Original Article

Folia Primatol 2007;78:56–68
DOI: 10.1159/000095686

Received: February 22, 2006
Accepted after revision: May 26, 2006

One-Male Harems and Female Social Dynamics in Guinea Baboons

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Key Words
Guinea baboons · Mating system · Harem · Female social relationships · Kinship

Abstract

Little is known about the mating system and social organization of Guinea baboons. This study investigated whether Guinea baboons have a harem-based mating system similar to that of hamadryas and gelada baboons and whether one-male mating units also correspond to social units. Ten adult females in a captive multi-male multi-female group of Guinea baboons were focally observed 2 h per week for 12 weeks, and all observed copulations within the group were recorded. Some males copulated with a single female while others had harems of 2–4 females. All females copulated with a single male except 1 female that switched harems early in the study. The focal females had higher rates of social interaction with their harem members, especially their harem male, than with individuals outside the harem. Females appeared to be subordinate to the harem male but little or no physical aggression or herding behavior from the male was observed. Variation in female social interactions within the harem was not accounted for by their sexual interactions with the male or their genetic relatedness with the females. Females, however, appeared to maintain social relationships with their female relatives in other harems. Taken together, the results of this study show that both mating and affiliative interactions in Guinea baboons are concentrated within one-male units and that the social dynamics within and between these units share some similarities as well as differences with those of hamadryas and gelada baboons.

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0015–5713/07/0781–0056$23.50/0

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Introduction

The species and subspecies of baboons belonging to the genera *Papio* and *Theropithecus* exhibit two basic forms of social organization and mating system. The 3 subspecies of savanna baboons, yellow *(Papio hamadryas cynocephalus)*, olive *(Papio hamadryas anubis)* and chacma baboons *(Papio hamadryas ursinus)*, live in large multi-male multi-female groups in which both males and females engage in highly promiscuous mating. In these subspecies, females typically remain in their natal groups and form strong bonds with their female relatives whereas males emigrate at puberty and join new groups. On the other hand, the hamadryas baboon *(Papio hamadryas hamadryas)* and the gelada baboon *(Theropithecus gelada)* have a multi-layered social system in which at least 3 types of social groupings are distinguished [Stammbach, 1987]. The grouping in which most social behavior and mating activities take place is the one-male unit, or harem, which consists of 1 or 2 males and several adult females and their offspring. Several adult males and their harems may aggregate to form higher-order groupings known as clans or teams, and many harems and clans travel and sleep together in bands or herds of hundreds of individuals (hamadryas [Kummer, 1968; Abegglen, 1984; Colmenares, 1992, 2004; Colmenares et al., 2006]; gelada [Mori, 1979; Dunbar, 1984]). The one-male units of hamadryas and gelada baboons differ in several important respects. In hamadryas baboons, harems are formed and maintained by males through kidnapping and herding of females. As a result, the hamadryas females within the same harem are typically unrelated to one another and direct most of their affiliative behavior toward the harem male [Abegglen, 1984; Kummer, 1968; but see Swedell, 2002a, b]. In gelada baboons, in contrast, the females within the same harem are typically related to one another [Dunbar, 1984; but see Mori et al., 1999] and form strong bonds and agonistic coalitions with their relatives so that even the male's access to individual females is constrained by the females' own social preferences [Dunbar, 1984]. These differences in social organization between hamadryas and gelada baboons are generally consistent with differences in patterns of feeding competition and sex-biased dispersal and philopatry between these species, and more generally with the prediction of socioecological theory [Sterck et al., 1997].

The Guinea baboon *(Papio hamadryas papio)* is the least known of all the baboon species and subspecies. Preliminary field studies have suggested that, similar to the hamadryas and the gelada baboons, Guinea baboons travel (or aggregate at sleeping sites) in bands or herds of hundreds of individuals, while most of their affiliative and reproductive activities appear to be concentrated in smaller, male-centered units [De Keyser, 1956, cited by Boese, 1975; Bert et al., 1967; Dunbar and Nathan, 1972; Byrne, 1981; Anderson and McGrew, 1984; Galat-Luong et al., in press]. Behavioral studies in captivity, primarily involving the colony of Guinea baboons at Brookfield Zoo in Chicago, have shown that adult males maintain 'harems' of 2–5 females with which they mate, and that most females within the group copulate with only 1 or 2 males [Boese, 1975; Anthoney, 1975; Maestripieri et al., 2005]. However, the extent to which these mating units also correspond to social units is largely unknown. Furthermore, if harems do exist as distinct social groupings, it is not clear whether the social dynamics within these harems are more similar to those of hamadryas baboons or those of geladas.

