

RESEARCH ARTICLE

Social Organization and Space Use of a Wild Mandrill (*Mandrillus sphinx*) GroupTIMO BROCKMEYER^{1,2}, PETER M. KAPPELER², ERIC WILLAUME³, LAURE BENOIT¹, SYLVÈRE MBOUMBA⁴, AND MARIE J.E. CHARPENTIER^{1*}¹CEFE-CNRS UMR 5175, Montpellier, France²Behavioral Ecology and Sociobiology Unit, German Primate Center, Göttingen, Germany³SOPEPAL, Bakoumba, Gabon⁴USTM, Franceville, Gabon

Mandrills (*Mandrillus sphinx*) are enigmatic Old World primates whose social organization and ecology remain poorly known. Previous studies indicated, for example, that groups are composed of only adult females and their young or that several units composed of one adult male and several females make up larger permanent social units. Here, we present the first data on group composition and male ranging patterns from the only habituated wild mandrill group and examine how home range size and daily path length varied with environmental and demographic factors over a 15-month period. Our study site is located in southern Gabon where we followed the group on a daily basis, collecting data on presence, ranging, behavior, and parasite load of its individual members. Throughout the study, the group was made up of about 120 individuals, including several non-natal and natal adult and sub-adult males. One-male units were never observed. The mandrills traveled an estimated 0.44–6.50 km/day in a home range area of 866.7 ha. Exploratory analyses revealed that precipitation, the number of adult males present, and the richness of protozoan parasites were all positively correlated with daily path length. These results clarify the social system of mandrills and provide first insights into the factors that shape their ranging patterns. *Am. J. Primatol.* 9999:XX–XX, 2015. © 2015 Wiley Periodicals, Inc.

Key words: space use; social organization; mandrill; male ranging; home range

INTRODUCTION

Mandrills (*Mandrillus sphinx*, Papionini; Cercopithecinae) are omnivorous forest-dwelling Old World primates inhabiting dense equatorial forests, from Southern Cameroon through Equatorial Guinea (Rio Muni) and Gabon to Southern Congo [Abernethy et al., 2002]. Mandrills have proven very difficult to study in the wild because they are semi-arboreal, live in dense forest habitats, and because they tend to form large itinerant groups that are difficult to habituate. Most information on mandrill socioecology, therefore, comes from studies on large semi-free ranging social groups housed in a medical research center in Southern Gabon (CIRMF; e.g., [Charpentier et al., 2005, 2007; Setchell et al., 2002]). These studies suggested that mandrills form matrilineal societies, with female philopatry and male dispersal [Abernethy et al., 2002; Setchell et al., 2006]. Reproduction is moderately seasonal in captivity, with a birth peak between January and March, and females give birth to a single offspring almost every year after a gestation length of just less than 6 months [Setchell et al., 2002]. Mandrills are also characterized by an extreme

sexual dimorphism, with males being more than three times heavier than females [Setchell et al., 2001] and showing bright colorations of the face and the genitalia [Setchell & Dixson, 2001]. Intra-sexual competition between males is intense in this species, resulting in alpha males' monopolization of reproduction [Charpentier et al., 2005]. One direct consequence of such intense competition is that, in

Contract grant sponsor: Deutsche Forschungsgemeinschaft; contract grant number: DFG, KA 1082-20-1; contract grant sponsor: Station d'Etudes en Ecologie Globale; contract grant number: INEE-CNRS; contract grant sponsor: Laboratoire International Associé; contract grant numbers: CIRMF, INEE-CNRS.

Conflict of interest: The authors declare no conflict of interest.

*Correspondence to: Marie JE Charpentier, CEFE-CNRS UMR 5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France. E-mail: marie.charpentier@cefe.cnrs.fr

Received 5 January 2015; revised 22 May 2015; revision accepted 23 May 2015

DOI: 10.1002/ajp.22439
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

captivity, male mandrills tend to live only up to 20 years old while females may live longer than 35 years (MJEC, pers. obs.).

The few studies on wild mandrill groups have yielded contrasting results regarding their social organization, defined as the size and composition of their groups [Kappeler & van Schaik, 2002]. Some authors proposed that mandrills form multi-level societies, as observed in some other papionins, such as hamadryas baboons (*Papio hamadryas*) and geladas (*Theropithecus gelada*) [Aegglen, 1984; Dunbar & Dunbar, 1975; Grueter et al., 2012] and that large groups observed in the wild are the result of aggregations of one-male units [Hoshino et al., 1984; Jouventin, 1975]. Others suggested that the huge hordes observed are stable societies centered on a nucleus of females in which adult and sub-adult males are only present during the receptive period of the females and otherwise roam alone [Abernethy et al., 2002]. However, none of these studies performed long-term follows of a particular group where members could be individually recognized and were consequently limited in their power to assess the dynamics of mandrill social organization.

The aims of this study were twofold. First, we studied the social organization of a wild mandrill group with special regard to the presence of breeding-age males. If mandrill societies represent aggregations of one-male units, we expect several adult males to be present year-round and we should observe several adult females clustering around a particular adult male. If mandrills live in hordes of females with which adult males only associate during the reproductive season, we would expect male presence to increase during the females' receptive period. To address these questions, we collected individual-based data on the presence of adult males and females during a 15-month study. We used genetic paternity analyses to determine whether males were born in the group or whether they were immigrants.

Second, we relate the group's space use to changes in demographic and environmental variables to provide first insights into these aspects of the socioecology of mandrills. The energetic demands of individuals should affect daily path length (DPL, [Clutton-Brock & Harvey, 1977a]) since in order to obtain higher food intake, more food needs to be found. We, therefore, expected DPL to increase when large proportions of the females of the group face higher caloric needs due to gestation or lactation [Hinde et al., 2009]. The food requirements of a group should also depend on the number of its constituent members and their cumulative body mass. Due to the strong sexual dimorphism in mandrills, one adult male contributes about three times as much body weight to the group than one female [Setchell et al., 2001]. Moreover, since females are the philopatric sex in this species, the number of adult males is more likely to vary during the year. We thus expected a

positive correlation between the number of adult males and DPL.

Additionally, DPL should also depend on the abundance and distribution of food resources [Clutton-Brock & Harvey, 1977b; Isbell et al., 1998]. Frugivorous species are, therefore, expected to travel less during periods of high fruit abundance, because they might satisfy their daily food requirements from only a few rich patches of fruiting trees. Because we have no direct measures of food availability, we used precipitation and temperature to assess the effects of seasonal variation on variation in DPL in a first approximation [as per: Chapman et al., 1999; van Schaik et al., 1993].

Finally, environmental parasite pressures may be an additional determinant of ranging patterns. The temporal use of sleeping trees by baboons has been proposed to reflect a behavioral strategy for parasite avoidance [Hausfater & Mead, 1982]. In mangabeys, fruit availability was found to be the main determinant of group movement and space use during the wet season but during drier periods, fecal contamination may force mangabeys to leave areas of high fruit density [Freeland, 1980]. Because orofecally transmitted parasites can likely be transmitted through a contaminated environment, we estimated contamination risk using gastro-intestinal parasite richness. We expected that with increasing parasite richness, the group would change locations more frequently in order to avoid contaminations, therefore, resulting in longer DPLs. Since several of these variables are correlated, disentangling the respective effect of each one on DPL can pose statistical problems due to multicollinearity. We, therefore, employed commonality analysis to illuminate the correlated structure of these variables

METHODS

Ethical Statement

This study complies with ethical protocols approved by the CENAREST institution (authorization number: AR0003/12/MENESRSIC/CENAREST/CG/CST/CSAR). The research adhered to the legal requirements of Gabon and to the American Society of Primatologists principles for the ethical treatment of nonhuman primates.

