

## **Group Composition of Guinea Baboons (*Papio papio*) at a Water Place Suggests a Fluid Social Organization**

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**Abstract** Baboon social systems are among the most studied in primates. Solid knowledge of the hamadryas and savannah baboon systems has accumulated, leading to a dichotomic view of baboon social systems. Hamadryas baboons live in multilayered troops based on 1-male units whereas savannah baboons live in multimale multifemale groups based on a network of related females. Less attention has been paid to their West African congeners, the Guinea baboons, *Papio papio*. To fill this gap, in 2007 we initiated a long-term study of a baboon troop ranging in the Niokolo Koba National Park in southeastern Senegal. Earlier studies suggested a tendency for a multilayered social system in Guinea baboons, similar to the hamadryas baboon organization. Therefore, as a first approach to analyzing variability in party size and composition, we observed members of the troop crossing an open area from a fixed point for 3 mo during the dry and wet seasons. We counted individuals and recorded changes in composition of both arriving and departing parties. Party size and composition were highly variable on both a daily

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and a seasonal basis; 45.9% of the arriving parties changed in composition while crossing the open area, either splitting into smaller parties or fusing into larger ones, suggesting a fluid organization. Our data support the existence of neither a hamadryas baboon-like multilayered social organization nor a stable medium-sized multimale multifemale group as in savannah baboons. In light of our data we may need to revise the dichotomic view of baboon social systems and include space for greater variability of their social systems.

**Keywords** Fixed-point observation · Guinea baboons · *Papio papio* · Social organization

## Introduction

Baboons are among the most extensively studied primate taxa, and data on their ecology and social systems have been used in comparative socio-ecological analyses to assess the variability and plasticity of social systems in closely related primate species (Barrett 2009; Barton 2000; Barton *et al.* 1996; Dunbar 1988; Henzi and Barrett 2005; Kummer 1990, 1995). However, compared to other baboon species, little is known about Guinea baboons (*Papio papio*; Barton 2000; Galat-Luong *et al.* 2006; Henzi and Barrett 2003; Maestripieri *et al.* 2007). Despite several studies, a great deal of inconsistency remains within the scientific literature concerning the social organization and group structure of this species. It is essential to understand better the social organization of Guinea baboons to gain a more complete understanding of the evolutionary history of baboon social systems.

Olive (*Papio anubis*), yellow (*P. cynocephalus*), and chacma baboons (*P. ursinus*), referred to as savannah baboons, live in multimale, multifemale groups (MMUs) of medium size (mean 50 individuals, based on data in Swedell 2011). However, group sizes are variable, mainly due to habitat conditions such as food availability or predation risk (Melnick and Pearl 1987). Savannah baboon groups are usually stable but may split up for short periods (Henzi and Barrett 2003), e.g., when foraging in harsher habitats (Barton *et al.* 1996). Females are predominantly philopatric, and a network of related females comprises the core of the MMU (Barton 2000). Female–female bonds are strongest between close kin, and stable dominance hierarchies exist (Barton 2000; Gouzoules and Gouzoules 1987; Hausfater *et al.* 1982). Females have multiple mating partners (Melnick and Pearl 1987), and males and females form sexual consortships during females' receptive periods (Smuts 1985). These consortships are exclusive pair bonds lasting from several hours up to 6 d, during which most of the matings are performed. In addition, females' intersexual social interactions are focused on only one or a few males with which they may form “friendships” that last beyond phases of sexual receptivity (Barton 2000; Huchard *et al.* 2010; Nguyen *et al.* 2009; Palombit 2009). Adult sex ratios are 1:1.1 (*Papio anubis*; Rowell 1966 [cited in Swedell 2011])–1:3.3 (*P. ursinus*; Hall and DeVore 1965).

In contrast, hamadryas baboons (*Papio hamadryas*) live in a multilayered organization, i.e., smaller social units are nested within larger ones. The basic social entities are stable 1-male, multifemale units (OMUs), consisting of 1 male (Kummer 1968), 1–10 females, and their offspring (for an overview of

multilayered societies including hamadryas baboons see Grueter and Zinner 2004; Stambach 1987). Some OMUs may contain an additional follower male (Kummer 1968). These OMUs are distinguishable through spatial and social segregation (Grueter and Zinner 2004; Kummer 1968; Stambach 1987). Two or three hamadryas OMUs associate, forming the next higher layer, a clan (Abegglen 1984; Schreier and Swedell 2009). Several clans and additional single males form a band, which is a stable and exclusive unit and constitutes the next layer. This layer is thought to be homologous to the multimale units of savannah baboons (Dunbar 1988). Up to 4 bands may form a sleeping unit, the troop (Stambach 1987). Bands often fission into clans or single OMUs when foraging (Kummer 1968). Males within a clan are assumed to be related (Abegglen 1984; Stolba 1979), but so far there is no genetic evidence confirming this assumption. Mean OMU size is *ca.* 7 (range 5–9) individuals, clan size *ca.* 24 (range 20–29), and band size *ca.* 86 (range 40–165) (Hill *et al.* 2008), and troops may contain several hundred (up to 800) individuals (Kummer 1968; Zinner *et al.* 2001). Females leave their natal OMU when sexually mature, but mostly stay within their bands (Sigg *et al.* 1982). Adult sex ratios are similar to those in savannah baboons: 1:1.3 (Swedell 2006)–1:2.9 (Zinner *et al.* 2001).

