner score ($\chi^2 = 7.99$, $df = 1$, $P < 0.005$). Similarly, the low rate at which Aloof females were approached could not be attributed to their aggressiveness, because rates of aggression and rates of being approached were not significantly correlated ($\beta = 0.182$, SE = 0.072, $t = 0.251$, $P > 0.10$). The low rate at which Loners were approached may have been a result of their high frequency of being alone, because there was a significant correlation between these two measures ($\beta = -0.155$, SE = 0.070, $t = -2.212$, $P = 0.028$).

The availability of kin had no effect on the rate of being approached.

Discussion

Three principal components accounted for a significant proportion of the overall variance in the data matrix. The loadings of different behaviors onto these components allowed us to identify three suites of functionally distinct behaviors (32), or personality dimensions, that were not redundant with dominance rank, age, or the availability of kin. We characterized these dimensions as Aloof, Loner, and Nice.

Several observations validated our approach. First, by at least one measure, females behaved differently toward individuals with different component scores. They approached females scoring high on the Nice dimension at the highest rates, seldom approached females scoring high on Loner, and were least likely to approach females scoring high on Aloof. These differences could not be explained by differences in dominance rank or aggressiveness, although Loners may have been avoided because they were so often alone. Thus, the baboons themselves appeared to be sensitive to the distinctions among personality dimensions.

Second, the different personality dimensions were correlated in different ways with stress. Females who scored high on Loner had higher GC levels than would have been predicted based on their rank alone.

Third, the different personality dimensions were correlated in different ways with two indices that measure the strength of females' dyadic bonds and are correlated with fitness (7, 8). Scores on Aloof were unrelated to CSI, which reflects overall levels of sociality, but showed a significant positive correlation with PSI, which reflects the stability of partner preferences over time. Scores on Nice showed a significant positive correlation with CSI and a near-significant positive correlation with PSI, but scores on Loner showed a significant negative correlation with CSI. Loner scores were less extreme when kin were present.

To summarize, borrowing terms from studies of human personality, the three personality dimensions showed: relative stability over time (test-retest reliability) (31); discriminant validity because they were not redundant with dominance rank or the availability of kin; and predictive validity because they were correlated with one physiological measure and two measures of dyadic social bonds that were not used to construct the personality dimensions and are known to be associated with reproductive success.

The different personality dimensions also appeared to reflect the strategic decisions that individuals made in different social circumstances. Animals scoring high on Aloof and Loner grunted most often to higher-ranking females in contexts in which they themselves were likely to benefit, either by gaining access to an attractive infant (Aloof) or by reducing the risk of aggression (Loner). In contrast, animals scoring high on Nice grunted even to lower-ranking females without infants, a context in which they themselves derived no immediate benefit. For Aloof and Loner animals, grunting appeared to be prompted primarily by personal gain, whereas for Nice animals it seemed motivated by the desire to signal benign intent and alleviate the recipient's anxiety.

Although PCA results yielded distinctly different personality dimensions, cluster analysis that combined females' scores on all three dimensions revealed considerable overlap among personality styles. As in humans, baboons' personalities showed some plasticity (15, 27, 28), and females did not always retain the same personality styles across time. Nonetheless, females were significantly more likely to retain, rather than change, their personality style from one year to the next. It remains to be determined whether shifts in personality were because of the overlap in personality styles, pivotal social or demographic events, or individual differences in consistency.

It is difficult to compare our results with other studies of personality in nonhuman primates, for several reasons. First, with some exceptions (e.g., ref. 33), most previous studies have relied wholly or in part on assessments by human observers, using trait classifications originally designed for human personality studies [a top-down approach, (e.g., refs. 17–21)]. We instead adopted a bottom-up approach (31), using the behavior of the baboons themselves to determine whether any personality dimensions emerged, without any assumptions about what these dimensions might be.