Study Population

The study population originated from 65 captive-born mandrills housed at CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) that were released into a private park (the Lékédi Park, Bakoumba, Gabon) on two occasions (36 individuals released in 2002 and 29 in 2006; see for details [Peignot et al., 2008]). This park contains large forest patches typical for the region and several

potential mandrill predators like raptors and leopards occur within its boundaries. Several matrilineal groups with individuals of all ages and both sexes constituted the core of the released group, including subadult and adult males. Two months after the first release, adult females were seen cycling and almost half of them gave birth the same year. We observed the same fertility rate the second year post-release, but infant survival (to >6 months) increased from 40% to 100% ($N=5$ in each case, [Peignot et al., 2008]). About 18 months after the first release, wild adult males were regularly seen immigrating into the study group and copulating with cycling females (MJEC, pers. obs.). Since early 2004, this mandrill population has been regularly visited by park guards and tourists (two visits/week on average of ~30 min each). These regular contacts allowed keeping the captive-born individuals habituated while wild-born infants and immigrants became increasingly habituated to the presence of humans.

Mandrills forage freely in the park and its vicinity but their diet has been supplemented about five times a week with bananas and monkey chow during the first years after the release events. However, in order to boost their foraging behavior, supplementation at no point provided their full caloric requirements, so that the group still needed to forage independently. The supplementation rate decreased over time and was down to once or twice a week by 2012. At the beginning of the present study (October 2012), mandrills had not been fed for the previous 6 months, except during trapping events (one trapping season of 10 days occurred during the study period), where only a few bananas were provided in small pieces to the entire group.

From January to October 2012, field assistants were trained and the habituation of the mandrills was intensified. Progressively, human observers were able to stay with the group for a few hours (0.5–2 hr) to full days (06:30–17:30 hr). At the beginning of this study, 53 individuals (31 females and 22 males of all ages) of the population were individually known and regularly followed. At the end of the study (December 2013), the number of known individuals increased to 76 individuals (41 females and 35 males of all ages). During the study, the group was composed of 100–120 individuals of which almost all adult individuals and all sub-adult males (6–9 years old) were individually known. Genetic analyses (see below) led us to conclude that about 80% of the individuals constituting the population in 2012 were composed of wild-born animals. Birth dates of captive-born individuals were exactly known while the age of wild-born individuals was estimated using general condition (a combination of size, stature, and signs of senescence) and for some of them, patterns of tooth eruption and wear [Galbany et al., 2014].

Climate data have been collected since the beginning of 2012 at a weather station (Davis Vantage PRO2 radio) in the village nearby Lékédi Park (Bakoumba). The station automatically records several weather parameters (precipitation, temperature, humidity etc.) every 30 min.

Behavioral Observations

Starting in October 2012, we conducted near daily all-day follows of the mandrill group, assisted by radio-collars (Telonics, Mesa, AZ) fitted on 2–3 adult females. We spent on average 7 hr/day in visual contact with the group. We performed daily censuses and observations of individually recognized animals, using handheld computers (PSION workabout pro) and software specifically designed for behavioral observations (ELA Innovation, Montpellier, France). During 5-min focal animal sampling, the frequency and duration of three behavioral states (foraging, resting, and traveling) were recorded. For our analyses below, we retained only data from those days where at least 25% of all known individuals were seen (generally some very well habituated adult females and all adult males). On other days, observation conditions were too difficult because of e.g., heavy rain to obtain reliable estimates of group composition.

We estimated the reproductive status of adult females by visual inspection of sexual swellings. We attributed a qualitative measurement of the size of the swelling on a scale of 0 (no swelling) to 3 (maximally turgescence swelling). Pregnant females also exhibit a typical pink tumescence [Setchell, 2005]. These observational data combined with a posteriori patterns of births allowed us to determine periods of pregnancies and periods of sexual receptivity. Finally, we distinguished natal males (males born in the group post-releases, but also the males born at CIRMF and released as juveniles) from wild males that immigrated into the group. With respect to their developmental status, we distinguished between adult males and males that have not yet reached full sexual maturity. Before reaching adulthood at an approximate age of 10 years, male mandrills experience a growth spurt at 6–9 years old that is associated with sexual development [Setchell & Dixson, 2002]. We refer to males falling into that age category as sub-adult males. Dominance rank of adult males was established based on the frequency of approach-avoidance behavior between all studied males (following Setchell et al. [2006]).

Genetic and Paternity Analyses

Since early 2012, we conducted three trapping sessions in which 67 individuals of the group were trapped. Animals were darted in the forest, and anesthetized by blowpipe intramuscular injections of

ketamine (Imalgène 1000; 7 mg/kg body weight for adults and 5 mg/kg body weight for juveniles) and xylazine (rompun; 3 mg/kg body weight for adults and 5 mg/kg body weight for juveniles). Various morphological and physiological data, including blood samples, were collected on each occasion. Animals were anti-sedated with atipamezole (Anitsedan ND, 0.5 mg/ml) to facilitate awakening.

Blood samples were centrifuged in our laboratory located 7 km away from the park. DNA extractions were performed on site from buffy coats using QIAamp DNA Blood Mini Kits (Hilden, Germany). DNA samples were then shipped to France for genetic analyses performed on 12 microsatellite markers. The 12 primer pairs were associated in seven PCR mixes (see Supplementary Material S1) and were amplified in the same reaction using the same protocol (see Charpentier et al. [2005] for details on the protocol).

Paternity analyses were performed using Cervus 3.0 software to assign both maternity and paternity of wild-born animals, using previously described procedures [Charpentier et al., 2005]. Briefly, Cervus calculates parentage inference likelihood ratios and generates a statistic based on the difference between the two most likely parents. Cervus also provides likelihood ratios for the two most likely triads (mother–father–offspring). We considered the default rate of scoring error (5%) and the proportion of candidate parents sampled to be 70%. Maternities and paternities were confirmed for the 19 captive-born individuals still living in the group. Maternity was assigned for 34/41 (83%) individuals born in the study group for whom we collected blood samples. Mothers were not found for seven wild-born individuals, probably because these mothers were never trapped. Paternities were assigned for 36/41 (88%) wild-born individuals. Unassigned paternities likely resulted from non-genotyped, unknown males that reproduced before the beginning of the study. Maternity and paternity were also not assigned for the eight immigrating males. We further generated Queller and Goodnight estimates of relatedness [Queller & Goodnight, 1989] based on the 12 genetic markers and using the software GenAlEx 6.501 available for Excel [Peakall & Smouse, 2006, 2012].