In the present study, we investigated the distribution of sexual and social behavior in the Guinea baboon colony at Brookfield Zoo with the following aims:

(1) to assess whether the distribution of copulations within the group is consistent with the one-male harem structure suggested by previous studies of the same colony; (2) to assess whether harems are not only mating units but also social units and, in particular, whether females exchange more affiliative interactions and fewer agonistic interactions with members of their harems than with nonmembers; (3) to assess whether interindividual variation in female social interactions with adult males and females is accounted for by variation in their sexual interactions with males and genetic relatedness with females, respectively.

Materials and Methods

Subjects and Housing

The study was conducted with the group of Guinea baboons at Brookfield Zoo in Chicago, Ill., USA. At the beginning of the study, the group consisted of 11 adult males (age range: 9–22 years; mean ± SD = 14.0 ± 4.16) and 23 adult females (age range: 11–21 years; mean ± SD = 14.36 ± 2.89). There were no infants, juveniles or subadults**.** All adult males except 1 were vasectomized while all females except 1 were intact and cycling. The intact male had been introduced into the group along with 3 new females a few months prior to the beginning of the study. The genealogical history of most individuals in the group was well known. In particular, there were 4 distinct matrilines within the group (M, F, A and S matrilines; see Results).

The group is housed in a multi-level, outdoor grotto comprised of artificial rocks and measuring 57.3 × 47.2 m. The animals also have access to an indoor holding and feeding facility, in which they are given an unlimited supply of water and monkey chow. At approximately 11.00 a.m. each day, the group is fed a combination of various fruits and vegetables.

Procedure

Ten randomly selected intact females were each focally observed in two weekly 1-hour observation sessions over 12 weeks. Thus, 24 h worth of focal data for each female were available at the end of the study. In addition, all copulations (defined as male mounts with intromission and thrusting) observed in the group during the study period were recorded with the behavior sampling method [Martin and Bateson, 1986]. Data were collected 5 days a week, between 7.30 a.m. and 4.30 p.m. The order in which the focal females were observed was randomized. All behavioral data were collected by one observer using binoculars, an audio tape recorder and a stopwatch. For the purposes of the present study, data analysis focused on copulations between males and females, the frequency and duration of contacts (any bodily contact lasting more than 5 s) made and received by the focal females, the number of approaches made and received by the focal females and the duration of proximity (defined as being within arm's reach of another animal without making contact), the number and duration of grooming episodes initiated and received by the focal females, the number of episodes of spatial avoidance (withdrawal in response to an approach) initiated and received by the focal females and the number of episodes of noncontact aggression (open-mouth threats, lunges and chases) initiated and received by the focal females. Since most noncontact aggression was accounted for by threats, this category of behavior will be referred to as threats. Aggression involving physical contact (e.g. hitting or biting) was too rare to be analyzed. Male herding behavior (e.g. holding and restraining females, or pulling and dragging them) was virtually nonexistent. Although all males except 1 were vasectomized and their copulatory behavior was nonreproductive, we assumed that the vasectomy did not affect any other aspect of their sexual behavior and therefore we referred to it as mating.

Statistical data analyses included mixed-design analyses of variance for repeated measures and correlations (Pearson's correlation coefficient). Data were log-transformed whenever they were nonnormally distributed or the variances were nonhomogeneous. All tests are two-tailed, and probabilities of ≤ 0.05 are considered statistically significant.