Second, most assessments of personality in nonhuman primates have relied on relatively crude designations, like "boldness," without controlling for attributes, such as dominance rank, that may affect these designations. In contrast, none of our personality dimensions could be fully explained by an individual's rank or the availability of kin. Females with high Loner scores were likely to be low-ranking, but rank alone could not explain

why they had higher GC levels. The presence of kin mitigated individuals' scores on Loner, but kin alone could not explain why they were so often isolated and so rarely approached. Such results confirm what many observers of cercopithecine primates have long suggested: that although dominance rank and matrilineal kinship are important organizing principles of female society, they do not explain all aspects of behavior. Indeed, in baboons, offspring survival and female longevity are best predicted not by dominance rank or the presence of kin but by the strength (CSI) and stability (PSI) of a dyad's social bonds (7, 8), and CSI and PSI are related in different ways to scores on personality dimensions.

Our results allow us to extend previous work by painting a more detailed picture of the costs and benefits of particular personality characteristics and their relation to other measures of sociality. For example, selection would appear to act against females scoring high on Loner, because these individuals were under more stress than others and formed dyadic bonds that yielded low CSI scores and low partner stability. This finding begs the obvious question of why any female would adopt the Loner strategy. Loners were not isolated and unfriendly solely because of their subordinate status or lack of kin. Although these demographic factors contributed to their scores on Loner, their behavior exacerbated them. Moreover, some Loners did have close kin whereas other females, consistently scoring high on Nice, did not. If Loners are often the victims of circumstances, what skills or motivation allow some individuals to overcome these circumstances while others do not?

In contrast, selection would appear to favor individuals scoring high on Aloof and Nice, because these dimensions were correlated with the formation of dyadic bonds that led to high scores on either PSI (Aloof) or both CSI and PSI (Nice). There were, however, subtle differences between these two apparently adaptive personality dimensions. Individuals scoring high on Nice were rarely aggressive and very friendly, grunting to all individuals. Perhaps as a result, they were often approached by others and formed the strongest dyadic bonds. However, their bonds were somewhat less stable than those formed by individuals scoring high on Aloof. One might speculate that the rather intense, indiscriminate social activity of Nice females carried costs that impaired their ability to maintain focused, stable bonds with the same few individuals.

Individuals scoring high on Aloof were notably aggressive, much less friendly, and much more exclusive in their grunting. Perhaps as a result, they were rarely approached and their dyadic bonds were less strong. Nonetheless, their partner stability was very high. One might speculate that these individuals' behavior led them to form bonds with a small number of close companions but prevented them from forming bonds that were strong enough to generate a high CSI. It remains for future research to determine which of these personality styles is more adaptive, or whether variation in personality styles is maintained by contrasting effects on fitness (e.g., ref. 34).

Methods

Field Observations. Data were derived from a long-term study of wild chacma baboons (*Papio hamadryas ursinus*) in the Moremi Game Reserve, Botswana (35, 36). The group had been observed since 1978. Maternal kinship was known for all individuals. The primary causes of mortality were infanticide and predation.

As in other species of cercopithecine primates, female baboons are philopatric and assume dominance ranks similar to their mothers' (36). Adult female dominance ranks were calculated monthly based on the direction of approach–retreat interactions. For most of the study, the female dominance hierarchy remained stable.

Analyses were based on 7-y observation (2001–2007) of 45 adult females, a period during which we had continuous data on all females. Eleven females were present for seven consecutive years, 7 females for 5 y, 9 females for 4 y, 6 females for 3 y, 11 females for 2 y, and 1 female for 1 y ($n = 189$ female years).

Research was approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol 19001).

Behavioral and Hormonal Data. Ten-minute focal animal observations (37) were conducted almost daily using a common protocol. All approaches, vocalizations, and friendly and aggressive interactions were recorded on a continuous basis. We also noted all grooming interactions and their durations (22).