Parasitological Analyses

Coprological analyses were routinely performed since the beginning of the project from fecal samples collected on unambiguously identified animals. Direct microscopic observations were performed after concentration and sedimentation of the fecal material. We performed qualitative analyses of the samples and recorded nematode eggs and protozoan trophs and cysts by taxon according to characteristic morphology (see for details: [Poirotte et al., unpublished data]). We evaluated parasite richness

at the population level as the average number of species recorded in all fecal samples collected during one week. We recorded both nematode eggs and protozoan species and calculated average richness for the two groups of parasites separately. While both sets of species are oro-fecally transmitted, nematodes need a period of maturation in the environment before being transmissible from host to host. In contrast, protozoans are transmissible through direct host–host contacts with infected fecal material. Hence, in the following analyses, we considered the weekly averaged number of nematode species as richness in long-life cycle parasites (LLC) and the weekly averaged number of protozoan species as richness in short-life cycle parasites (SLC) (as defined in: [Poirotte et al., unpublished data]).

GPS Data

GPS data were collected by field assistants using two handheld devices (Garmin GPSMap62). The devices were turned on only when the observers were with the mandrill group and switched off when direct contact was lost, ensuring that they recorded only group movements. We cross-checked that devices were switched off correctly by comparing recordings with notes from the behavioral observations and discarded points that were recorded 15 min after the last behavioral observation. We calculated the velocity of each GPS point as the distance to the preceding point divided by the time between the two points. To avoid biases by points having a large measurement error, we discarded all points indicating a velocity >10 km/hr, since it is highly unlikely that the observers moved at that speed in the field. The devices took GPS fixes in irregular intervals. To avoid biases due to varying sampling densities, we reduced the data set to the largest interval (30 min) over the whole 15 months using a linear interpolation function. In the end, we retained 19797 GPS points collected on a total of 413 observation days.

Mandrills are active on average 10 hr a day (see below). To estimate daily path lengths (DPL), we determined the average distance the group traveled per hour each day and extrapolated it to a 10-hr period. Since data availability varied between days, this value estimates the distance traveled per day by the group on each given observation day. To minimize biases linked to insufficient sampling, we included only those days where at least 10 GPS points were recorded (i.e., with at least 5 hr of observations; $N = 194$ days).

Home range area was calculated as the 95% envelope of the utilization distribution based on all cleaned GPS fixes. We used the software BRB/MKDE (Biased Random Bridges for Movement-based Kernel Density Estimation, [Benhamou, 2011; Benhamou & Cornélis, 2010]) to calculate the diffusion coefficient (150 m²/min) and the utilization distribution.

We set the minimum smoothing parameter to 20 m to allow for GPS error and the threshold assuming immobility to 50 m. We chose this value because it approximately corresponds to the spread of the group when not traveling. Human observers carrying the GPS will, therefore, also move within this radius through the stationary group. DPL, in contrast, was directly estimated from the interpolated values of the GPS tracks, and we did not include additional criteria about stationarity.

Statistical Analyses

To study the relationship between the number of males or their time spent in the group and the percentage of cycling females, and also to compare the distribution of relatedness among immigrant versus resident dyads, we used non-parametric statistics (Spearman rank correlations and Mann–Whitney tests, respectively; two-tailed tests). To study the variables influencing DPL, we performed a four-step analysis. First, we tested whether time budgets of focal individuals correlated with group DPLs (Pearson's product-moment correlation). We included only those days where GPS points collected during at least 5 hr and at least three focal observations were available. This was the case for 162 days over the study period that included a total of 3,326 focals.

Second, we determined whether DPL differed between seasons and forest zones visited by the group using a two-way ANOVA on the full data set with 194 observation days. Four seasons were defined by adjusting the typical perennial seasons of southern Gabon so that they overlapped well with local climatic measurements (long rainy season: February–May, long dry season: June–September, short rainy season: October–November, short dry season: December–January). Six forest zones of the area occupied by the mandrills were defined manually using local geography such as vegetation, valleys, rivers and forest patch connectivity, based on our knowledge of the field. This was done in order to account for unmeasured local factors that might influence group movements.

In a third step, we constructed a linear model to explain the seasonal variance by replacing the four distinct seasons with informative variables about group composition, parasite richness, and climate. As not all measures were available in sufficient quality on a day-to-day basis, we averaged all measurements within one week intervals (except in the case of precipitation, where we summed the daily measurements over the week). We constructed a full model containing average temperature, weekly precipitation, mean number of adult males in the group, mean percentage of lactating females in the group, and mean parasite richness for SLC and LLC parasites as predictor variables. Mean DPL was

ln-transformed in order to meet assumptions of normality. We weighted observations by the number of days where GPS data were available during each week. Using commonality analysis (see below), we were able to explore the effects of multicollinearity between these explanatory variables.

In a fourth step, we aimed to select from our set of variables the combination of predictors with the highest explanatory power, using Akaike's second order information criterion (AICc, [Burnham & Anderson, 2002; Hurvich & Tsai, 1989]). In order not to test all possible combinations of variables, we chose subsets of variables from the full model based on their biological meaning. For example, we removed all variables related to group composition (number of males present and percentage of lactating females) from the full model and constructed two other models including only one of the two variables; we did the same for climatic effects and parasite richness. Finally, we ranked all models by their AICc-value. We checked for distribution and autocorrelation of residuals in all models. All analyses were conducted using the R software package, version 3.0.3 [R Development Core Team, 2014].

Commonality Analysis

Multicollinearity is a common problem in multiple regressions when predictor variables are correlated with each other. Since we expected the explanatory variables in our models to be correlated to different degrees, we employed commonality analysis [Nimon & Oswald, 2013; Ray-Mukherjee et al., 2014] to explore how multicollinearity affected the parameter estimates. This method aims to increase the interpretability of a regression analysis through the calculation of additional coefficients, notably structure coefficients, and commonality coefficients. Structure coefficients are the Pearson's correlation coefficients between the explanatory variable and the predicted values from a regression outcome [Nathans et al., 2012] and are thus, in contrast to the regression coefficients, independent of collinearity with the other variables. Commonality coefficients decompose the variance explained (R^2) by a predictor variable in a given model into variance uniquely attributable to that specific predictor and common variance that is shared with other predictor variables. This common part can be seen as the additional variance explained in a model when two or more predictor variables are included, as opposed to the sum of variances explained if each predictor would be included separately into the model. It is a sign of collinearity if the shared variance between two variables is negative, indicating that the R^2 of the model does not increase to the sum of the R^2 of the models in which each of the variables would be included solely.

RESULTS

Group Composition and Male Migration Patterns

At the end of this study (December 2013), the group was composed of about 120 individuals, almost half of them being non-reproductive individuals (infants and juveniles; Table I). The large majority of unrecognized individuals belonged to the juvenile class (about a third were individually recognized).

We found that adult males varied in their degree of association with the group (Fig. 1). Some “social” males (ID 33, 54, 74) stayed for long periods of time and were seen almost every day (simultaneously or not) during those periods, while less social males were present only during shorter periods (ID 53) or were seen with varying frequency (ID 57). Another adult male (ID 36) of high rank remained associated with the group for a long period but during this time was seen only with low frequency. This was probably due to intense competition with the other high-ranking male at that time (ID 54; MJEC, pers. obs). As expected, the respective alpha males spent almost 100% of their time within the group

during their tenure. Sub-adult males tended to be present almost all the time, with the only exception being male 57, who started to progressively disperse from his natal group at age 9. Patterns of group association across males did not seem to be related to the male’s origin: natal reproductive males were still present in the group at the time of the study.