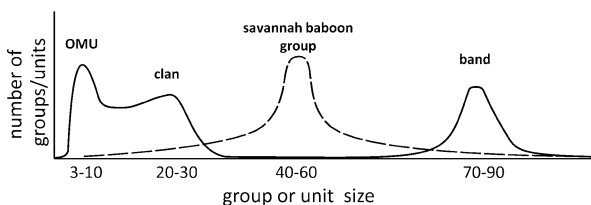
The data available for Guinea baboons suggest that their society differs from other baboon social organizations. Studies of free-ranging Guinea baboons report multimale troops of up to 300 or even more individuals in a multilayered organization (Sharman 1981). Individuals aggregate in these large groups when traveling and at sleeping sites. Foraging and resting seem to take place in smaller groups (Anderson and McGrew 1984; Boese 1973; Dunbar and Nathan 1972; Galat-Luong *et al.* 2006; Sharman 1981). Contradictory suggestions have been made concerning their social organization. Some authors suggest that they are organized in OMUs that aggregate into larger parties, resembling the social organization of hamadryas baboons. For instance, Boese (1973, 1975) observed that the composition of OMUs in a zoo population remained stable over a longer period of time, that female–male bonds are strong, and that males show herding behavior, like hamadryas males. However, he also reported that females interact freely with females of other OMUs and also with other males besides their OMU males; traits that are uncommon in hamadryas baboons (Kummer 1968). Boese also observed OMUs aggregating into larger parties in a field study (Boese 1973). In a more recent study of captive Guinea baboons, Maestripieri *et al.* (2007) observed both mating and social activity taking place within OMUs, and just 1 of 16 sexually active females copulating with >1 male. However, the OMU male threatened “his” females more often than other individuals did and the females did not threaten the male. Again, the researchers observed no typical hamadryas herding behavior, which was also confirmed in a study on free-ranging groups by Galat-Luong and colleagues (2006). Similarly, Dunbar and Nathan (1972) and Anderson and McGrew (1984) describe OMU-like subgroups in free-ranging Guinea baboons, but emphasize that females have more freedom in their social interactions than hamadryas baboon females. Sharman (1981) even observed females copulating with >1 male and, moreover, he reported consortships when females were in estrus, suggesting direct competition among males for receptive females, a trait typically found in savannah baboon multimale societies and not in hamadryas baboons. Boese (1973) suggested

that the social organization of Guinea baboons represents an evolutionary precursor to the more rigid multilayered social organization of hamadryas baboons. Sharman (1981), in contrast, maintained that the male-centered units in Guinea baboons more likely represent maternal kin groups than male-policed harems as in hamadryas baboons, thus possibly resembling the social organization of the geladas (Dunbar 1978, 1983a, b, 1988).

We observed a large troop of Guinea baboons when they crossed an open area. This condition allows for better visibility than previous studies that estimated group size in a forested habitat (Bert *et al.* 1967; Dunbar and Nathan 1972; Galat-Luong *et al.* 2006) and allowed us to obtain more detailed data on group composition. Researchers have used similar fixed-point observation to detect temporal and spatial organization patterns in groups of other nonhabituated primates (*Pan troglodytes*: Itani 1966 [cited in Sugiyama 1968]; *Mandrillus sphinx*: Abernethy *et al.* 2002; *Rhinopithecus bieti*: Zehua *et al.* 2007) and other mammalian taxa, e.g., chital (*Axis axis*: Barrette 1991).

We focus on the question of whether Guinea baboon social organization resembles that of savannah or hamadryas baboons (Fig. 1) and test the following predictions:

- 1) If Guinea baboons constitute a coherent social group of medium size similar to that of savannah baboon bands, we expect a steady flow of complete, discrete groups crossing the open area, with stable group sizes over time. This does not exclude the possibility that we may occasionally observe subunits of this medium-sized group. However, OMUs should rarely occur. Thus we predict a narrow unimodal distribution of group size with only small variation over the observation period.
- 2) If Guinea baboons are organized in a multilayered way, similar to hamadryas baboons, we expect them to either enter or cross the open area as a coherent band of large size, as clans of medium size or as single OMUs. This predicts (a) a bi- or trimodal frequency distribution of party size with maxima for OMU size, possibly clan size and band size (Fig. 1). (b) If subgroups are predominantly organized as OMUs, we expect to find specific spatially or temporally segregated clusters of 1 adult male, possibly subadult followers, and several adult females and their offspring in the same composition throughout all observations. Moreover, (c) if larger subgroups reflect a temporary association of several OMUs a comparison of sex ratios in OMUs and these larger MMUs should reveal no difference (Abernethy *et al.* 2002).



