CHAPTER FIVE

The Social and Ecological Flexibility of Guinea Baboons: Implications for Guinea Baboon Social Organization and Male Strategies

Anh Galat-Luong, Gérard Galat, and Suzanne Hagell

CHAPTER SUMMARY

The social organization and behavioral ecology of Guinea baboons is poorly understood compared to other baboon taxa. Most data contributing to our current knowledge of their behavior come from either very short field studies or captive populations. In this chapter, we attempt to augment the knowledge base of Guinea baboon behavior with data from a wild population of Guinea baboons inhabiting the Niokolo Koba National Park in Senegal.

Anh Galat-Luong • **Gerard Galat** • UR 136 Aires protégées, Institut de Recherche pour le Développement (IRD), France **Suzanne Hagell** • City University of New York and the New York Consortium in Evolutionary Primatology, New York, NY, USA

Our results indicate that Guinea baboons have adapted to a wide range of habitats with many different climates and that they vary in their social structure over time depending on habitat and season. Apparently, Guinea baboons have a multilevel social structure that is superficially similar to that seen in hamadryas baboons. The basic social group is the one-male unit, but when necessary these small groups aggregate into successively larger groups. This may occur through a combination of female flexibility and male–male tolerance and cooperation. Fission and fusion of groups during the day are components of foraging and antipredation strategies. Seasonal changes are also possible, as the number of individuals in each of the intermediate group structures is flexible as well. In this way Guinea baboons optimize their group size given their highly variable habitat without placing undue demands on individual social time budgets and risking permanent fragmentation of the one-male unit. It seems likely that Guinea baboon social organization has evolved independently into a multilevel structure that is different from both hamadryas baboons and other savanna baboons. Moreover, Guinea baboons are unique in their response to the demands of the diversity of West African habitats.

1. INTRODUCTION

The Guinea baboon of West Africa, *Papio hamadryas papio,* is both the least studied and poorly understood of the five major subspecies of *P. hamadryas* (Henzi and Barrett, 2003). Although their total distribution area is small, ca. 250,000 km^2, Guinea baboons have a wide north–south spread (Figure 1), and, as a consequence, they inhabit a wide range of habitats with many different climates. These include sahelian steppe in Mauritania, soudanian shrubby savannas in Senegal and Mali, subguinean mosaic woodlands in Senegal, and secondary high forest in Guinea. They live at sea level in the mangrove forests of Senegal as well as at altitudes of more than 1,000 m in the foothills of the Fouta Djalon mountains of Guinea. The annual rainfall of Guinea baboon habitats varies from less than 200 mm in Mauritania to more than 1,400 mm in the south of their range in Guinea, and the mean daily maximum temperature ranges from ca. 20 to 50°C. Unfortunately, despite being the third most abundant large mammal in the Mafou protected area of the Haut Niger National Park in Guinea (Brugière et al., 2002), several recent surveys have indicated that Guinea baboon distribution overall has declined in recent years (Galat et al., 2002; Galat-Luong and Galat, 2003a).