Over the study period, the number of fully developed adult males varied from three to five and was positively correlated with the percentage of cycling females (Fig. 2; Spearman rank correlation: $r = 0.68, P = 0.005$). The number of sub-adult males varied from two to five during the same period but was uncorrelated with the percentage of cycling females (Fig. 2; $r = 0.1, P = 0.72$). Restricting our data set to maximally tumescent females did not change the quality of the results and the correlation with the number of adult males persisted (not shown).

In general, the monthly time spent in the group for each male did not depend on the percentage of cycling females present (Fig. 1): one adult male and two sub-adult males appeared to increase their fraction of time spent in the group as a function of the presence of cycling females, but we found the reverse effect for two other males (Fig. 1). These few exceptions, however, did not persist when applying a Bonferroni correction with a corrected significance level of 0.004 (0.05/12), except for one sub-adult male (ID 12). Taken together, these results suggest that the observed effects occurred by chance rather than representing a real effect of the presence of cycling females on the time spent in the group for each individual male.

TABLE I. Group Composition in December 2013

Infants		Juveniles		Females		Males	
0–1 yr	1–3 yrs	Adult (>4yrs)	4–5 yrs	6–9 yrs	Adult (>10yrs)		
17 (20)	19 (60)	28 (30)	3	5	3		

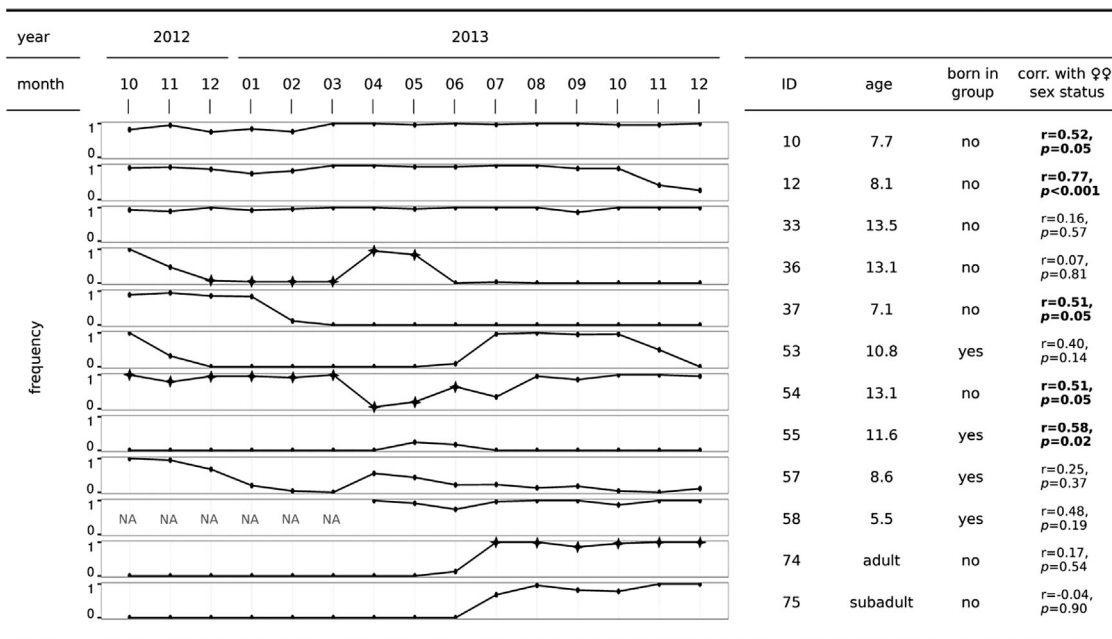


Fig. 1. Frequency of monthly male presence. Stars indicate the alpha male (the dominance was unclear between males 36 and 54 from December 2012 to May 2013). NA: non-appropriate age class (too young). Ages were assigned in October 2012.

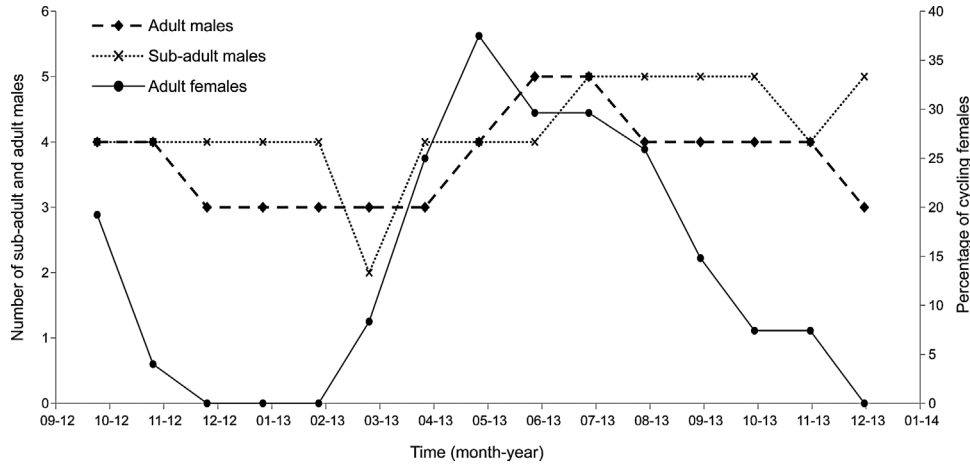


Fig. 2. Monthly presence of adult and sub-adult males (dashed lines) in the group and percentage of cycling females (solid line).

Paternity analyses revealed that eight of the 12 studied males (Fig. 1) were wild-born and immigrated into the group. During the study period, we witnessed the immigration of one fully developed adult male (ID 74, aged 10–11 years) and one sub-adult male (ID 75; aged 7–8 years). Additionally, two other unknown males (one sub-adult and one adult) were also observed close to the study group for a day, during the 2013 mating season. These two males were never seen again, but because the zone where the mandrills live is sometimes used by poachers, we were unable to distinguish between emigration events and mortality.

Paternity analyses further allowed tracking fathers of wild-born individuals from the group conceived as early as 2005. We found that adult males still present in the group in 2013 (ID 33) reproduced as early as 2007. One other adult male that was present and dominant in 2012 already reproduced in 2009. Altogether these observations suggest that males sometimes enter and leave the same social group several times during their life.

Finally, when examining the relatedness coefficients between immigrating males, we found that on average, these males were not more related to each other than any pairs randomly chosen in the population (Mann–Whitney test: $W = 16,155$, $P = 0.35$) and the most closely related dyad was not found among these males (mean \pm SD and range among immigrating males: 0.02 ± 0.15 , -0.21 to 0.40 ; among random individuals: -0.01 ± 0.19 , -0.46 to 0.65). We found, however, some evidence that two of these males (ID 36 and 37) were related ($R = 0.40$), probably as half-brothers.