**Fig. 1** Examples of potential distributions of unit or group sizes for (1) a bi- or trimodal distribution similar to a hamadryas-like organization (solid line) where OMUs join up into larger clans and bands, and (2) a unimodal distribution as expected for a savannah baboon organization (dashed line).

## Methods

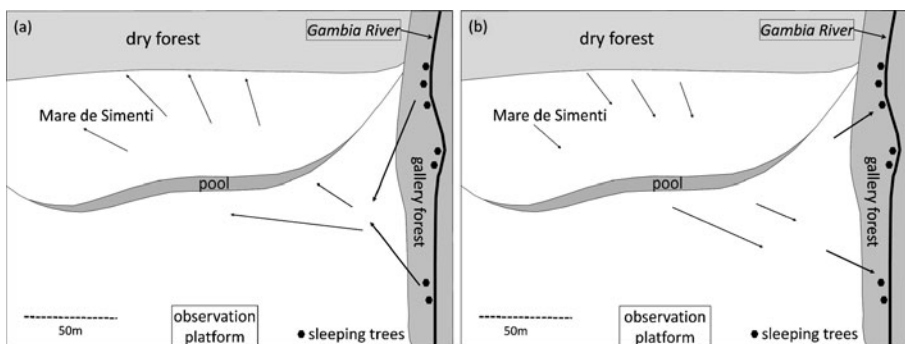
### Study Site

Our focal troop ranges close to the field station of the German Primate Center (DPZ), the Centre de Recherche de Primatologie (CRP) at Simenti (13°01'34"N, 13°17'41"W) in the Niokolo Koba National Park in southeastern Senegal. The climate is highly seasonal with a dry season from November until June. The mean annual rainfall of 1000–1100 mm (Dupuy 1971) is mostly concentrated in the rainy season from July to October. Vegetation varies from grassland savannah, dry and evergreen, to deciduous and palm tree forest as well as gallery forest along the banks of the Gambia River. Galagos (*Galago senegalensis*), green monkeys (*Chlorocebus sabaues*), Western red colobus (*Piliocolobus badius*), and patas monkeys (*Erythrocebus patas*) occur sympatrically with Guinea baboons. Potential predators are lions (*Panthera leo*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*) (Galat-Luong et al. 2006).

We conducted the study at the Mare de Simenti. The Mare is a seasonally flooded plain of ca. 6.6 ha next to the field station, with mainly herbaceous vegetation, surrounded by bushes and palms as well as deciduous forest. It is used by grazers such as warthogs (*Phacochoerus africanus africanus*) and kobs (*Kobus kob kob*). A muddy pool usually remains in the center during the dry season and is used for wallowing by warthogs and for drinking by other animals, including the baboons.

### Data Collection

Observations took place while habituation was still under way. We collected data over 3.5 mo in the dry and rainy seasons. We observed and recorded the arrival and departure of baboons using binoculars (10×40) from an outlook used as a hideout by tourists. Our observation post was situated at the edge of the Mare, between the sleeping site and the forest. The baboons usually crossed the Mare in the morning before foraging in the forest and crossed back again on returning to the sleeping trees (Fig. 2). They occupied an area of short grass at a distance of 30 to ca. 320 m from our observation point. Visibility was unobstructed. Two observers collected data on size and composition of arriving and departing parties independently for 2 wk



**Fig. 2** Movement directions of the baboon troop when **a** leaving the sleeping site in the morning and **b** coming back from foraging in the afternoon. The location of the observation platform is also indicated.

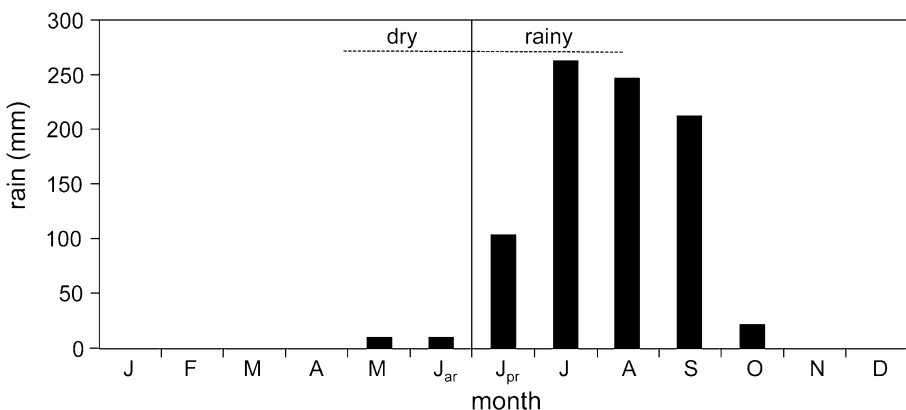
check for concordance, which was 93.5%. For the rest of the observation period the 2 observers collected data alternately.

Next to the Mare the baboons use large trees along the Gambia River as sleeping sites (Fig. 2). We refer to these baboons as a troop, and to any cluster of  $\geq 4$  individuals as a party. We preferred the term party instead of group or subgroup because the term is generally used to describe social entities of fission–fusion societies (Aureli *et al.* 2008). Once we recorded a party comprising 330 individuals in the rainy season leaving the Mare. Our estimation of the total troop size is thus based on this maximum count.