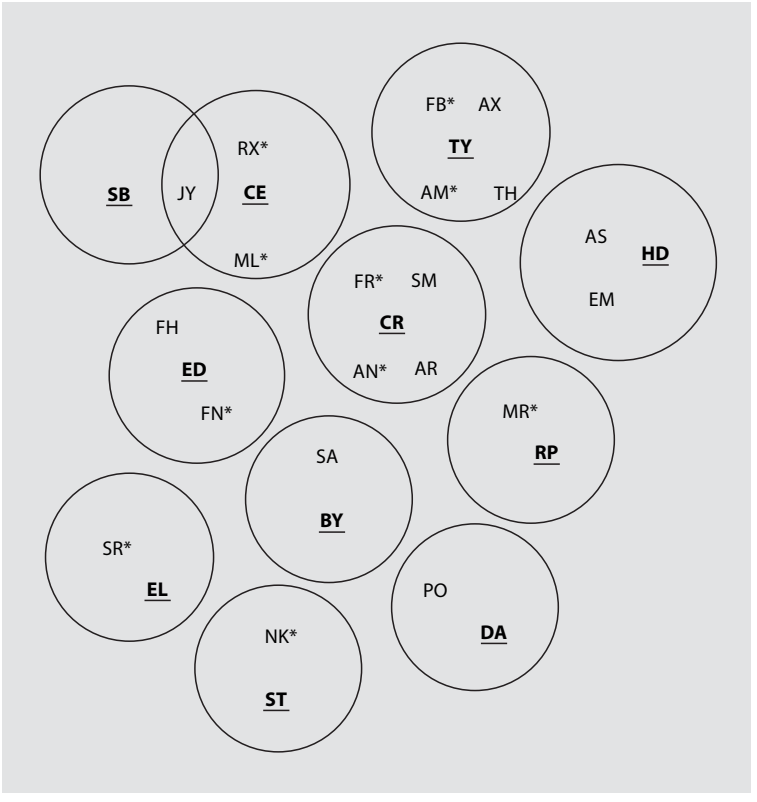

Fig. 1. Diagrams of male mating harems. Males are in bold and underlined. The 10 focal females are identified with an asterisk, and the females belonging to the same matriline have codes beginning with the same letter. Three more females, MO, VA and FL, were not observed copulating and therefore were not assigned to any harems.

Results

Identification and Structure of Male Harems

During the study period, 64 copulations were observed. Of the 23 females present in the group, 16 were seen copulating at least once. Four additional females were observed copulating during pilot observations conducted prior to the study. The number of observed copulations per female ranged from 1 to 13 (mean = 2.91, SEM = 0.67). Except for 1 female (Jy) who was observed copulating with 2 different males, all females copulated with only 1 male. All of the 11 males present in the group were observed copulating at least once. The number of females with which each male copulated ranged from 1 to 4. In figure 1, the 20 females who were observed copulating were grouped with the male with which they copulated. The circles in the figure therefore represent the males' harems. Three more females (MO, VA and FL) were not observed copulating and therefore were not assigned to any harems. The female Jy had copulated with the intact male SB prior to their introduction into the group

and was seen copulating with him again at the beginning of the study. However, the male SB quickly 'lost' his female to another male and was not seen copulating again for the duration of the study. Since the female Jy copulated with the male CE for most of the study, she was assigned to his harem for the purposes of data analysis. This female was however not one of the focal subjects and therefore her contribution to the data set was negligible. In figure 1, the focal subjects are identified with an asterisk and the females belonging to the same matriline have codes beginning with the same letter. Of the 5 harems with more than 1 female, 3 of them included at least 2 related females while the other 2 included only unrelated females.

Comparisons of Female Affiliative and Agonistic Interactions with Individuals within and outside the Harem

Frequency and duration measures of contact, proximity and grooming between the focal females and other individuals were generally highly correlated. Therefore, only frequency measures were analyzed. Figure 2a depicts the total number of episodes of contact, proximity, grooming, threat and avoidance initiated by the focal females with both harem and nonharem males and females. These data provide a snapshot of the distribution of female affiliative and agonistic behavior within the group. In figure 2b the same measures are controlled for the number of individuals available in each category (harem male, nonharem male, harem female and nonharem female). These data provide more direct information on the social preferences of the focal females and/or the quality of their social relationships with particular individuals. Figure 3a and b presents similar information but for interactions in which the focal females were recipients. Statistical analyses focused on the average behavioral measures per individual per category, i.e. the data presented in figures 2b and 3b.

Analyses of variance revealed statistical main effects of harem membership for all affiliative behaviors initiated by the focal females (contact, $F_{1, 15} = 9.01$, $p < 0.01$; proximity, $F_{1, 15} = 49.84$, $p < 0.0001$; grooming, $F_{1, 15} = 19.40$, $p < 0.0005$) as well as for threats ($F_{1, 15} = 4.63$, $p < 0.05$) and avoidance ($F_{1, 15} = 14.59$, $p = 0.001$). In all cases, the focal females initiated more interactions with harem members than with nonmembers. Main effects of partner sex emerged for proximity ($F_{1, 15} = 13.01$, $p = 0.002$), grooming ($F_{1, 15} = 6.11$, $p < 0.05$) and threats ($F_{1, 15} = 8.11$, $p = 0.01$), but not for contact ($F_{1, 15} = 2.12$, $p = 0.16$) or avoidance ($F_{1, 15} = 0.08$, $p = 0.77$). Females initiated proximity and grooming more frequently with males than with females but threatened other females more than they threatened males (fig. 2b). Finally, there was a statistically significant interaction between harem membership and partner sex for the three measures of affiliation (contact: $F_{1, 15} = 5.52$, $p = 0.03$; proximity: $F_{1, 15} = 13.01$, $p = 0.002$; grooming: $F_{1, 15} = 24.59$, $p = 0.0002$) and threats ($F_{1, 15} = 8.11$, $p = 0.01$) but not for avoidance ($F_{1, 15} = 0.06$, $p = 0.81$). Within their harem, the focal females initiated affiliative interactions more with the male than with the females, whereas with nonharem members, they affiliated more with females than with males (fig. 2b). Females never threatened any males, but they threatened other females within their harem more than females outside the harem (fig. 2b).