Home Range and Ranging Behavior

Mandrills are active about 10 hr/day. They move with constant speed throughout the course of

the day, except during the hours just after sunrise (Supplementary Material S2). Based on the extrapolation of the measured mean daily velocity to 10 hr/day, we estimate that mandrills traveled on average 2.42 km/day (SD: 1.04, range: 0.44–6.50, $N = 194$ days). During the study period, they occupied a home range of 866.7 ha (Fig. 3). Mandrills appeared to equally use all of the forest patches within the polygon encompassing their home range area (Fig. 3). However, they avoided savannas and open habitats. DPL was positively correlated with time spent moving ($r = 0.326$, $P < 0.0001$) and negatively correlated with time spent resting ($r = -0.160$, $P = 0.043$), but it was not correlated with time spent foraging ($r = -0.028$, $P = 0.728$).

The two-way ANOVA revealed significant effects of both season ($F_{3,170} = 3.975$, $P = 0.01$) and forest zone ($F_{5,170} = 6.936$, $P < 0.0001$) on DPL. Post-hoc tests revealed that DPL was higher during the short rainy season, compared to the three other seasons (Tukey Honest Significant Differences: $P < 0.05$ in all comparisons involving the short rainy season), and that mandrills traveled faster only in one forest zone (zone labeled 1 in Fig. 3) than in the five others (Tukey Honest Significant Differences: $P < 0.01$ in all comparisons involving forest zone 1).

The initial full model based on weekly averaged values revealed that weekly precipitation and the average number of adult males present were both significantly associated with DPL (Table IIA). Additionally, SLC parasite richness showed a strong correlation with the predicted values (structure coefficient). Commonality analysis revealed that the average number of adult males made the highest contribution to the total variance explained by the model (Fig. 4). The second highest proportion corresponded to richness of SLC parasites. The high proportion of shared variance with other predictors (Fig. 4), however, indicates that its

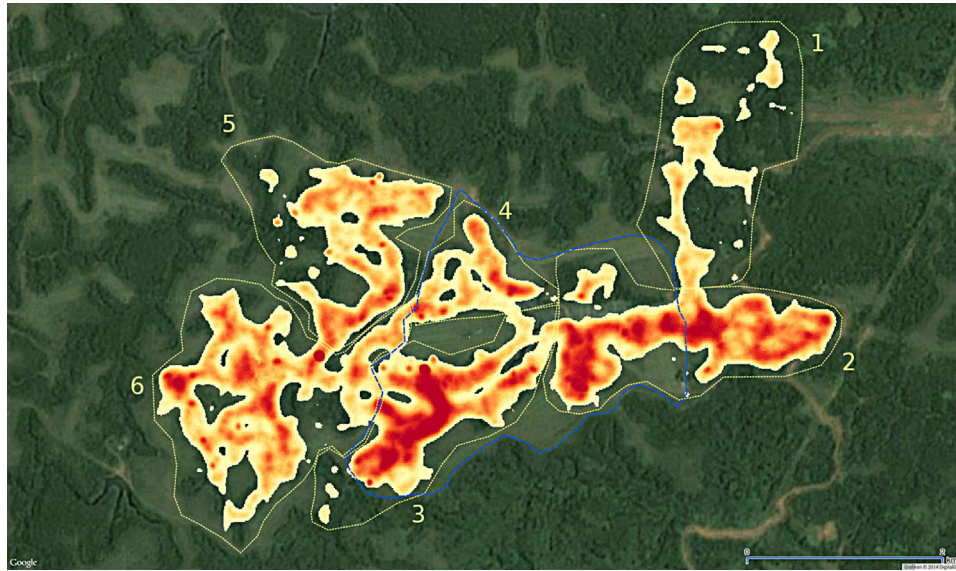


Fig. 3. Mandrill's home range. Utilization distribution (variations in yellow and red colors) is displayed on the figure, based on the GPS data points. Red indicates higher utilization density. The outer limits represent the 95%-envelope that was used to calculate the home range area. Yellow lines delimit the six forest zones we defined; zone 1 is the zone where mandrills showed longer DPLs. The blue line marks the fence surrounding one of the modules of the park. Note that mandrills range freely and are not restricted in their movements by these boundaries.

regression estimates in the full model might be obscured by multicollinearity. Weekly precipitation captured a unique part of the variance that was not captured by other variables, although contributing only the second smallest proportion to the total explained variance. Weekly mean temperature was strongly correlated with other predictor variables and showed no correlation with the predicted values from the model (Table IIA and Supplementary Material S3). Since its proportion of explained variance in the full model was close to zero, any effect of mean temperature in the model is likely due to correlation with other predictor variables and we thus excluded it from further models.

In a complementary analysis, we tested nine different models with varying variable sets (models 2–10 in Supplementary Material S4) and ranked them by their AICc. The highest rank was given to the model including all variables except the percentage of lactating females, followed by the models excluding either percentage of lactating females, LLC parasite richness, or mean temperature. Models excluding the two parasite richness variables or climatic effects ranked last. This exploration stage based on model selection criterion indicated that three variables: average number of adult males, SLC parasite richness, and weekly precipitation, were of highest explanatory power. Consequently, we

TABLE II. Regression Results and Structure Coefficients

Predictor	Coefficient	SE	<i>t</i> -value	<i>P</i> -value	Str. coeff.
A (Full model)					
Intercept	−0.5905	1.1483	−0.514	0.6108	–
Number of males	0.1632	0.0778	2.097	0.0442	0.6461
% Lactating females	0.0687	0.3826	0.180	0.8587	−0.4314
Mean temperature	0.0202	0.0470	0.429	0.6706	−0.0230
Weekly precipitation	0.0031	0.0014	2.170	0.0378	0.3111
Parasite rich. (SLC)	0.1281	0.0776	1.651	0.1089	0.6272
Parasite rich. (LLC)	0.0328	0.1177	0.279	0.7824	0.2044
B (Optimal model)					
Intercept	0.1428	0.1688	0.846	0.4024	–
Weekly precipitation	0.0022	0.0010	2.245	0.0301	0.3113
Parasite richness (SLC)	0.1234	0.0510	2.420	0.0199	0.6335
Number of males	0.1006	0.0372	2.701	0.0099	0.6625

Str. coeff: structure coefficient.
Significant *P*-values are shown in bold.

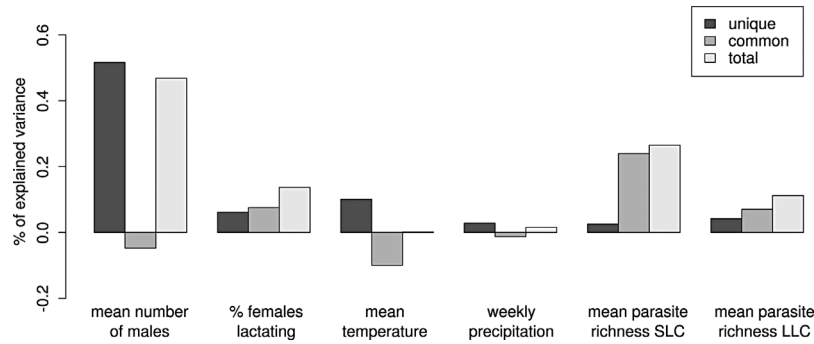


Fig. 4. Proportion of the variance explained by each of the variables in the full model. Unique variance is the variance solely explained by that variable, while common variance is the proportion shared with other variables in the model, total variance is the sum of both.