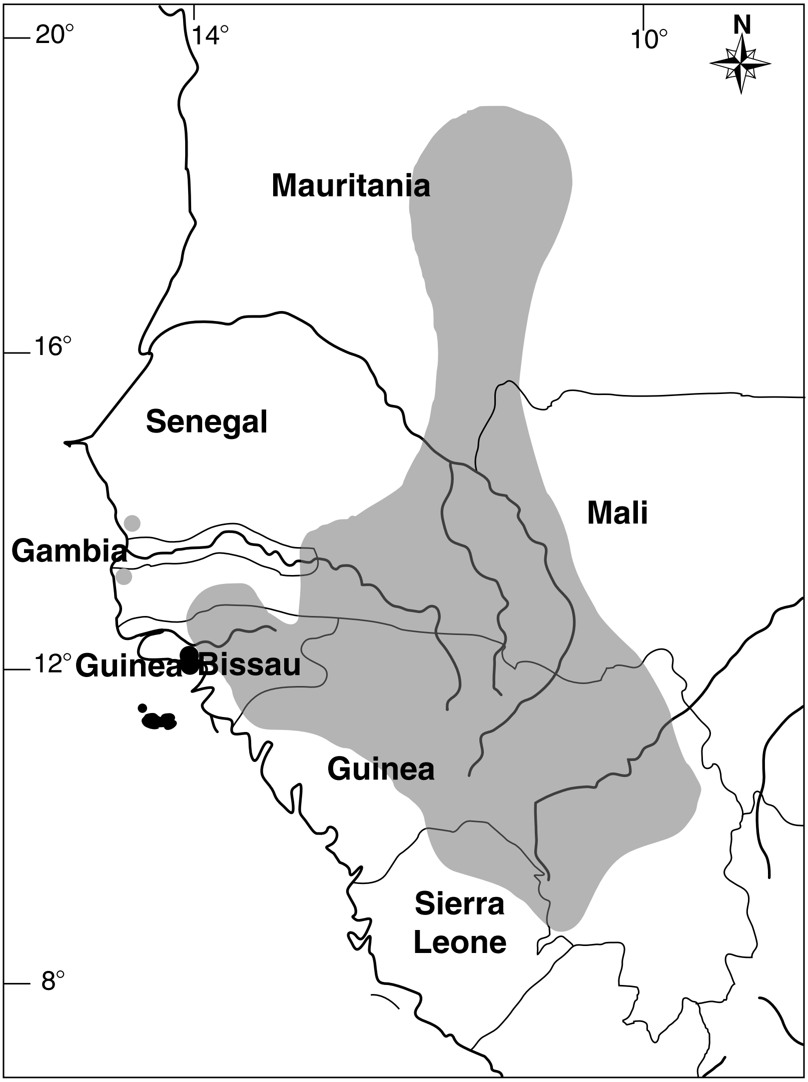

Figure 1. Distribution of the Guinea baboon.

How the social organization and mating system of Guinea baboons compares to that of other baboon subspecies is still somewhat unclear. Olive baboons (*Papio h. anubis*), the immediately neighboring baboon population to Guinea baboons, exemplify the social organization common to most other *Papio* subspecies: multimale and multifemale groups in which females are philopatric. In these societies, social and mating behavior is relatively unstructured and indiscriminate among group members. Hamadryas baboons (*Papio h. hamadryas*), on the other hand, are unique among *Papio* baboons in having a highly structured, multilevel social system based around individual one-male units (OMUs) in which females are forcibly herded into permanent consortships with a leader male. The mating strategy of hamadryas males would seem to be to maintain continuous reproductive access to females by controlling social interactions throughout their reproductive cycle. The strategies of females in hamadryas baboon groups have been less discussed, but it seems that females may also benefit from associating with a single protective male (see Beehner and Bergman, this volume; Swedell and Saunders, this volume; Swedell, 2006). Previous studies suggest that Guinea baboons lie somewhere between these two extremes, with a social system that is somewhat intermediate between that of hamadryas and olive baboons (Boese, 1973, 1975).

Most data concerning Guinea baboon behavior and ecology come from one location, the Niokolo Koba National Park in Senegal (e.g., Dekeyser, 1956; Fady, 1972; Dunbar and Nathan, 1972; Boese, 1973; Sharman, 1981; Anderson and McGrew, 1984). Interestingly, although all these authors collected data at the same location, they disagree about the social structure and social organization of these animals. Both Anderson and McGrew (1984) and Dunbar and Nathan (1972) observed sleeping aggregations of Guinea baboons and reported OMU-like subgroupings, but they also witnessed a degree of female flexibility in social relationships not seen in hamadryas. Both of these sets of authors concluded that the Guinea social system more closely resembles olive than hamadryas baboons.

Boese (1973, 1975), who conducted by far the longest study of Guinea baboons, also saw females interacting more freely than in hamadryas, but he observed permanent one-male subgroups, strong male–female bonds, and herding behavior as well. Boese concluded from his observations that Guinea baboons have an OMU system that is intermediate between olive and hamadryas baboon social organization. Boese suggested that male Guinea baboons maintain sexual exclusivity with particular females but are more tolerant of extrasubgroup interactions than hamadryas males. Close social bonds between females and males, as in hamadryas, were attributed to a habitat in which female and immature animals periodically require male protection

(Boese, 1975). Boese's conclusions, however, were drawn mainly from his observations of Guinea baboons in captivity at the Brookfield Zoo in Chicago. Captivity has the potential to enhance aggressive behavior, strengthen dominance hierarchies, and allow the spread of idiosyncratic behaviors within groups, hence observations of zoo populations should be corroborated by observations of wild populations as well.