The analysis of behaviors received by the focal females (fig. 3b) revealed some similarities as well as differences with the analysis of the behaviors performed. Significant main effects of harem membership were found for approaches ($F_{1, 15} = 53.14$, $p = 0.001$), grooming ($F_{1, 15} = 5.79$, $p = 0.02$) and threats ($F_{1, 15} = 29.61$, $p = 0.0001$) but not for contact ($F_{1, 15} = 2.84$, $p = 0.11$) or avoidance ($F_{1, 15} = 2.22$, $p = 0.15$). The focal

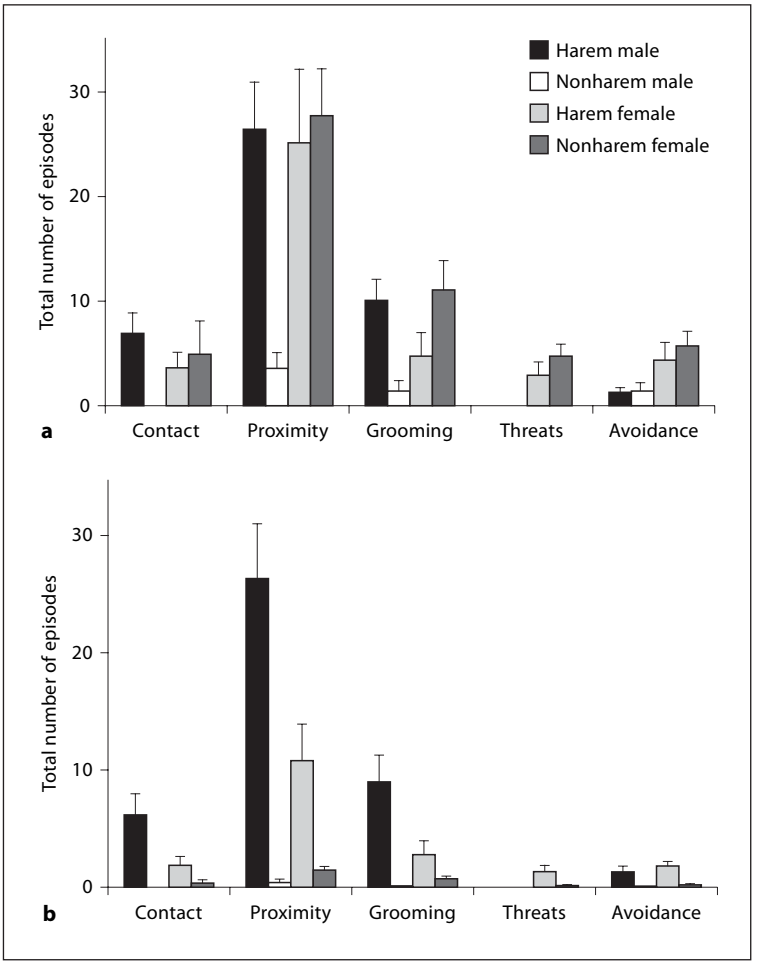

Fig. 2. a Mean number (and SEM) of episodes of contact, proximity, grooming, threat and avoidance initiated by the focal females with harem and nonharem males and females during the study period. **b** Mean number of episodes of contact, proximity, grooming, threat and avoidance initiated by the focal females with harem and nonharem males and females divided by the number of individuals in each partner category.

females received more approaches, grooming and threats from their harem members than from other individuals (fig. 3b). There were significant main effects of partner sex for all variables. Females received more contact, grooming and avoidance from other females than from males (contact: $F_{1, 15} = 4.21$, $p = 0.05$; grooming: $F_{1, 15} = 6.26$, $p = 0.02$; avoidance: $F_{1, 15} = 7.28$, $p = 0.01$) but received more approaches and threats from males than from females (proximity: $F_{1, 15} = 20.73$, $p = 0.0004$; threats: $F_{1, 15} = 5.79$, $p = 0.02$; fig. 3b). Finally, there was a significant interaction between harem membership and partner sex for proximity ($F_{1, 15} = 45.44$, $p = 0.0001$), threats ($F_{1, 15} = 8.63$, $p = 0.01$) and avoidance ($F_{1, 15} = 4.98$, $p = 0.04$) but not for contact