The troop's sleeping site extends over *ca.* 500 m of the Gambia River, and the baboons pass the night resting in tall trees, e.g., *Borassus aethiopicum*, *Ceiba pentandra*, that are difficult to access for predators. In the mornings scattered parties arrived at the Mare. The baboons either crossed the Mare immediately or spent some time in the open field and used the Mare for foraging, drinking, and socializing (median 10 min; range 0–122 min;  $N=163$  of 198 parties entered and left the Mare in the same composition. For the remaining 35 parties the data set was not complete.). They stayed either as 1 party or mingled or later moved on into the forest with other parties. Further, some parties left the sleeping site at the Gambia into other directions without crossing the Mare. In the afternoon, scattered parties returned from foraging in the forest. As in the morning, the baboons spent time on the Mare for foraging, drinking, and socializing before they took off to their sleeping trees. Because of this pattern we hardly ever saw all the *ca.* 330 individuals within 1 session.

We collected data on 78 d from April 30, 2007 to August 12, 2007 when the Mare flooded and baboons were no longer able to cross it. We classed data collected until the first heavy rain (June 16, 2007) as dry season data and data collected thereafter as rainy season data (Fig. 3). We gathered data during 20 morning and 32 afternoon observation sessions in the dry season and 28 morning and 29 afternoon sessions in the wet season (total=109 sessions).

Morning observation sessions started at dawn (between 06:15 h and 07:00 h, depending on sunrise) and lasted until 10:00 h. We resumed our observations



**Fig. 3** Precipitation in 2007. J<sub>ar</sub> = June before first heavy rain; J<sub>pr</sub> = June after first heavy rain. The dashed line marks the observation period in the dry and rainy seasons.

when the baboons started to return to their sleeping site and crossed the Mare in the afternoon (15:00 h–17:00 h). Observations lasted until darkness (18:30 h–19:15 h, depending on the season). Whenever the baboons entered or left our field of view, we recorded their arrival and departure times respectively, direction of movement, party composition (number of males, females, juveniles, and infants), and fission and fusion events. We recorded a fission event when one part of a party left the area while the other part stayed behind, and a fusion event when 2 parties entered the area at different times or from different directions but left the area together at the same time and in the same direction. It was difficult to obtain an exact head count at times, especially when parties were large, dense, or in motion (Sharman, 1981). In such cases, we estimated party size to the nearest 10, e.g., 100–110 individuals; 68 of 366 events with parties >50 individuals, and used the intermediate value in analysis (thus, in the former example we would have taken 105 as party size value). Moreover, we may have missed individuals or counted them twice. Thus the error in estimating exact party size and composition likely increased with party size.

Guinea baboons show a pronounced sexual dimorphism, which makes identification of the adult sexes easy. Males are much larger than females (males on average 21 kg, females 14 kg; Boese 1973) and have a shoulder mantle, which is not as pronounced as in hamadryas baboons, but more developed than in olive baboons. However, distinguishing females from juvenile males was sometimes difficult when the baboons were in greater distance and might have resulted in an over- or underestimation of females and subadult males. However, because this error should apply for all types of clusters in the same magnitude, it should not bias sex-ratio estimations for OMUs and MMUs. We used temporal or spatial criteria, or both, to distinguish one party from another and defined parties as:

- 1) Clusters of  $\geq 4$  individuals if these clusters came from (or left in) the same direction but were separated by an interval of  $\geq 5$  min. 130 of the 132 recorded time gaps between 2 consecutively arriving clusters were  $\geq 5$  min.
- 2) Clusters of  $\geq 4$  individuals if these clusters came from or left in different directions (defined as  $>45^\circ$ ), even if they arrived or left at the same time.

While resting at the Mare, parties were not only spatially separated, with a spatial distance of  $<5$  m among but  $\geq 50$  m between individuals or clusters, but also behaviourally separated from each other, i.e., no interaction between the parties took place (Sharman 1981). This is also valid for newly formed aggregations in cases of fission and fusion taking place on the Mare.

## Data Analysis

We determined the sizes of 496 parties, including 366 parties that entered the observation area (arriving parties). The remaining 130 parties were departing parties that resulted from fission–fusion events on the Mare. To avoid inflating sample size by counting the same party when it arriving, rested in, and left the observation area, we used only data for arriving parties in the analysis. We were able to determine the group composition of 241 of 366 arriving parties, i.e., all individuals within a party could be assigned to an age/sex class.



We explored the impact of time of day on the number of parties arriving and party size with a Mann-Whitney  $U$  test (Statistica 9.0, StatSoft Inc., [www.statsoft.com](http://www.statsoft.com)). We used 1 data point for each party during each observation period, resulting in a sample size of 109. We used a  $t$ -test to compare sex ratios in OMUs and MMUs (Statistica 9.0, StatSoft Inc., [www.statsoft.com](http://www.statsoft.com)). We compared the frequency distributions of party sizes in the rainy and dry seasons with an exact  $\chi^2$  test (SsS 1.0b Rubisoft Software GmbH).