In this chapter, we report original data collected at the Niokolo Koba National Park in Senegal and compare our results to other studies of Guinea baboons as well as other baboon subspecies and sympatric cercopithecines. We attempt to describe the current state of knowledge concerning Guinea baboon ecology and social organization, and draw some general conclusions about the origins of Guinea baboon social organization and its relationship to male social and mating strategies.

2. METHODS

2.1. Ecology

Data were collected by Galat-Luong and Galat at the Niokolo Koba National Park during surveys of large mammals conducted in Senegal and Guinea between 1975 and 2001. Using the line-transect method (and Distance software from Laake et al., 1996), we estimated the density of Guinea baboons and compared the results of 1990–1993 censuses with those from 1994 to 1998 to estimate changes in Guinea baboon abundance over time. We also recorded the habitat in which the animals were found: shrubby savanna, arboreal savanna, forest, or open grassland, and additionally described the area as "unburned," "recently burned," or "burned with secondary grass growth." "Recently burned" areas were covered with ashes, with no visible green grasses or leaves. "Burned with secondary grass growth," which replaces "recently burned" areas in 1–10 days, refers to areas in which ash was accompanied by fresh, recently grown grasses. Visibility conditions in these two types of areas are similar and better than in unburned areas. Use of a particular type of area was determined by measuring the percentage of encounters in each area. As the absolute area of each habitat has not been determined and visibility varies for each of these habitats, our determination of "preference" for particular habitats is valid only in comparison with data collected on other species during this study.

2.2. Social Structure, Organization, and Behavior

The number of instantaneously visible individuals was counted during each group encounter and used as a comparative index of group sizes. This index is sensitive to variations in visibility and it is thus mainly used for the same site and for the same period of the year (mid-February). Age/sex classes were based on Boese (1973) as well as the authors' own experience.

Time budgets of one population of baboons in the park were estimated from hourly scan samples of individuals (ca. 205 observation hours). These observations were made when the baboons were highly visible at the transition period between the dry and rainy seasons in May and June 1997, when the groups frequented the same water pool.

The authors also opportunistically recorded social interactions among adult baboons (37 observation hours) focusing on interactions related to social organization, i.e., affiliative and agonistic behavior as well as submissive/dominant interactions (Table 1). These behaviors were defined as in Boese (1973, 1975). For example, a male "prance–rump–push" was recorded when a male pushed a female using his rump, a behavior that occurred as part of the "prance" stereotypical display described by Boese (1975).

3. RESULTS

3.1. Ecology

The results of our analysis of habitat use at Niokolo Koba are very similar to those of Sharman (1981). Guinea baboons at Niokolo Koba spent about 50 percent of their observed time in shrubby savanna, one-third in tree-savanna, and the balance in forest or open grassland (Figure 2). In the savanna, baboons were found most often in recently burned areas (56 percent of encounters, N=333) and were encountered less often in unburned areas (25 percent) or in burned areas with secondary grass growth (19 percent). As other large mammals did not show the same preferences, it is unlikely that this result reflects a visibility bias. Grimm's bush duiker (*Sylvicapra grimmia*), for example, was observed to prefer areas with secondary grass growth, whereas the red-flanked duiker (*Cephalophus rufilatus*) did not. Among the other sympatric primates, the green monkey (*Cercopithecus (aethiops) sabaeus*) showed the same preferences as the Guinea baboons for recently burned land, whereas the patas monkeys (*Erythrocebus patas*) did not. Patas were found

Table 1. List of behavioral interactions recorded

Friendly/submissive	Agonistic/dominant	Herding/corralling
Approach (go and sit nearby another animal)	Fight	Adult male leads OMU
Present (lateral to rear presenting)	Chase	Adult male leads group
Standing Present (abdominal to inguinal presenting, with or without hands on shoulder or head of receiver; usually, the receiver sniffs the abdominal or inguinal area of the initiator)	Kick	Group of adult males leads group
Groom	Run Away	Corral (change direction, accelerate using shaking, jumping, prancing, or running)
Solicit groom	Social Mount	Adult male recruit
Head lunge (with or without look away)	Solicit social mount	Follow adult male
Prance–rump–push	Prance and supplant	Shrieking recruit
Wait	Supplant	
	Sexual	Male Maternal Behavior
Embrace	Sexual mount	Adult male manipulates infant
Hold	Sexual mount and sit	Adult male kidnaps infant with ventral carry
Muzzle	Solicit sexual mount	
Sniff	Adult female dart (withdraw after sexual mount)	
	Adult female sniffs male genital area	
	Masturbation	