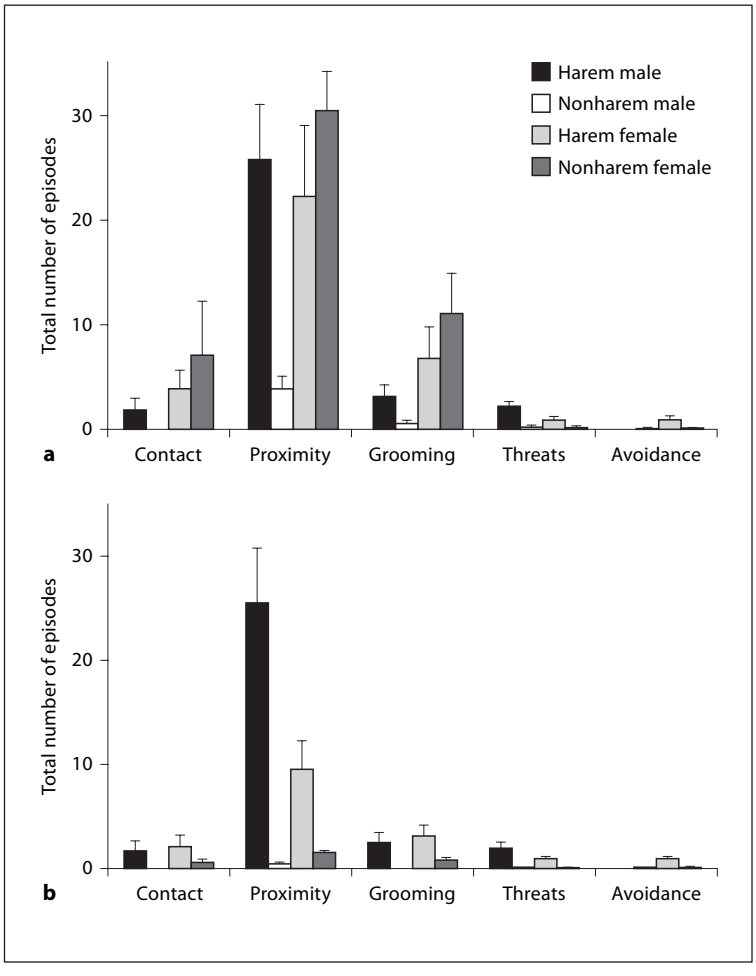

Fig. 3. a Mean number (and SEM) of episodes of contact, proximity, grooming, threat and avoidance received by the focal females from harem and nonharem males and females during the study period. **b** Mean number of episodes of contact, proximity, grooming, threat and avoidance received by the focal females from harem and nonharem males and females divided by the number of individuals in each partner category.

($F_{1, 15} = 0.05$, $p = 0.89$) or grooming ($F_{1, 15} = 1.92$, $p = 0.18$). Within their harem, the focal females were approached more by males than by females, whereas outside the harem the opposite was true (fig. 3b). Finally, the higher amount of avoidance received from females and the higher number of threats received from males were greater for harem members than for non-members (fig. 3b).

Taken together, these results indicate that although females exchanged affiliative and agonistic interactions with individuals within and outside their harems, both types of interactions were more frequent with harem members than with nonmembers. In particular, females had relatively high rates of affiliation, especially

proximity, with their harem male, intermediate levels with other harem females and low levels with other females outside the harem. Females had virtually no interactions, whether affiliative or agonistic, with nonharem males. Interactions within the harem had a strong agonistic component as well, with females receiving the most threats from their harem male and the most avoidance from the harem females. In order to gain a better understanding of the social dynamics within the harem, we compared the affiliative and agonistic interactions done and received by the focal females with the harem male and the harem females.

Comparisons of Interactions Initiated and Received with Male and Females within the Harem

Approaches were the most frequent interactions between the focal females and other harem members (fig. 2, 3). There was no significant difference between approaches made and received by focal females ($F_{1, 12} = 0.72$, $p = 0.41$) but there was a significant main effect of partner sex ($F_{1, 12} = 34.71$, $p = 0.0001$): the focal females exchanged more approaches with the harem male than with the females (fig. 2b, 3b). The interaction between these variables was not significant ($F_{1, 12} = 0.78$, $p = 0.39$).

