# RESEARCH ARTICLE

# Associations Between the Drill (*Mandrillus leucophaeus*) and Sympatric Monkeys in Korup National Park, Cameroon

CHRISTOS ASTARAS[1]*, STEFAN KRAUSE[2], LUTZ MATTNER[3], CHRISTOPH REHSE[1], AND MATTHIAS WALTERT[1]
[1]*Centre for Nature Conservation, Department of Conservation Biology, Georg-August-Universität Göttingen, Germany*
[2]*Fachbereich Elektrotechnik und Informatik, Fachhochschule Lübeck, Germany*
[3]*FB IV – Mathematik, Universität Trier, Germany*

Studies of polyspecific associations among African forest primates have primarily focused on arboreal *Cercopithecus* and *Procolobus/Colobus* species. We examined the association frequency of the terrestrial drill (*Mandrillus leucophaeus*) with six sympatric monkey species in Korup National Park, Cameroon, testing reports that *Mandrillus* associations are infrequent and transient. We conducted 3,284 km of trail walks for 12 months (February–June 2006; July 2007 to January 2008), recording species composition in 612 primate clusters. Using a Markov chain Monte Carlo test, we compared the observed frequency of dyadic associations against null models of ''no association.'' A novel conservative statistical approach which addresses possible dependence of observations close in time was also used, further strengthening confidence in our findings. Drills associated with all monkeys throughout the study period, and were with at least one other species (range 1–5) in half of the encounters. The association frequency of drills with red-capped mangabeys (*Cercocebus torquatus*) was greater than expected by chance, which is interesting given the morphological adaptation of the *Mandrillus-Cercocebus* clade for the exploitation of the same dietary niche, hard seeds. The difference we observed in the use of forest strata by drills and mangabeys may reflect a strategy to reduce food competition while in association. The nature and duration of observed drill associations varied. Although some associations seemed to be chance encounters, others lasted for hours with the involved species foraging together. Am. J. Primatol. 73:127–134, 2011.　© 2010 Wiley-Liss, Inc.

## INTRODUCTION

The formation of polyspecific associations among rainforest primates is a well documented phenomenon across Africa [Chapman & Chapman, 1996; Cords, 1990; Gartlan & Struhsaker, 1972; Gautier-Hion & Gautier, 1974; Moreno-Black & Maples, 1977; Oates & Whitesides, 1990]. Among possible functional explanations for them, antipredator and foraging advantages have frequently been proposed [e.g. Gautier-Hion et al., 1983; McGraw & Zuberbühler, 2008; Noë & Bshary, 1997]. Competitive advantages do not have to be equally distributed among involved species, and many associations may be simple chance encounters and consequently of limited evolutionary significance [Hutchinson & Waser, 2007; Waser, 1982, 1984; Whitesides, 1989].

Most studies of African forest primate associations have investigated habituated groups of arboreal *Cercopithecus* and *Procolobus/Colobus* species at long established research sites [e.g. Chapman & Chapman, 2000; Cords, 1987; Höner et al., 1997]. The few reports on terrestrial forest monkeys derive from studies focusing on habituated arboreal species [McGraw & Bshary, 2002] or from limited encounters made during community-wide association studies [Mitani, 1991]. The typically elusive nature and large home ranges of terrestrial primates make them hard to habituate and consequently less likely to become the subjects of long-term studies.

In this study, we examine the primate associations of the terrestrial drill (*Mandrillus leucophaeus*)

in the ancient, lowland Atlantic forests of Korup National Park (KNP) in southwest Cameroon, a region identified as a priority area for primate research and conservation [Oates et al., 1987]. To date, no study has examined the frequency of primate associations including *Mandrillus* or KNPs diurnal species (*Pan troglodytes*, *Cercocebus torquatus*, *Cercopithecus nictitans*, *C. mona*, *C. pogonias*, *C. erythrotis*, *M. leucophaeus*, and *Procolobus preussi*, the latter three being endemic to the Cross-Sanaga Rivers ecoregion [Oates et al., 2004]).

Preliminary data analysis from the study's first field season [Astaras et al., 2008] seemed to contradict Gartlan and Struhsaker's [1972] suggestion that all primate associations of the drill are "insignificant" and "infrequent." We tested this claim statistically by evaluating whether the observed frequency of associations between the drill and the semi-terrestrial red-capped mangabey (*C. torquatus*) could be attributed to chance. An association between the mandrill (*Mandrillus sphinx*), the drill's sole congener, and the red-capped mangabey was suspected by Mitani [1991], but limited data restricted analysis. The close phylogenetic relationship of the *Mandrillus* and *Cercocebus* genera [Disotell et al., 1992; McGraw & Fleagle, 2006] and their shared craniomandibular adaptations for exploiting hard seeds as a unique dietary niche [Fleagle & McGraw, 1999] makes studying drill–mangabey associations particularly relevant for understanding the potential of niche separation as a means of easing primate association costs [see Gartlan & Struhsaker, 1972; Struhsaker, 1978, for a review].