To test whether the observed distribution of party sizes of Guinea baboons is due to a random process of general attraction to a group or whether they form any higher social organization, we fitted the observed distribution with a 0-truncated Poisson distribution and a 0 truncated negative binomial distribution (StataCorp. 2010. Stata Statistical Software: Release 11.1.). We compared models using Akaike's Information Criteria (AICs). The model having the lowest AIC is regarded as a better fit (Akaike 1973), and a difference in AIC of  $>10$  suggests virtually no support for the model with the larger AIC (Burnham and Anderson 2002). If the membership or size of a group does not influence the attraction of an individual to join a group, then the frequency distribution of the group should follow a 0-truncated Poisson distribution (Cohen 1971; Wilson 2000). If individuals join a group because of specific membership or the size of the group, then the frequency distribution should follow a 0-truncated binomial distribution. If this is the case, we can conclude that Guinea baboons form higher social aggregations. Descriptive data are presented as means and standard deviations (SD), median, and IQR or proportions.

## Results

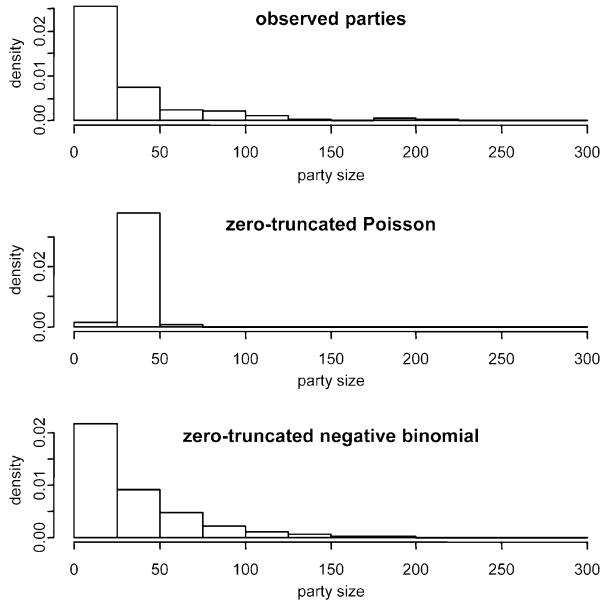
Troop cohesion was rather loose, and the composition of arriving parties was highly variable, both on a daily and on a seasonal basis. In the dry season we observed only 1 arriving party  $>100$  (in that particular case, 125) individuals (0.5% of 191 parties), whereas in the rainy season 13.1% of the parties (23 of 175) comprised  $>100$  individuals.

Using our 2 criteria for different occasions, we identified 212 arriving parties according to our spatial criterion, arriving from different directions, and 132 by our temporal criterion ( $\geq 5$  min lag). Time intervals between arriving parties ranged from 5 to 113 min (median 20 min; IQR 10–30;  $N=131$ ). In 22 of 109 observation sessions, only 1 party passed the observation area, which adds to a total of 366 arriving parties. The average size of arriving parties was 20.0 (median; IQR 11–40; range 4–300). 58.5% (214/366) of all arriving groups comprised 6–25 individuals, while 12.3% (45/366) comprised 40–60 individuals (the equivalent of savannah baboon groups) and 4.9% (18/366), 70–90 individuals (the equivalent of hamadryas bands).

A 0-truncated negative binomial distribution (AIC=3325.3) fitted the distribution of sizes for arriving parties better than a 0-truncated Poisson distribution (AIC=14089.6; Fig. 4), suggesting that party size was not random. The negative binomial dispersion parameter ( $\alpha$ ) of the 0-truncated model was 0.88 (95% CI: 0.75–1.04) and significantly larger than 0 ( $z=12.1$ ,  $p<0.001$ ). This further suggests that there is



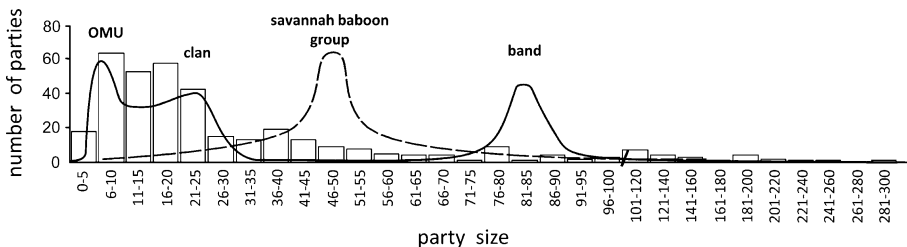
**Fig. 4** Comparison of observed data with 0-truncated Poisson and 0-truncated negative binomial distributions.



overdispersion in the data set and a 0-truncated Poisson model is not appropriate (when the overdispersion parameter is 0 the negative binomial distribution is equivalent to a Poisson distribution.) The observed distribution matched neither the bi- or trimodal distribution expected for hamadryas baboons nor the unimodal distribution expected for savannah baboons (Fig. 5).