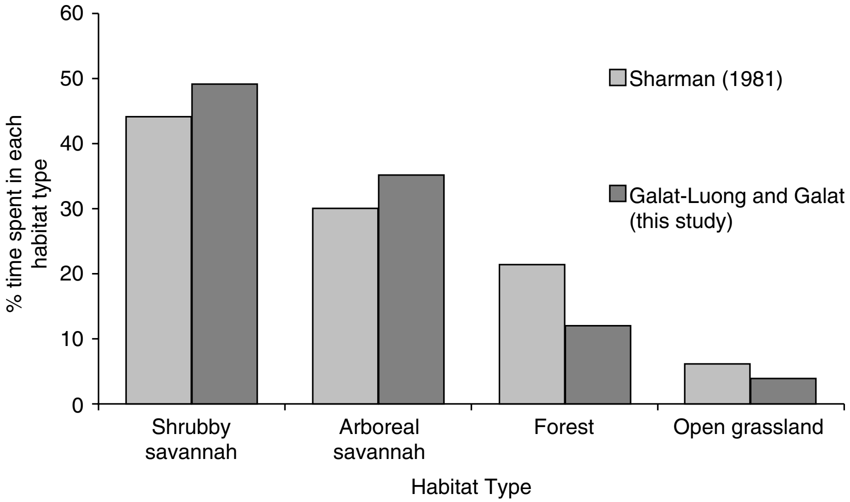

Figure 2. Use of habitat types by Guinea baboons in the Niokolo Koba National Park.

most commonly in areas of secondary grass growth (58 percent, *N* = 107). Green monkeys were encountered on 56 percent of occasions in recently burned savanna, 26 percent in unburned areas, and 18 percent in burned areas with second grass growth vegetation (*N* = 237).

Predation risk at Niokolo Koba is high, and the hunting of Guinea baboons by lions (*Panthera leo*) in particular has increased since 1994 (Galat-Luong and Galat, unpublished data). During this study, an attack by a spotted hyena (*Crocuta crocuta*) was observed as well as the barking and shrieking of baboons when lions were close by. On one occasion, a troop of green monkeys was observed to direct alarm calls at a hyena, which then ran away. The baboons, however, were never observed to mob predators in this way.

3.2. Social Structure, Organization, and Behavior

The variation in size of the Guinea baboon population in the Niokolo Koba National Park is shown in Figure 3. Observations made during this study point to a multilevel social structure in Guinea baboons similar to that described by Kummer (1968) for hamadryas baboons, in which four hierarchical levels can be distinguished. The smallest subunits, and basic social groups, were composed of 8–10 individuals and resembled hamadryas OMUs. These subgroups were most obvious during feeding, foraging, and

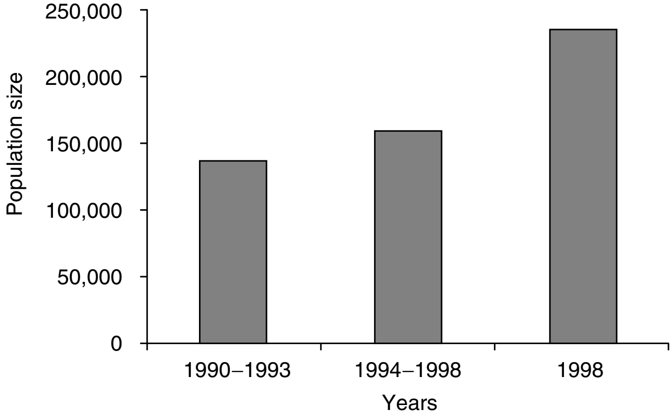

Figure 3. Population size changes of Guinea baboons in the Niokolo Koba National Park, Senegal.

resting during the day. When resting, an adult male was frequently in the center of the group. When moving, each OMU was led by an adult male. These OMU-like groups were visibly (spatially) distinct from temporary females or immature parties.