## METHODS

### Study Area

Our study site was a 38 km² area in the southern sector of KNP, a 1,260 km² predominantly primary forest in southwest Cameroon (4°54′ to 5°28′N, 8°42′ to 9°16′E). Precipitation is seasonal, with a single wet season from May to October (peak in August) and a distinct dry season from December to February. Mean annual rainfall is >5,000 mm, temperature varies little (monthly mean maximum 30.6±SD 1.6°C), and plant phenology shows strongly seasonal patterns with a wet season peak in fruiting [Chuyong et al., 2004]. The topography of the study area consists of rolling hills and low-lying stream valleys with rocky outcrops to the north (Fig. 1). Vegetation is characterized as Biafran coastal forest, a closed-canopy lowland moist forest dominated by Caesalpinioideae species [Letouzey, 1968].

In KNP, the main primate predators are humans, the crowned eagle (*Stephanoaetus coronatus*), pythons (*Python* spp.), and historically the extirpated leopard (*Panthera pardus*). There are no documented reports in the region of chimpanzees eating monkeys. Hunting pressure in the study area is light-to-moderate, because the area is far (>5 km) from villages and researchers are present [see Linder, 2008].

### Data Collection

We regularly walked the study area's 68 km trail network in February–June 2006 and July 2007 to January 2008, covering 3,284 km (15–20 days/month; 274±SD 38 km/month). These walks took place throughout the day from dawn until dusk. The trails extend across the study area's elevation gradient (Fig. 1). Encountered monkeys were recorded as "clusters." Following Whitesides [1989] and others [Chapman & Chapman, 1996; Höner et al., 1997; McGraw & Bshary, 2002; Oates & Whitesides, 1990], we considered individuals part of the same cluster if
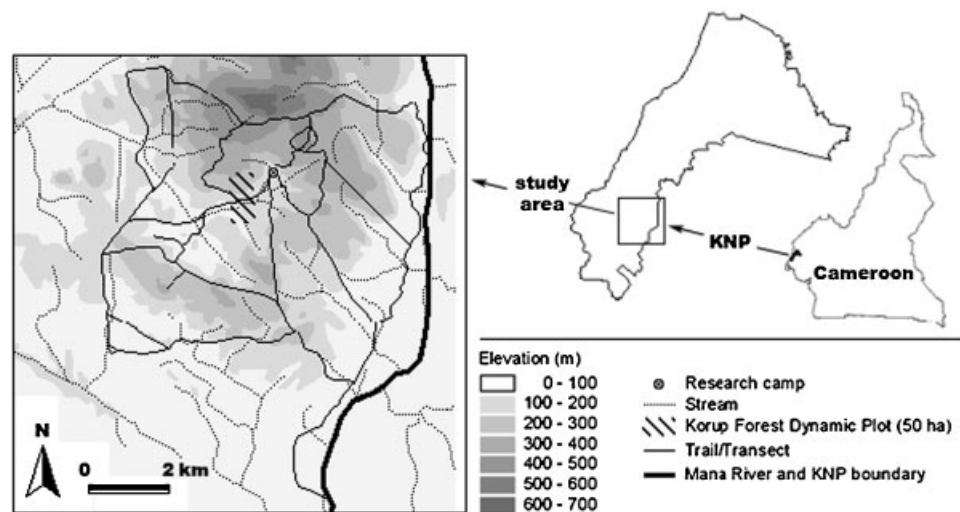


Fig. 1. Topographic map of the study area depicting its trail network and location within Korup National Park (KNP) and Cameroon. (Elevation data were digitized from a 1:200,000 map of Cameroon's National Cartographic Center–1979.)

they were within 50 m of each other. Chimpanzees (*P. troglodytes)* were never seen in association and were hence excluded from analysis. The two field teams each consisted of an experienced exhunter as a guide and either the first author or a trained field assistant as a data collector. To increase our chances of encountering even the least conspicuous monkeys and smaller groups, we walked slowly (mean 2 km/hr) and quietly, stopping often to scan the surrounding forest. We remained with encountered clusters for at least 3 min and recorded the time, trail, species composition, detection method (visual or audio), approximate distance from observers, and reliability of the collected data. With drill and red-capped mangabey groups, we also estimated by sight the height above ground of the first animal seen. Teams were periodically trained in estimating distance and height in order to ensure accuracy and comparability of observations.