**Party Composition and Sex Ratio**

The average party size was 16 individuals (median; IQR 9–23; range 4–90;  $N=241$ ), with a mean of 3.1 adult males (17.1%; SD 2.6; range 0–18;  $N=241$ ). 63 of 241 parties with known composition (26.1%) included only 1 adult male, whereas 175 parties were MMUs (Table I). Three of 241 parties (1.2%) included no adult males.



**Fig. 5** Frequency distribution of party size categories (histogram;  $N=366$  arriving parties) in relation to an expected bi- or trimodal distribution for a hamadryas-like organization (solid line) where OMUs join up into larger clans and bands and a unimodal distribution expected for a savannah baboon organisation (dashed line). The distribution of hamadryas baboon unit sizes is based on data in Hill *et al.* 2008 (summary of 8 different study sites); the distribution for savannah baboons is based on data in Swedell 2011 (summary of 11 *Papio anubis*, 2 *P. cynocephalus*, and 10 *P. ursinus* study sites).

**Table 1** Composition and sex ratio of multimale units (MMU:  $n=175$ ) and 1-male units (OMUs:  $n=63$ )

	Party size	Adult males	Adult females	Adult sex ratio
MMUs				
Mean	23.0	3.8	9.1	1:2.5
SD	15.6	2.6	6.3	1:1.1
Range	4–90	2–18	1–40	1:0.5–1:7.0
OMUs				
Mean	8.8	1.0	3.3	1:3.3
SD	4.1		1.5	1.5
Range	4–24		1–7	1:1.0–1:7.0

A large proportion (65.0%, 52/80) of the small parties ( $\leq 10$  individuals), however, were OMUs. The number of females per male was lower in MMUs than in OMUs (sex ratio: 1:2.5 vs. 1:3.3;  $t=4.35$ ,  $p<0.001$ ,  $N_{\text{MMU}}=175$ ,  $N_{\text{OMU}}=63$ ).

We recorded 2 small all-male units (AMUs, i.e., units of exclusively adult males) containing 3 and 2 adult males, respectively. We also noted 16 solitary males, 15 of which we observed in the dry season. Although we observed some party compositions up to 6 times during our study period, we only once saw a party of the same size and composition twice on 2 consecutive days. The mean time lag between observations of the same party compositions was 25 d (median 13 d; IQR 8–35.6; range 1–86;  $N=78$ ).

### Changes in Party Size by Time of Day and Season

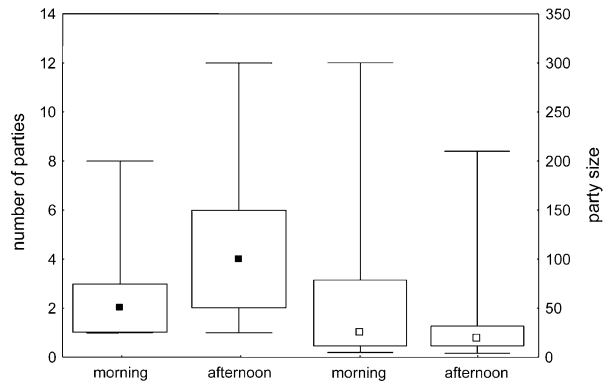
More and smaller parties arrived in the afternoon than in the morning (Fig. 6). In the morning, an average of 2 parties (median; IQR 1–3; range 1–8;  $N=49$ ) arrived at the Mare whereas 4 parties arrived in the afternoon (median; IQR 2–6; range 1–11;  $N=60$ ;  $Z=-3.969$ ;  $p<0.001$ ). Median party size was 25 in the morning (IQR 11.5–78.5; range 5–300;  $N=115$ ) and 19 in the afternoon (IQR 11.5–32; range 4–210;  $N=251$ ;  $Z=3.670$ ;  $p<0.001$ ).

Parties were larger during the rainy season vs. the dry season (Fig. 7;  $\chi^2=205.6$ ,  $df=3$ ,  $p<0.001$ ). Party size was 16 in the dry season (median; IQR: 8.5–24; range 4–125;  $N=191$ ), and 30 in the rainy season (median; IQR 16–58; range 5–300;  $N=175$ ;  $Z=-7.28$ ;  $p<0.001$ ).

### Fission and Fusion

The fate of the parties arriving at the Mare is shown in Fig. 8. 198 parties (54.1%) arrived and left the Mare without any change in size and composition. The average size of these parties was 19 (median; IQR 11–39, range 4–300; Fig. 8a). In the remaining 168 parties we observed fissions, fusions, and fusion–fission by intermingling of parties while the baboons crossed the Mare (Fig. 8b–d).

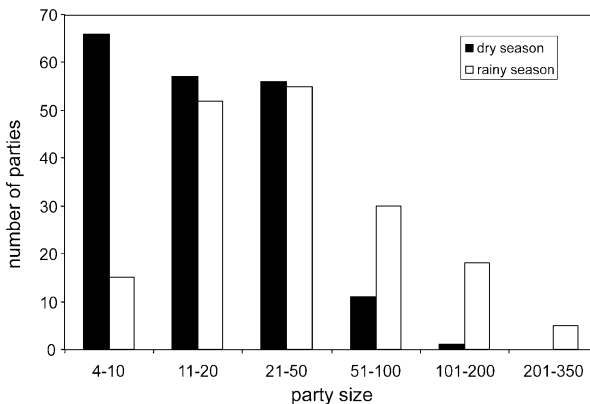
**Fig. 6** Number of parties arriving (black squares) and party size (white squares) according to time of day (morning and afternoon; median, IQR, range).