OMUs joined into larger, second-level subgroups when beginning to move or when sleeping at night. The mean size of these second-level subgroups was 19 individuals (5–65; $N = 45$). At night, the second-level subgroups slept either spatially separated from or together with other second-level subgroups. During longer periods of movement, second-level groups were still spatially distinguishable as they walked in long columns with other second-level groups. Several of these second-level groups comprised larger, third-level groups. At Niokolo Koba, the mean size of the third-level group was 62 (22–249; $N = 111$). During a survey outside the Park in 1988, we observed a mean third-level group size of 72 individuals (24–200; $N = 14$). Several third-level groups were observed to share the same sleeping site, forming a fourth-level group. Occasionally, subgroups of females and immatures as well as individual juveniles, adult males and females were seen moving through these larger groups. The number of individuals within groups varied from year to year as well as by time of day.

Time budgets do not have absolute values here and comparisons are limited to the studied population at the waterhole. The Guinea baboons spent more time feeding at the beginning of the rainy season than at the end of the

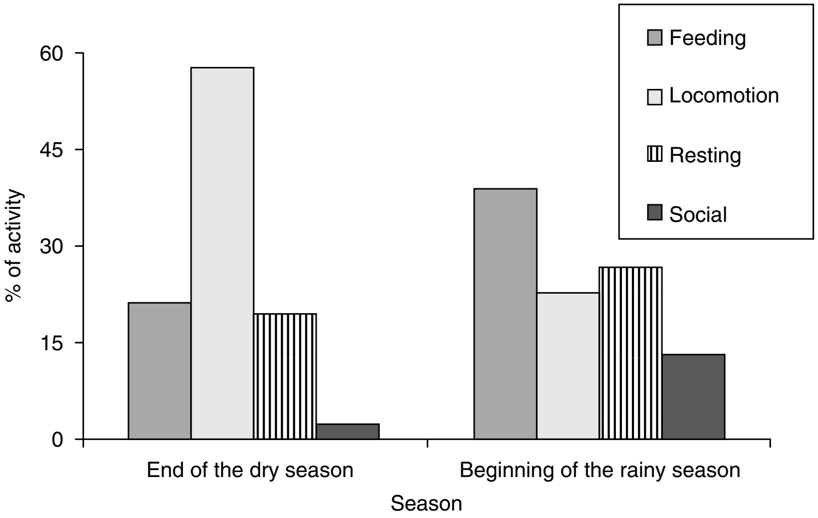

Figure 4. Time budgets of Guinea baboons at a waterhole in the Niokolo Koba National Park in May and June 1997.

dry season (Figure 4). The transition between seasons is marked by a change in the distribution and density of grasses, which are widely available, high and dense during the rainy season and reduced and restricted to water pools during the dry season. As grasses became widely available, Guinea baboons were observed to decrease their time spent in locomotion and to increase their social time. Time spent resting did not change during the observation period.

The social behaviors observed in this study were classified as friendly/submissive (e.g., approach, groom), agonistic/dominant, herding/corralling, male maternal behavior, or sexual interactions (Table 1). The frequency of interactions among adults (Table 2) shows a high level of male tolerance. Only three instances of aggressive chasing or fighting were observed during the study, and most agonistic behavior consisted of dominance interactions (e.g., mounts, supplants). Although grooming appeared to be evenly distributed among adults of both sexes, males gave and received most other friendly interactions in the group. Males initiated friendly contact with both males and females equally, and initiated most of the friendly contacts with other males as well. Males initiated copulation only slightly more often than females did. Males were more often affiliative than agonistic with other males.

Herding with violent neck-biting behavior, typical of hamadryas baboons (e.g., Kummer, 1968) and described in Guinea baboons by Boese (1975), was not observed in this study. All kinds of individuals were seen to move

Table 2. Adult social interactions. Number of interactions recorded in 37 hr of observation

Receiver/initiator	Adult female	Adult male	Total	Adult female	Adult male	Total
Friendly/submissive				Presenting interactions		
Adult Females	3	21	24	1	4	5
Adult males	17	18	35	2	5	7
Total	20	39	59	3	9	12
Agonistic/dominant				Approach followed by "contact"		
Adult females	1		1		4	4
Adult males	6	19	25	7	16	23
Total	7	19	26	7	20	27
Sexual interactions				Solicitation interactions		
Adult females		9	9	2	4	6
Adult males	13		13	5	6	11
Total	13	9	22	7	10	17
Grooming interactions						
Adult females	1	9	10			
Adult males	6	2	8			
Total	7	11	18			

through subgroups while foraging. Males were, however, observed to control group movements with a behavior that we describe as "corralling," that is, by running to speed the progression of the group and by shaking, jumping, and prancing to change the direction of group movement. Adult males were observed leading OMUs (*N* = 3 occurrences) and larger groups (*N* = 3) as well as corralling a larger group (*N* = 2). Three males led a larger group together once and several males corralled a large group together once. Adult males were also observed to wait for other individuals while assuming vigilance when at the edge of an exposed location. Subgroups were observed to wait for alternate access to a restricted water source.