There was no significant difference between contact or grooming done and received (contact: $F_{1, 12} = 1.35$, $p = 0.27$; grooming: $F_{1, 12} = 2.56$, $p = 0.13$) or between contact or grooming exchanged with males and females (contact: $F_{1, 12} = 1.01$, $p = 0.33$; grooming: $F_{1, 12} = 2.79$, $p = 0.12$) but there was a significant interaction for both variables (contact: $F_{1, 12} = 4.8$, $p = 0.05$; grooming: $F_{1, 12} = 10.79$, $p < 0.05$). The focal females initiated more contact and grooming with the harem male than they received from him, whereas with the other harem females the difference was negligible and in the opposite direction (fig. 2b, 3b). There were no significant differences in threats or avoidance done and received with males and females.

Correlational analyses of behaviors done and received were used to infer whether affiliative relationships between the focal females and other harem members were symmetrical or asymmetrical. For interactions between the focal females and the harem male, there were significant positive correlations between contact made and received ($r = 0.77$, $p = 0.008$), approaches made and received ($r = 0.77$, $p = 0.009$), and grooming done and received ($r = 0.77$, $p = 0.009$). Therefore, the more females initiated affiliation with the male, the more they received affiliation from the male. For interactions between the focal females and other harem females, there were significant positive correlations between contact made and received ($r = 0.92$, $p = 0.003$) and between approaches made and received ($r = 0.85$, $p = 0.01$), but not between grooming done and received ($r = 0.01$, $p = 0.97$). No significant correlations were found between threats made or received, or between avoidance done and received, regardless of whether these interactions involved the harem male or the females.

Relationship between Mating and Affiliation with the Harem Male

We hypothesized that the affiliative interactions between females and their harem males might have a relationship with their mating interactions. Specifically, we predicted that the females who copulated more often with the harem male might affiliate more frequently with him, receive fewer threats from him and avoid him less often than the females who copulated less frequently. There was indeed a positive correlation between number of copulations and female initiation of contact, proximity and grooming with the male but none of these correlations was statistically sig-

nificant (contact: r = 0.21, p = 0.56; proximity: r = 0.35, p = 0.32; grooming: r = 0.31, p = 0.38). The same was true for contact, proximity and grooming initiated by the harem male (contact: r = 0.33, p = 0.34; proximity: r = 0.01, p = 0.97; grooming: r = 0.10, p = 0.77). There was no significant correlation between copulations with and avoidance of the harem male (r = 0.11, p = 0.76) or threats received (r = –0.11, p = 0.75). Therefore, how frequently females copulated with their harem male did not account for variation in their affiliative interactions with him.

Affiliative Interactions with Harem and Nonharem Females: The Role of Kinship

On average, the focal females exchanged higher rates of both affiliative and agonistic interactions with harem females than with nonharem females. One possible explanation for this difference is that it was a by-product of proximity to the harem male. In other words, because all harem females stayed close to the harem male, they also ended up being closer to and interacting with each other more than with nonharem females. Other possible explanations are that higher affiliation between harem females reflects social attraction between them and higher agonism reflects competition (we will refer to this as 'the social attraction hypothesis'). Due to insufficient information on contact aggression, the dynamics of competition between harem females were not investigated in the context of the present study.

The social attraction hypothesis implies that females are more socially attracted to their kin than to non-kin and therefore that their patterns of affiliation with other females are kin biased. From this hypothesis we derived and tested the following predictions: (1) females who have more female relatives in their harem initiate and receive more affiliative interactions with other harem females than females who have fewer relatives; (2) females who have more female relatives outside their harem initiate and receive more affiliative interactions with nonharem females than females who have fewer relatives. The latter prediction implies that females maintain close social bonds with their relatives outside the harem and that the interactions with these relatives account for most of the affiliative exchanges with nonharem females.

There was no significant correlation between the contact, proximity and grooming episodes exchanged (initiated or received) between the focal females and other harem females and the number of relatives within the harem (or the proportion of harem females accounted for by kin). There was, instead, a tendency for the focal females to initiate contact and grooming less frequently when they had more relatives in the harem than when they had few or none (contact: r = –0.71, p = 0.06; grooming: r = –0.72, p = 0.06). Therefore, contrary to our prediction, having female relatives within the harem was not associated with higher rates of affiliation with harem females.