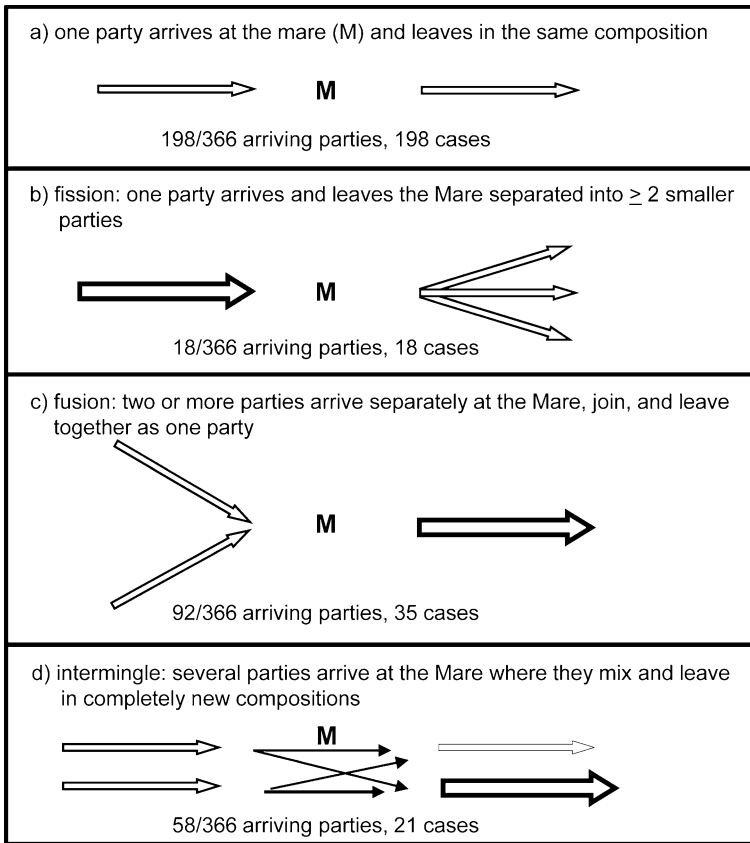
In 18 cases, 1 party arrived and left the Mare split into  $\geq 2$  smaller parties (Fig. 8b). The average size of these parties before splitting was 101 (median; IQR 46.5–151; range 9–220). On average, 2.7 (mean; SD 0.86; range 2–4;  $N=42$ ) parties were formed out of 1 arriving party with an average size of 22 baboons (median; IQR 12.5–37.25; range 4–137).

In 35 cases,  $\geq 2$  parties arrived independently at the Mare, joined, and left together as 1 party (Fig. 8c). The mean number of parties to converge into a single party was 2.8 (mean; SD 1.37; range 2–7;  $N=95$ ) with an average size of 20 individuals each (median; IQR 11–36; range 4–120), whereas the average size of the combined departing parties was 49 individuals (median; IQR 31–108; range 8–330;  $N=38$ ).

In 21 cases, several parties arrived at the Mare, where they mixed and then left as several newly composed parties (Fig. 8d). An average of 2.9 parties (mean; SD 1.59; range 1–6;  $N=58$ ) with an average size of 22 individuals (median; IQR 13.5–38.5; range 4–80) arrived. Those parties split and individuals of several parties mingled and formed new parties. On average 2.8 parties (mean; SD 1.57; range 1–8;  $N=50$ ) of 18 individuals (median; IQR 12–28.5; range 4–240) left.



**Fig. 7** Frequency distribution of party sizes in the dry and rainy seasons ( $N=366$  parties).



**Fig. 8** Fate of parties arriving at the Mare (M). Arrows indicate direction of movement and size of baboon parties. Total number of arriving parties=366.

## Discussion

### Social Organization

The baboons came to the Mare from their various sleeping sites in scattered parties in the morning, and in the afternoon when distinct parties came back from foraging before moving back to their sleeping trees. We therefore only rarely saw the whole troop at the same time. We observed mainly parties of  $\leq 25$  individuals. Aggregations of *ca.* 40–60 and 70–90 individuals, as expected for savannah and hamadryas baboons respectively, were rare, suggesting that the troop most likely did not consist of several stable groups or bands, unlike savannah or hamadryas baboons (Fig. 5). Thus predictions 1 and 2a are not supported by our data. The observed distribution of party sizes was best described by a 0-truncated negative binomial distribution, suggesting that Guinea baboons join a group because they are attracted by its membership and that they do not associate in a random fashion, which would be the case if a 0-truncated Poisson distribution was a better fit (Cohen 1971; Wilson 2000).