Specific behaviors observed included adult males presenting to a juvenile male as well as juveniles and subadults presenting to adult males. Adult males were also seen in contact with nonadults, both giving and receiving grooming. Adult males also handled infants (*N* = 3), and on one occasion a male kidnapped an infant, carrying it ventrally. An adult female was observed to carry a deceased infant for 3 days (cause of death unknown).

Postcopulatory behaviors included males and females sitting together (*N* = 2), females running away (*N* = 2), or a resumption of their previous activity, e.g., foraging or moving ($N = 11$). On two occasions a male was unsuccessful at soliciting copulation when the female was carrying an infant ventrally. Adult female solicitations for copulation were successful twice and unsuccessful twice.

If we analyze our data with reference to the "obedience" test used by Nagel (1971) in his comparative study of olive and hamadryas baboons, we rarely observed males and females to look behind at an individual while walking away from them following a period of contact (i.e., in order to check if this individual is actually following). This did occur, though, if a supplant seemed likely to occur, such as when moving to a water pool to drink.

4. DISCUSSION

The data presented here demonstrate the opportunistic way in which Guinea baboons use their habitats, changing their diet and time budgets in response to seasonally changing resources. We believe this to be a factor behind the fact that Guinea baboon populations in the Niokolo Koba Park have not declined despite the decrease in population size of most other large mammals in the park (Galat-Luong and Galat, 2003a,b). Another factor behind their success may be that the baboons are not hunted, while ungulates are. Guinea baboons, however, as shown by the 1998 outburst of reproductive success (Figure 3), also appear to show a fast reactivity to fluctuating environmental conditions, which may indicate an adaptation for ecological flexibility. This coincides with the flexibility seen in their social organization.

While we cannot say anything yet about the stability of Guinea baboon social units through time or the pattern of sex-biased dispersal, we can draw some parallels between Guinea baboon social structure and that of hamadryas baboons. Both subspecies are characterized by multiple levels of social structure that fragment and coalesce depending on ecological conditions. Additionally, in both subspecies the smallest social unit consists of one adult male and several females. Boese (1973) suggested that the Guinea baboon social structure represents an evolutionary precursor to the more rigid multilevel social structure seen in hamadryas. Sharman (1981) suggested, however, that Guinea baboon OMUs likely represent matrilineal kin groups rather than the male-policed harems found in hamadryas baboons and that the two subspecies are thus only superficially comparable. We would suggest that the two systems are indeed *not* homologous and that the use of Kummer's terminology for hamadryas baboons—i.e., harem, clan, band, and troop—may thus not be appropriate.

If Guinea baboons do represent a social organization intermediate between the relaxed, multimale societies of olive baboons and the multileveled structure of hamadryas, then this would accord nicely with the provisional findings of Jolly and Phillips-Conroy (this volume) in which testis size in captive Guinea baboons was found to be intermediate between that of hamadryas and olive baboons. Jolly and Phillips-Conroy's findings would suggest that Guinea baboons have a mating system that is less polyandrous than olive baboons but more so than hamadryas, which would make sense given a social system that, while organized around OMUs, also includes a greater degree of female flexibility than in hamadryas society.

Though limited, our data seem to confirm the suggestion by Boese (1975) that the multileveled system seen in Guinea and hamadryas baboons is rooted in male–male tolerance. Such tolerance results in the fusion of OMUs into large troops when predation pressure is highest, particularly when traveling through more risky areas in the terrain. This suggests that leader males may coordinate their units so that each OMU in the troop receives protective benefits. At Niokolo Koba, Guinea baboons are exposed to lions concealed in the high grasses of the savanna, as well as to leopards when in gallery forests along rivers, and it is when traveling in these areas that Guinea baboons are observed to form large columns. Additionally, Boese (1975) has suggested that adult males permit the presence of subadult males in OMUs so that they may assist in vigilance. In this way, the OMU structure that Guinea baboons form during the day allows for a reduction in food competition as well as moderate protection from predation. Tolerance of nonadult males within an OMU has also been described by Kummer (1968) and Swedell (2006) for hamadryas baboons.