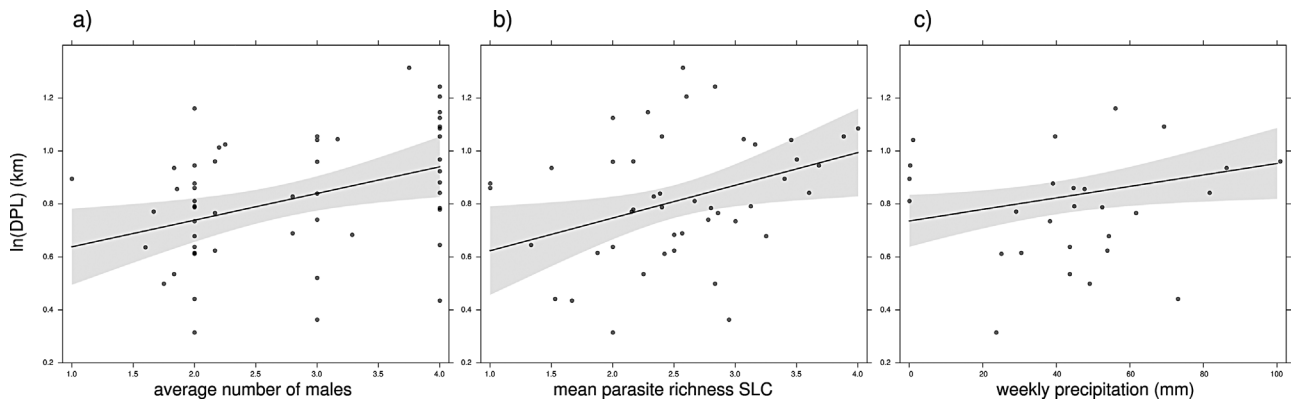


Fig. 5. Regression lines for the predictors of DPL in the optimal model. **a:** Effect of the average number of adult males present in the group. **b:** Effect of the mean richness of SLC parasites. **c:** Effect of weekly amount of precipitation. Shaded areas indicate 95% confidence intervals.

constructed a minimal model including only these three predictors. We found no autocorrelation of errors in the highest-ranking model among the tested models, residuals were normally distributed, and all variables were significant and had a positive effect on DPL (Table IIB, Fig. 5). In other words, mandrills tended to increase their DPL when precipitation increased, when more adult males were present in the group and when parasite pressure was higher.

Since we found that one forest zone influenced DPL, we repeated our analysis excluding the 5 weeks in which the study group visited this forest zone. The effects are weaker due to decreased sample size, but remain qualitatively comparable (data not shown).

DISCUSSION

In this study, we presented data on group composition and adult male ranging movements in a poorly studied Old World monkey. The unique circumstances of studying a habituated mandrill population allowed daily follows and recognition of

the majority of group members. We clarified several aspects of mandrill social organization. In particular, we did not find any support for the hypotheses that mandrill societies are aggregations of one-male units or that all adult males are absent during some periods of the year, as previously suggested [Abernethy et al., 2002; Hoshino et al., 1984]. Using GPS-based technology, we further estimated home range size and daily ranging distances. We employed recently developed exploratory statistics to examine the relative contribution of demographic and environmental variables on DPL, highlighting the importance of group composition and parasite load for daily travel patterns.

Social Organization

We found that several adult males were present in the group year-round, and some of them were observed during several consecutive years. The presence of adult males throughout the year is in accordance with early studies on wild mandrills [Hoshino et al., 1984] and is also consistent with oral

reports from Gabonese forest-dwellers mentioning at least one big male leading the groups (MJEC, pers. obs). However, a previous study on several wild mandrill social groups living in Lopé National Park observed adult males with the groups exclusively during the reproductive season [Abernethy et al., 2002]. The social organization reported for these groups could be a biological reality due to differences in habitat ecology or might be an artifact resulting from the difficulties of following wild mandrills in dense equatorial forests. The Lopé groups of mandrills differed in two important characteristics from the other studied groups. First, groups were composed of up to 845 individuals [Abernethy et al., 2002], a figure that has not been reported elsewhere. Second, the habitat structure of Lopé National Park differs from the vast forests that are typical for the mandrills' distribution range from southern Cameroon, across Gabon to southern Congo. Lopé National park is composed of a mosaic of forests and savannas where large forest blocks are absent. This mosaic differs from the surrounding forests in terms of fruit availability [Tutin, 1999].

While we do not question the size of Lopé mandrill groups (several other unpublished observations reported huge group sizes in this area), the habitat of the present study group living in the Lékédi Park is also composed of a mosaic of forests and savannas. The habitat structure is thus likely not the cause of the male absence outside the reproductive season suggested for Lopé. We, therefore, suspect that videos of mandrills crossing open savannas used to count individuals might lead to an underestimation of the number of males present, especially, since adult males usually occur peripherally [Setchell & Dixson, 2002]. Additionally, the proportion of adult males is generally low in mandrills, particularly outside the breeding season. Oversight of a few male individuals might thus rapidly lead to biased estimates.

In this study, we observed an adult ratio of 1:27 to 1:32.4 depending on the estimate of group size (between 100 and 120 individuals, respectively). Other studies on wild mandrills reported values ranging from 1:13.9 [Hoshino et al., 1984] and 1:21 [Rogers et al., 1996] to as high as 1:71.4 [Hongo, 2014] and 1:775 [Abernethy et al., 2002]. Again, the Lopé groups appear as an outlier and the two last mentioned studies are based on counts from videos in open areas.

Additionally, a total temporal absence of males in the group does not correspond with what we know from captive or wild male mandrill behavior. Adult males are always associated with adult females and numerous infants that actively seek their proximity (MJEC, pers. obs.). In mandrills, paternal care is not as evident as for baboon species where adult males are known to actively protect infants [Buchan et al., 2003]. Mandrill fathers, however, tend to be spatially

closer to their genetic offspring than to other infants [Charpentier et al., 2007], suggesting a form of paternal protection. Adult male mandrills also frequently intervene during conflicts involving young individuals or adult females (MJEC, pers. obs.). These males are, therefore, fully integrated into their respective societies in which they actively participate.

We found, however, an effect of the females' sexual cycle on the number of adult males: there were more breeding-age males with the group during the reproductive season. While some adult males were highly social and were almost always present throughout the study, others were more elusive. Yet, sub-adult males tended to be continuously associated with the group, independent of their origin. During our 15-month study, we witnessed the progressive emigration of a 9-year-old natal male as well as two immigration events (one sub-adult and one adult male). This immigration rate roughly corresponds to the rate previously observed for this group (EW, pers. obs.). Historical data on these mandrills suggested that wild sub-adult (6–9 years old) and adult males emigrated at all ages, and that secondary dispersal occurred. Genetic evidence also indicated that related males immigrated into the study group but whether they immigrated together or at different times is still unknown. Detailed studies on male dispersal are needed to fully describe this important milestone in male mandrills' life.