However, our prediction concerning kinship and affiliation with nonharem females was supported by the data. Among the 10 focal females, there was a significant positive correlation between number of contact and grooming, but not proximity, episodes initiated and received, on average, with a nonharem female and the total number of relatives the focal females had outside their harem (contact made: r = 0.76, p = 0.01; contact received: r = 0.68, p = 0.03; grooming done: r = 0.66, p = 0.03; grooming received: r = 0.62, p = 0.05; approaches made: r = 0.39, p = 0.26; approaches received: r = 0.42, p = 0.22). Data on contact and grooming exchanged (done and received added together) between the focal females and nonharem females in rela-

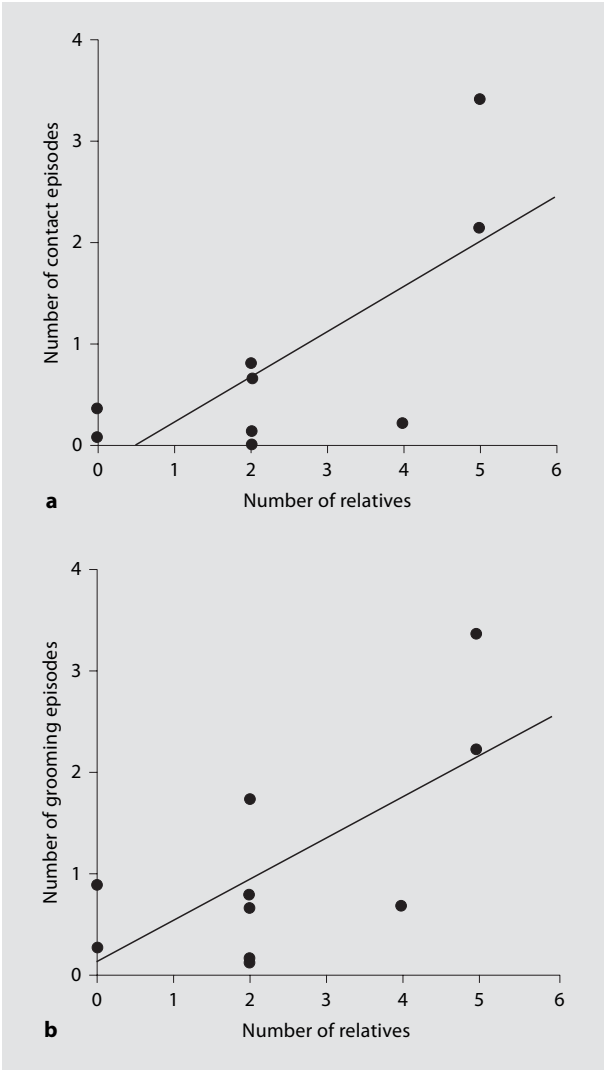

Fig. 4. a Correlation between the mean number of contact episodes exchanged (initiated + received) between the focal females and nonharem females and the number of female relatives outside the harem. **b** Correlation between the mean number of grooming episodes exchanged (initiated + received) between the focal females and nonharem females and the number of female relatives outside the harem.

tion to the number of relatives outside the harem are presented in figure 4a and b. Similar correlations were also found if instead of using the total number of female kin outside the harem, the analysis was conducted using the proportion of nonharem females accounted for by kin (contact made: $r = 0.76$, $p = 0.01$; contact received: $r = 0.70$, $p = 0.03$; grooming done: $r = 0.64$, $p = 0.04$; grooming received: $r = 0.63$, $p =$

0.05; approaches made: r = 0.33, p = 0.34; approaches received: r = 0.39, p = 0.26). Therefore, the more relatives the focal females had outside their harem, the more they affiliated with nonharem females.

Discussion

The results of this study are consistent with preliminary field studies of wild Guinea baboons [Dunbar and Nathan, 1972; Galat-Luong et al., in press] and previous studies of this captive colony [Boese, 1975; Maestripieri et al., 2005] in suggesting that Guinea baboons have a harem-based mating system similar to that of hamadryas and gelada baboons. Specifically, in our captive group of 11 adult males and 23 adult females, some males copulated with a single female while others had harems of 2–4 females (see also the study by Maestripieri et al. [2005], in which maximum harem size was 5 females). In this study, all females copulated with only 1 male (with the exception of 1 female who switched harems) while in a previous study of the same group we reported that about one third of the females copulated with 2 males [Maestripieri et al., 2005]. In the first study, however, more females switched harems than in the second study. Indeed, the harem structure of the group at the end of the first study was virtually identical to that observed in the second study, and the overall mating structure of this group is very similar to that observed in the same setting, but with different individuals, over 30 years ago [Boese, 1975]. Although the distribution of affiliative behavior within this captive group may have been affected by the lack of immature individuals and pregnant and lactating females, the stability of its mating structure over time suggests that the observed mating patterns are representative of the mating system of Guinea baboons [see also Galat-Luong et al., in press].