Dunbar (1992, 1994) proposed that the mean size of social groups is influenced by the social budget allowed under local ecological conditions. According to this model, as group size increases, so does the burden on individual group members to balance vigilance and time spent feeding with time for socializing. At a certain group size, these individuals are no longer able to maintain cohesiveness and the group will fragment. Guinea baboons represent another strategy, in which group structure can be adjusted with a given season and time of day to optimize the number of individuals. Leader males may retain semiexclusive access to mates, while cooperating with subadult males within the group for assistance with vigilance. Females and immatures (including the subadult males) benefit from forming strong associations with a male who will protect them from predation and extragroup harassment. Both females and subadult males are also provided a certain degree of freedom to interact outside the group.

Seasonal flexibility can be shown by comparing group counts at different times of the year. Sharman (1981) recorded that the size of the troop (third-level structure) changed from 50-90 individuals during the dry season to 135–250 during the rainy season. This may reflect an adjustment of group size to food availability, which is highest in the rainy season. Heavy rainfalls occurred in 1997, 2.4 times more than during the preceding years, and in 1998 the Guinea baboons reacted with an outburst of reproductive success (Figure 3) that has subsequently caused crop depredations (Galat-Luong and Galat, 2003a).

Galat and Galat-Luong surveyed group sizes of green monkeys along the same north–south gradient in Senegal, and these monkeys show interesting parallels to Guinea baboons. Green monkeys were observed to live in small territorial groups of 8–33 individuals when in relatively species-rich areas of high and constant vegetal diversity (Galat and Galat-Luong, 1976). In the more arid areas of northern Senegal, the green monkeys lived in larger groups of up to 174 individuals with little territorial behavior (Galat and Galat-Luong, 1977). In this habitat, vegetal diversity is severely impoverished, deciduous trees have disappeared, and *Acacia nilotica* is the dominant species. When the rainy season approached, OMU-like subgroups formed and males showed a tendency to herd females; half of these females were pregnant or carrying newborn infants. As with the Guinea baboons, the OMUs were most visible when foraging or resting during midday in trees. At twilight these OMUs aggregated into large clumps for sleeping. Coincidentally, Guinea baboons are no longer found in the northerly area of Senegal where green monkeys also form these larger aggregates.

The Niokolo Koba National Park is located at the center of the Guinea baboons' north–south range. Because the park encompasses several habitat types, the environment permits adaptations to both desert and forest habitats. We would predict that in more northerly populations, where resources are more scattered and unpredictable, Guinea baboons would show more conspicuous OMUs and larger third-level aggregations. In the south, on the other hand, where the forest is denser, the populations should exhibit less conspicuous OMUs as well as larger second-level groups and age-graded units as seen in green monkeys in these areas. In green monkeys, OMUs and second-level groupings may be more efficient for foraging in separate trees, whereas larger groups would not be able to maintain cohesiveness due to restricted visibility. In fact, Brugière et al. (2002) reported the mean number of instantaneously visible individuals of Guinea baboons (which we think to be mainly tied to the size of the second-level groups) in the Haut Niger National Park, approximately 300 km south of Niokolo Koba, to be 27 (*N*=3), which is much greater than at Niokolo Koba (6–15), though the figure should be biased toward a lower value as visibility in more dense vegetation is likely reduced.

In conclusion, the social organization of Guinea baboons can be viewed as a highly adaptable social network capable of responding quickly to ecological fluctuations. Although this multilevel social organization is superficially similar to that seen in hamadryas baboons, most of the behavioral elements we have observed suggest that it may not be homologous. The fusion and coordination of separate subgroups is only possible through the tolerant and affiliative behavior of males. Some males receive submissive behaviors from individuals of different OMUs. Some males are able to lead small OMUs as well as larger groups. Males also cooperate in the leading and corralling of these groups. In this study, males were not observed to herd females in their OMU in the manner seen in hamadryas baboons, and female movements through groups appeared to be less rigid. Based on the limited observations reported so far, Guinea baboons do not appear to possess the same restrictive, harem structure seen in hamadryas baboons. Rather, they are characterized by a multilevel system that, while it includes one-male harem-like groupings, also includes a greater degree of female flexibility than seen in hamadryas. It seems more likely that Guinea social organization has evolved independently toward a fission–fusion structure that is different from both hamadryas baboons and other savanna baboons and that they are unique in their response to the demands of the diversity of the West African habitats they occupy.