This study also clarified the previous notion that mandrill societies result from temporal aggregations of several one-male units [Hoshino et al., 1984; Jouventin, 1975]. This interpretation might originate from the observation that female mandrills appear to have favorite adult male partners in the wild (MJEC, pers. obs.) as they do in captivity [Setchell, 2005]. This might lead to the formation of temporal clusters within the group that resemble those of one-male societies. However, mandrill behavior does not correspond to what is known on baboon species forming one-male units. For example, in hamadryas baboons, adult males are highly aggressive to females and reproduction is often coercive (e.g., [Grueter et al., 2012; Kummer, 1968, 1984]). In contrast, female mandrills have a higher degree of control over male group membership through female–female coalitions [Setchell et al., 2006] mating success and social partner choice [Charpentier et al., 2005]. This pattern rather compares to the male–female relationships found in gelada baboons, where females can exert control over their male partners via their social relationships [Dunbar, 1983]. Interestingly, Patzelt et al. [2011] found that the social structure of Guinea baboons is more fluid than can be classified by the traditional distinction between one-male units and multi-male–multi-female social organizations, suggesting that baboon social systems might be more variable across baboon species. Further studies on association patterns between female and male

mandrills will clarify whether these bonds are transient or enduring and whether several of these clusters occur simultaneously in the same group.

Spatial Ecology

The second aim of this study was to analyze how group composition as well as environmental factors affected space use. We found that mandrills traveled between 0.44 and 6.50 km/day in an area of approximately 8.6 km². They ranged freely in forest patches in and outside the park and were not restricted by the fences that mark the park's physical boundaries. They avoided open savannas where they are presumably more vulnerable to predators or poachers. These results fall into the range reported in previous studies on this species. Hoshino [1985] reported home range sizes from 5 to 28 km² and daily path lengths of 2.5–4.5 km/day in Cameroon. Jouventin [1975] estimated daily distances of 1.3–8 km/day in Gabon. The large home range size determined by White et al. [2010] for a group of ca. 700 individuals (59–118 km²) also corresponded to the findings of this study if we consider the smaller size of the study group (using the regression model from [Clutton-Brock & Harvey, 1977a]; compare with Figure 5 in [White et al., 2010]). Not surprisingly, mandrill's home range areas and daily path lengths are greater than in many other forest-dwelling primate species that have mainly arboreal life styles and are smaller in body and group size [Gillespie & Chapman, 2001; Nunn & Barton, 2000; Olupot et al., 1997; Palacios & Rodriguez, 2001].

We also found that mandrills seemed to travel more in one particular forest block, which is the closest to human settlements. Since human disturbances and poaching activity were noticeably higher in this area than in other parts of the park, we suspect this likely caused more frequent displacements of the group. Meanwhile, we found a strong seasonal variation on DPL. During the short rainy season (October–November), mandrills traveled farther per day than during any other season. This increase likely reflects changes in the environment rather than changes in group size because no major changes in the group were noticed during that period of the year. Moreover, the short rainy season just follows the long dry season and leads to stark changes in the vegetation and thus likely as well in food availability and quality [Hoshino, 1985]. This interpretation of the seasonal effect is supported by the positive relationship we found between precipitation and DPL. A possible explanation for this pattern is that mandrills shifted their diet to include more fruits (in higher density during the rainy seasons [Chapman et al., 1999; van Schaik et al., 1993]), which mainly occur clumped in irregularly spaced fruiting trees. This would require the group to bridge the distances between fruit patches, while other food items such as leaves and roots are usually more evenly distributed.

Using cutting-edge statistical methods, we were further able to tease apart the contributions to space use of correlated effects of environmental factors, such as temperature and precipitation, and other factors, such as parasite load and demographic variables. We found a positive effect of the number of adult males present on the distance traveled by the group. Due to the strong sexual dimorphism in mandrills, adult males should have higher energy expenditure. Therefore, an increase in the number of adult males might raise the cumulative caloric demands of the group and lead to the need to explore more foraging sites during one day [Milton & May, 1976]. As an alternative explanation, a larger number of immigrating males may increase the exploratory propensity of the group as males possibly migrate into the group from distant sites and have knowledge of a larger territory. If true, this mechanism could have wider implications for the relationship between philopatry and dispersal patterns, and more generally range shifts in many species.

In contrast, we did not find an effect of the presence of lactating females on DPL. Lactation is thought to be the most energy demanding stage of reproduction in mammals [Gittleman & Thompson, 1988; Hinde et al., 2009] and in the study group, up to 60% of the females were lactating at the same time. On the other hand, it might be possible that females carrying newborn are restricted in their movements and therefore do not influence DPL per se.

Finally, we found a positive relationship between the richness in SLC parasites and DPL: the more the group was parasitized with directly transmitted protozoans, the more DPL increased. Interestingly, richness in parasites that need a period of maturation in the environment before being contaminant (LLC), such as nematodes, did not influence DPL, possibly because the risks of contamination in staying for short periods of time in the same area is lower. Long-distance migrations in several taxa have been proposed as a strategy to lower parasite exposure by leaving them behind [Altizer et al., 2011]. Although these studies were carried out on the spatial scale of continents, the mechanism may also work on a smaller spatial scale, as long as parasite contamination decreases between revisits.

We, therefore, suggest that the daily travels of mandrills could be seen as a way to escape contaminated habitats on a local scale. In addition, there could also be an interaction between food availability and parasite load as observed in red colobus [Chapman et al., 2006] and snowshoe hares [Murray et al., 1998], where food availability had a negative effect on parasite infections. It is, therefore, possible that we measured in part an effect of food availability on DPL via parasite richness. While, we cannot completely rule out this possibility, we would then expect such an effect to be also true for LLC parasites, which we did not find any evidence for. A

fine-grained study on patterns of occupation and re-occupation of mandrills' home ranges is, therefore, needed to clarify the relationship between parasite load and DPL.

CONCLUSIONS

This study provides the first continuous long-term observation of a wild mandrill social group. By individually recognizing group members and following adult male movements over a 15-month period, we were able to infer new details about the role of males in mandrill social organization. In particular, our results indicate that mandrills live in multi-male–multi-female groups that are not composed of one-male units and that some males are present all year long. We were further able to show the influence of group composition, in particular the number of adult males present and parasite load on daily group movements. We present also the first GPS-based estimate of home range size in mandrills. This study will help to build hypotheses and provide a starting point for future studies of mandrill ecology on male dispersal, female–male bonds and the role of parasite pressure in group movements.

ACKNOWLEDGMENTS

We are grateful to past and present staff of the Mandrillus Project for their assistance in data collection. We also would like to thank Simon Benhamou for helpful discussions on the analysis of GPS data and help with the BRB/MKDE software. This study was funded by a grant of the Deutsche Forschungsgemeinschaft (DFG, KA 1082-20-1) to MJEC and PMK, a “Station d'Etudes en Ecologie Globale” (INEE-CNRS) to MJEC, and a “Laboratoire International Associé” (CIRMF and INEE-CNRS) to MJEC. This study was approved by an authorization from the CENAREST institute (permit number: AR0052/12/MENESTFPRSCJS/CENAREST/CG/CST/CSAR). This is a Project Mandrillus publication number 5.