Similar to hamadryas and gelada baboons, the harems of Guinea baboons are not only mating units but also social units with relatively high rates of social interactions among their members. In this study, females exchanged higher rates of both affiliative and agonistic interactions with their harem members than with other individuals. Within their harem, females interacted more with the male than with females, whereas outside the harem they interacted more with females than with males. Females had few or no interactions with nonharem males.

Proximity between the male and the females seems to be a key feature of social dynamics within the harem. Females exchanged more approaches with the harem male than with the females, and their approaches to the male were generally reciprocated by him. Contact and grooming, however, were generally not reciprocated by the harem male. Although contact aggression was rare and male herding behavior was not observed, females received more threats from their harem male than from other individuals. This suggests that maintenance of proximity between the harem male and the females may be associated with some social tension and agonism. The finding that females were threatened by the harem male and avoided him, whereas they never threatened him or were avoided by him, suggests that harem females are socially subordinate to the harem male, similar to what is observed in hamadryas and gelada baboons [Kummer, 1968; Dunbar, 1984]. Individual differences among females in their affiliative and agonistic interactions with their harem male were not accounted for by their sexual interactions with him. This is also consistent with what

has been reported for gelada baboons, in which grooming rarely follows copulation and male-female affiliation in general is not affected by mating [Dunbar, 1984].

Some social tension and agonism may be present not only between the harem male and the females but also between the harem females, as the harem females exchanged threats and avoidance with each other more than with nonharem females. However, harem females also exchanged frequent affiliative behavior with one another. In fact, the focal females in our study received more contact and grooming from other harem females than from the male. Interactions involving contact, proximity and grooming within the harem were relatively symmetrical, as the amount of affiliation initiated by the focal females with both harem male and females was generally positively correlated with the amount of affiliation received from these individuals. The presence and number of female relatives within the harem did not seem to affect the exchange of affiliation or agonism between harem females. However, because only 3 harems in our study group contained female relatives, these results should be considered as preliminary. A more comprehensive understanding of the social dynamics within the harems would require studies with larger sample sizes and accurate information on the process of harem formation, changes in harem composition over time and female dominance ranks within the harem.

Although kinship was not a good predictor of female social interactions within the harem, it did predict variation in female affiliative interactions, particularly contact and grooming, with females outside the harem. Among our focal females, those who had more female relatives outside their harem initiated contact and grooming with nonharem females more than those with fewer nonharem relatives. Therefore, having female relatives in other harems may facilitate the exchange of affiliative interactions between harems. Similar affiliative interactions between females of different harems have also been observed in wild hamadryas baboons, although the extent to which they depended on kinship was unknown [Swedell, 2002a]. Social ties between females of different harems might be associated with relationships between their harem males, and with the formation of aggregations of harems similar to the clans observed in hamadryas baboons [Colmenares, 1992; Colmenares et al., 2006]. Clearly, we need to know more about the process of harem formation in wild Guinea baboons and how different harems are distributed in space to gain a full understanding of female relationships across harems and the formation of aggregations between harems.

Overall, the mating and social relationships of captive Guinea baboons share some similarities as well as differences with those of both hamadryas and gelada baboons. In all 3 species, mating and affiliation are concentrated in one-male units or harems, and the harem males are the focus of the females' attention and affiliation. Unlike in hamadryas baboons, in Guinea baboons proximity between harem members is maintained by frequent approaches by both males and females and not by male coercion. Therefore, male-female relationships in Guinea baboons may be more similar to those of geladas than to those of hamadryas baboons. On the other hand, social relationships between females within the same harem do not appear to be as dependent on kinship as in gelada baboons. These comparisons are only tentative because Guinea baboons have so far been mostly studied in captivity and because recent studies of new wild populations of gelada and hamadryas baboons have suggested that the social organization of these species is more variable than previously thought [Mori et al., 1999; Swedell, 2002a, 2002b]. More field studies of these 3 spe-

cies are needed to fully understand the similarities and differences in their mating system and social organization and explain them on the basis of their phylogenetic history and ecological adaptations.

Acknowledgments

The study was supported by intramural funds provided by the University of Chicago. We thank Melinda Pruett-Jones and all the staff of the Primate Department at Brookfield Zoo for providing helpful information about the study subjects and facilitating data collection.

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