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REFERENCES

Anderson, J. R. and McGrew, W. C., 1984, Guinea baboons at a sleeping site, *Am. J. Primatol.* **6**:1–14.

Boese, G. K., 1973, Behavior and social organization of the Guinea baboon *(Papio papio*). Ph.D. Dissertation, Johns Hopkins University.

Boese, G. K., 1975, Social behavior and ecological considerations of West African baboons, in: R. H. Tuttle, ed., *Socioecology and Psychology of Primates*, Mouton, The Hague, pp. 205–230.

Brugière, D., Dia, M., Magassouba, B., Diakité, S., Gbansara, M., Mamy, M., and Saliou, B., 2002, *Dénombrement des Moyens et Grands Mammifères de la Zone Intégralement Protégée Mafou du Parc National du Haut-Niger, Guinée*, Unpublished report to AGIR, Conakry.

Dekeyser, P. L., 1956, Mammifères, *Mémoires de l'Institut Français d'Afrique Noire.* **48**:35–79.

Dunbar, R. I. M. D., 1992, Time: A hidden constraint on the behavioral ecology of baboons, *Behav. Ecol. Sociobiol.* **31**:35–49.

Dunbar, R. I. M., 1994, Ecological constraints on group size in baboons, in: *Animal Societies: Individuals, Interactions, and Social Organization*, P. Jarman and A. Rossiter, eds., Holt, New York, pp. 253–292.

Dunbar, R. I. M. and Nathan, M. F., 1972, Social organization of the Guinea baboon, *Papio papio*, *Folia Primatol.* **17**:321–334.

Fady, J. C., 1972, Absence de coopération de type instrumental en milieu naturel chez *Papio papio*, *Behaviour* **43**:157–164.

Galat, G. and Galat-Luong, A., 1976, La colonisation de la mangrove par *Cercopithecus aethiops sabaeus* au Senegal, *Rev. Ecol. Terre Vie* **30**:3–30.

Galat, G. and Galat-Luong, A., 1977, Démographie et régime alimentaire d'une troupe de *Cercopithecus aethiops sabaeus* en habitat marginal au nord Senegal, *Rev. Ecol. Terre Vie* **31**:557–577.

Galat, G., Galat-Luong, A., and Keita, Y., 2002, Régression de la Distribution et Statut Actuel du Babouin, *Papio papio*, en Limite d'Aire de Répartition au Sénégal, *Afr. Primates* **4**:69–70.

Galat-Luong, A. and Galat, G., 2003a, La ressource grande faune terrestre du Sénégal oriental: ses potentialités, ses contraintes, in: *Potentialités, contraintes et systèmes d'exploitation au Sénégal Oriental et en Haute Casamance*, UCAD–IRD–DDR, eds., CD-ROM, Dakar.

Galat-Luong, A. and Galat, G., 2003b, Social and ecological flexibility in Guinea baboons as an adaptation to unpredictable habitats, *Am. J. Phys. Anthropol. Suppl.* **36**:98.

Henzi, P. and Barrett, L., 2003, Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations, *Evol. Anthropol.* **12**:217–230.

Kummer, H., 1968, *Social Organization of Hamadryas Baboons: A Field Study*, University of Chicago Press, Chicago.

Laake, J. L., Buckland, S. T., Anderson, D. R., and Burnham, K. P., 1996, *DISTANCE 2.2*, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

Nagel, U., 1971, Social organization in a baboon hybrid zone, *Proc. 3rd Int. Cong. Primatol. Zurich* **3**:48–57.

Sharman, M. J., 1981, Feeding, ranging, and social behavior of the Guinea baboon. Ph.D. Dissertation, University of St. Andrews.

Swedell, L., 2006, *Strategies of Sex and Survival in Hamadryas Baboons: Through a Female Lens*, Prentice Hall, Upper Saddle River, NJ.