References

- Abegglen JJ. 1984. On socialization in hamadryas baboons. Lewisburg: Bucknell University Press.
- Abernethy KA, White LJ, Wickings EJ. 2002. Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *Journal of Zoology* 258:131–137.
- Altizer S, Bartel R, Han BA. 2011. Animal migration and infectious disease risk. *Science* 331:296–302.
- Benhamou S, Cornéilis D. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. *Journal of Wildlife Management* 74: 1353–1360.
- Benhamou S. 2011. Dynamic approach to space and habitat use based on biased random bridges. *PLoS ONE* 6:e14592.
- Buchan JC, Alberts SC, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. *Nature* 425:179–181.
- Burnham KP, Anderson DR. 2002. Model selection and multi model inference: a practical information-theoretic approach. 2nd edition. New York: Springer-Verlag.
- Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* 15:189–211.
- Chapman CA, Wasserman MD, Gillespie TR, et al. 2006. Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology* 131:525–534.
- Charpentier M, Peignot P, Hossaert-McKey M, et al. 2005. Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behavioral Ecology* 16:614–623.
- Charpentier MJE, Peignot P, Hossaert-McKey M, Wickings EJ. 2007. Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. *Animal Behaviour* 73:37–45.
- Clutton-Brock TH, Harvey PH. 1977a. Primate ecology and social organization. *Journal of Zoology* 183:1–39.
- Clutton-Brock TH, Harvey PH. 1977b. In: Clutton-Brock TH, editor. Species differences in feeding and ranging behaviour in primates. London: Academic Press. p 556–584.
- Dunbar RIM. 1983. Structure of gelada baboon reproductive units. 3. The male's relationship with his females. *Animal Behaviour* 31:565–575.
- Dunbar RIM, Dunbar EP. 1975. Social dynamics of gelada baboons. Basel: Karger.
- Freeland W. 1980. Mangabey (*Cerocebus albigena*) movement patterns in relation to food availability and fecal contamination. *Ecology* 61:1297–1303.
- Galbany J, Romero A, Mayo-Alesón M, et al. 2014. Age-related tooth wear differs between forest and savanna primates. *PLoS ONE* 9:e94938.
- Gillespie TR, Chapman CA. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. *Behavioral Ecology and Sociobiology* 50:329–338.
- Gittleman JL, Thompson SD. 1988. Energy allocation in mammalian reproduction. *American Zoologist* 28:863–875.
- Grueter CC, Chapais B, Zinner D. 2012. Evolution of multilevel social systems in nonhuman primates and humans. *International Journal of Primatology* 33:1002–1037.
- Hausfater G, Meade BJ. 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23:287–297.
- Hinde K, Power ML, Oftedal OT. 2009. Rhesus macaque milk: magnitude, sources, and consequences of individual variation over lactation. *American Journal of Physical Anthropology* 138:148–157.
- Hongo S. 2014. New evidence from observations of progressions of mandrills (*Mandrillus sphinx*): a multilevel or non-nested society? *Primates* 55:473–481.
- Hoshino J, Mori A, Kudo H, Kawai M. 1984. Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. *Primates* 25:295–307.
- Hoshino J. 1985. Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. *Primates* 26:248–273.
- Hurvich CM, Tsai C-L. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- Isbell LA, Pruettz JD, Young TP. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behavioral Ecology and Sociobiology* 42: 123–133.
- Jouventin P. 1975. Observations sur la socio-écologie du mandrill. *La Terre et la Vie* 29:439–532.

- Kappeler P, van Schaik C. 2002. Evolution of primate social systems. *International Journal of Primatology* 23: 707–740.
- Kummer H. 1968. Social organization of hamadryas baboons: a field study. Basel: Karger.
- Kummer H. 1984. From laboratory to desert and back: a social system of hamadryas baboons. *Animal Behaviour* 32: 965–971.
- Milton K, May ML. 1976. Body weight, diet and home range area in primates. *Nature* 259:459–462.
- Murray DL, Keith LB, Cary JR. 1998. Do parasitism and nutritional status interact to affect production in snowshoe hares? *Ecology* 79:1209–1222.
- Nathans LL, Oswald FL, Nimon K. 2012. Interpreting multiple linear regression: a guidebook of variable importance. *Practical Assessment, Research & Evaluation* 17: 1–19.
- Nimon KF, Oswald FL. 2013. Understanding the results of multiple linear regression: beyond standardized regression coefficients. *Organizational Research Methods* 16:650–674.
- Nunn CL, Barton RA. 2000. Allometric slopes and independent contrasts: a comparative test of kleiber's law in primate ranging patterns. *The American Naturalist* 156:519–533.
- Olupot W, Chapman CA, Waser PM, Isabirye-Basuta G. 1997. Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *American Journal of Primatology* 43:65–78.
- Palacios E, Rodriguez A. 2001. Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a southeastern colombian rainforest. *American Journal of Primatology* 55:233–251.
- Patzelt A, Zinner D, Fickenscher G, Diedhiou S, Camara B, Stahl D, Fischer J. 2011. Group composition of Guinea baboons (*Papio papio*) at a water place suggests a fluid social organization. *International Journal of Primatology* 32: 652–668.
- Peakall R, Smouse PE. 2006. GENEALEX: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288–295.
- Peakall R, Smouse PE. 2012. GenALEX 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 28:2537–2539.
- Peignot P, Charpentier MJE, Bout N, et al. 2008. Learning from the first release project of captive-bred mandrills *Mandrillus sphinx* in Gabon. *Oryx* 42:122–131.
- Queller DC, Goodnight KF. 1989. Estimating relatedness using genetic markers. *Evolution* 43:258–275.
- R Development Core Team R. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing <http://www.r-project.org>
- Ray-Mukherjee J, Nimon K, Mukherjee S, et al. 2014. Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution* 5:320–328.
- Rogers ME, Abernethy KA, Fontaine B, et al. 1996. Ten days in the life of a mandrill horde in the Lopé Reserve, Gabon. *American Journal of Primatology* 40:297–313.
- Setchell JM, Dixson AF. 2001. Circannual changes in the secondary sexual adornments of semifree-ranging male and female mandrills (*Mandrillus sphinx*). *American Journal of Primatology* 53:109–121.
- Setchell JM, Dixson AF. 2002. Developmental variables and dominance rank in adolescent male mandrills (*Mandrillus sphinx*). *American Journal of Primatology* 56:9–25.
- Setchell JM, Knapp LA, Wickings EJ. 2006. Violent coalitionary attack by female mandrills against an injured alpha male. *American Journal of Primatology* 68:411–418.
- Setchell JM, Lee PC, Wickings EJ, Dixson AF. 2001. Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology* 115:349–360.
- Setchell JM, Lee PC, Wickings EJ, Dixson AF. 2002. Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *International Journal of Primatology* 23:51–68.
- Setchell JM. 2005. Do female mandrills prefer brightly colored males? *International Journal of Primatology* 26:715–735.
- Van Schaik C, Terborgh J, Wright S. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- Tutin CEG. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve. Gabon. *Primates* 40:249–265.
- White EC, Dikangadissi J-T, Dimoto E, et al. 2010. Home-range use by a large horde of wild *Mandrillus sphinx*. *International Journal of Primatology* 31:627–645.

Supporting Information

Additional supporting information may be found in the online version of this article.