In 2002–2005 and 2007, behavioral observations were supplemented with the collection of weekly fecal samples for the extraction of GC, steroid hormones associated with stress (9, 38, 39). Previous results have shown that females' GC levels are elevated during pregnancy and periods of social instability (e.g., the immigration of a potentially infanticidal male). Because we wished to determine whether variation in baseline GC levels was associated with variation in behavior, we restricted our analysis to samples obtained from lactating and cycling females during periods of social stability ($n = 99$ female years).

We used seven independent behavioral variables, calculated annually for each female, to construct the components of personality styles: (*i*) Alone: the proportion of focal samples in which a female did not interact with any other individual (excluding dependent infants) for the entire 10-min period. (*ii*) Friendly: the rate at which a female touched or embraced other females. (*iii*) Aggression: the rate at which a female behaved aggressively (head bobs, lunges, chases, bites) toward other females. Because high-ranking females have more available targets than do low-ranking females, we corrected each female's annual aggression rate for the proportion of females who ranked below her. Thus, a low-ranking female might score higher on 'aggression' than a high-ranking one. (*iv–vii*) Grunts: the frequency with which a female grunted when approaching (*iv*) a higher-ranking female who had a young infant (< 3 mo), (*v*) a higher-ranking female who did not have an infant, (*vi*) a lower-ranking female who had a young infant, and (*vii*) a lower-ranking female who did not have an infant.

We tested our results against three possible covariates (*i–iii*), three dependent variables previously shown to be associated with fitness (*iv–vi*), and one behavioral measure (*vii*). Each measure was calculated annually for each female: (*i*) Age. (*ii*) Dominance rank (calculated as the proportion of females dominated). (*iii*) The presence or absence of adult female kin (mothers, daughters, maternal sisters), a binary measure. (*iv*) Stress: a female's mean GC levels during periods of social stability. (*v*) Composite Sociality Index: The CSI is based on the rate of approaches, groom presents, grooming initiations, and the duration of grooming within dyads (both given and received) (7, 22). For consistency with previous analyses, we used females' average CSI with their top three partners. (*vi*) Partner Stability Index. The PSI assesses the consistency of a female's top 3 partners across successive years (25). The value of PSI could vary from 1 (for females who retained the same three partners across all years) to 0 (for females who had a completely different set of top 3 partners in each year). (*vii*) Rate of being approached (calculated as the rate at which other females approached to within 2 m of the focal individual).

Because rates of sampling varied over the study period, and because variation in demographic factors can influence rates of behavior (40), we converted all annual rates of behavior, including the CSI and PSI, to *z*-scores for statistical analysis. Annual GC levels were also *z*-scored. Thus, each female's annual *z*-score reflected her score on a particular measure relative to other females in that year.

Statistical Analysis. Statistical analyses were conducted using R statistical software (version 2.15, R Foundation for Statistical Computing, R Development Core Team, 2009). To test whether females were consistent relative to others in their rates of behavior or their scores on principal components, we calculated the Kendall coefficient of concordance (W) using the function kendall.w in the R package "concord." We calculated the value of W over *n* successive years for all individuals observed for that number of years. When sample sizes were small, we collapsed the data to increase the number of individuals and the number of years. For example, data on rates of aggression were available from six females over 5 y and nine females over 4 y, so we dropped the first year's data on the former group to create a sample of 15 females observed over 4 y. The dropped data always came from females' first year as adults (age 5).

For exploratory PCA, we used the principal function in the "psych" package in R, with the default varimax rotation. To test for a relation between scores on principal components and our dependent variables, we used linear mixed models (lmer in R), entering female ID and year as random factors. To compare models, we used the anova function (41).

To assign each female in each year to a particular personality style, we used the partitioning around medoids program in the "cluster" package in R. This function is "based on the search for *k* representative objects, or medoids, among the observations of the dataset" (R Development Core Team 2009). We used the "average silhouette width" to determine the value of k that best described the structure of the data (29, 30). After the function finds *k* medoids, each observation is assigned to a cluster by minimizing the sum of dissimilarities between the point and the medoid (29).

All probability values are two-tailed.

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