Two thirds of the smaller parties ( $\leq 10$  individuals) of known composition contained just 1 adult male and can be regarded as OMUs. We did not repeatedly observe specific

spatially or temporally segregated clusters of 1 adult male, possibly subadult followers, and several adult females and their offspring in the same composition throughout all observations, contradicting prediction 2b. Moreover, the different sex ratios in OMUs and MMUs suggest that MMUs do not reflect a temporary association of several OMUs. Thus, prediction 2c is also not supported. OMUs seem not be the modal basal social unit in Guinea baboons, suggesting that the social organization of our focal troop seems to be different from hamadryas baboon organization. However, these findings must be interpreted with caution as they do not exclude the possibility that observed MMUs do consist of several OMUs, but not always the same OMUs (unlike hamadryas baboons), resulting in a more flexible composition similar to that of geladas, as suggested by Sharman (1981). However, Sharman (1981) concluded that a harem structure (OMU organization) was improbable, as he frequently observed small social groups without any males, and argued that it would be impossible for males to control their females from a distance because visibility was highly restricted in the habitat where he studied the baboons. Similarly, at our study site, visibility is also largely restricted in certain habitat types.

An alternative explanation for the different sex ratios may be the presence of additional follower males that occasionally integrate into MMUs, which consist of OMUs, or defeated leader males that do not monopolize females anymore but remain attached to the unit, as is the case in both hamadryas and gelada baboons (Mori 1979; Stambach 1987). However, because there is a large proportion of OMUs among the smaller parties, but also a high percentage of MMUs in the entire data set, we suggest that both kinds of parties occur and that the MMUs do not consist of OMUs. The simultaneous occurrence of OMUs and MMUs that are not composed of single OMUs would match neither the savannah nor the hamadryas baboon social organization, suggesting that Guinea baboons have a distinct system that cannot be integrated into the established dichotomic framework of baboon social systems.

#### Daily and Seasonal Variation in the Number of Parties Arriving and Party Size

The number and size of parties arriving varied on both a daily and seasonal scale. Fewer but larger parties arrived at the Mare and split for foraging in the mornings, whereas more but smaller parties came back from foraging in the afternoon. This seasonal fluctuation in party size corroborates Sharman's (1981) observations of increasing group sizes in the rainy season (Anderson and McGrew 1984; Galat-Luong *et al.* 2006). Boese (1973), Sharman (1981), and Galat-Luong *et al.* (2006) hypothesize that seasonal changes in group size are an adaptation to food scarcity in the dry season and conclude that Guinea baboons optimize group sizes according to a given situation, avoiding unnecessary demands on individual time budgets. Moreover, because food availability increases in the rainy season and, consequently, food competition decreases, groups may no longer be forced to split up for foraging (Anderson and McGrew 1984; Galat-Luong and Galat, 2003; Galat-Luong *et al.* 2006). This seems plausible, but both phenological data and quantitative records of seasonal changes in food availability are lacking for Guinea baboons. Another possible cause for the formation of larger groups in the rainy season is restricted visibility owing to denser vegetation, which may lead to higher predation risk as predators become harder to detect (Henzi and Barrett 2003; Sharman 1981).

About half of the arriving parties split up or merged with others when crossing or resting at the Mare. Thus troop cohesion was rather loose, and parties were highly variable in size and composition, both on a daily and seasonal scale. These findings suggest a flexible social organization with a high tendency for fission–fusion. However, it remains unknown whether parties are stable over time and whether the fission–fusion resembles a molecular organization, with particular independent subgroups, e.g., family or breeding groups such as OMUs in hamadryas baboons, or whether individuals decide when and where to go and with whom, in an atomistic organization similar to that of chimpanzees (Rodseth *et al.* 1991).

Our results regarding the apparently undifferentiated and highly flexible social organization of Guinea baboons are in accordance with those of other authors (Boese 1973; Sharman 1981). We were unable to distinguish the baboons individually, but we observed them intermingling on a daily basis, and party sizes and compositions were different before and after the intermingling of arriving parties. OMUs analogous to hamadryas OMUs may have aggregated before arriving at the observation site. However, we observed both males and females switching between multimale parties, with females grooming and even mating with different males, which is not characteristic of the hamadryas system. Further, male–male distances in our Guinea baboons were often very small and males interacted extensively (unpublished data), which also does not suggest a hamadryas-like OMU organization. We suggest that the basal social entities of Guinea baboons are OMUs and MMUs, which are not made up of OMUs, i.e., some males may monopolize females whereas other males share females. Whether this social organization translates directly into the mating system and whether it represents 2 alternative male reproductive strategies needs to be explored.

## Conclusion

We found no stable temporal or spatial patterns in Guinea baboon group composition. Guinea baboons appear to have a highly complex social organization with very variable group composition, on both a daily and a seasonal basis. Their social organization appears to resemble neither the strict multilayered OMU-based organization of hamadryas baboons nor the typical multimale organization of savannah baboons. It is likely that the social organization of Guinea baboons, and with it most likely the complete social system (*sensu* Kappeler and van Schaik 2002), is neither a precursor of the hamadryas system nor intermediate between savannah and hamadryas systems. In light of our data, we may have to revise our view of baboon social systems as a dichotomy, as they seem to be much more variable than previously assumed.

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