We considered encounters unreliable when they occurred at distances that precluded data collection (e.g. *C. nictitans* calls at 200 m) and, less often, when they were too brief to meet the minimum duration limit or when they occurred under difficult observation conditions (e.g. heavy rainfall, dusk). A similar minimum observation duration has been used for primate transect surveys in the KNP and its support zone [Linder, 2008; Waltert et al., 2002], and it seemed sufficient for detecting species composition of most clusters up to ~50 m from the trail during an on-site pilot study by Astaras in 2005.

All species were represented by multiple groups within the study area, but we could not distinguish groups as the animals were not habituated to human presence. We followed drill groups off-trail, maintaining audio contact and avoiding detection for as long as possible, taking notes on the nature of drill associations (duration, interspecific interactions, and vocalizations).

Field research was conducted with the permission of the managing authority for Cameroon's National Parks (Ministry of Forestry and Wildlife) and the consent of the KNPs conservator, adhering to national legal requirements.

### Data Analysis

Species composition data were placed in a presence–absence matrix, where "1" in row "i" of column "j" denotes that the species "j" was present in cluster "i," while a "0" marks its absence. Data from both mono- and polyspecific clusters were included in the matrix.

To test the observed frequencies of dyadic associations in our matrix against the frequency expected if encounters occurred only by chance, we adopted as a null model of "no association" all presence–absence matrices with the same row and column sums as the observed one to be equally likely.

This null model can then be tested by choosing a test statistic and applying a Markov chain Monte Carlo approach according to Besag and Clifford [1989]. Krause et al. [2009] describe the correct implementation of the Besag–Clifford algorithm (BC) and also discuss its possible pitfalls. As a general test of the null hypothesis, without associations of a particular pair of species in mind, we used as our test statistic the association strength square sum score (ASSS-score) defined in Krause et al. [2009]. For each dyad of the seven monkey species under consideration, we counted the number of co-occurrences in the observed clusters. This yielded 21 numbers ($7 \times 6/2$) and the ASSS-score was the sum of the squares of these (without squaring, the score would be the same for all matrices with the same row and column sums). To test the null model for specific associating dyads, we took as our test statistic the number of the pair's co-occurrences (here, squaring would not make any difference in the analysis).

The above analysis rests on the assumption that our null model is an appropriate one for "no association." The assumption could be violated because of temporal dependences between observations. For example, a primate group observed in a cluster one day is less likely to be reobserved in another cluster that same day vs. the subsequent day. We addressed this potential nonindependence of cluster membership with two alternative, conservative analyses. The first was recently proposed by Sundaresan et al. [2009] and uses a blocked variant of the Besag–Clifford approach (BBC). In addition to keeping the sums of each column constant in the null model matrices, the sums within each subcolumn corresponding to an observation day ($N = 179$) are also kept fixed. The second analysis is a novel one, and uses the original Besag–Clifford method (BC) applied to a randomly chosen subsample containing just one observation per day. This modification, hereafter referred to as SBC, addresses potential dependences resulting from erroneous repeat counts of clusters reencountered in a day, which is a possibility when working with unhabituated animals in dense rainforest. The SBC analysis is conservative (losing statistical power if, in fact, no dependences are present under the null hypothesis) by making use of only part of the data. For example, in the present case, only 29% of the data is used in each matrix (179 of 612 observations). The resulting *P*-value is considered randomized as it depends on the particular subsample chosen. However, repeating the subsampling *M* times, an essentially non-randomized *P*-value can be calculated, which is valid even under the worst mathematically possible dependencies among same day observations. This nonrandomized *P*-value is the median of the *M* *P*-values times a certain correction constant $c_M$, if this product is at most 1, or 1 otherwise. Regardless of *M*, $c_M \leq 2$ (here $M = 1,000$ and $c_M = 1.846$). This

derandomization is a further source of conservatism in our analysis. See Mattner [2010] for mathematical details.

## RESULTS

We encountered drills visually 35 times (0.01/km), including solitary males on two occasions. We located drills via audible cues 23 additional times (0.007/km). The sightings involved at least two different groups of drills [Astaras et al., 2008].

We recorded reliable data on species composition of 612 primate clusters (52% of total encounters), 44% of which were polyspecific. All monkeys formed mono- and polyspecific associations (Fig. 2) and were observed together with all other species (Table I). Drills were in association during half ($N = 22$) of the encounters. Putty-nosed guenons (*C. nictitans*) were the most commonly encountered species ($N = 370$) and were present in 39% of drill encounters. In turn, drills were more frequently present in encounters of red-capped mangabeys (22% of $N = 51$) than those of any other species.

## Frequency of Drill Associations

Testing the null hypothesis of ''no association'' between Korup monkeys with a direct application of the Besag–Clifford algorithm (BC) yielded $P$-values that led us to reject the null hypothesis in the case of dyadic association frequencies in general ($P < 0.0001$) and those of the drill–mangabey pair ($P = 0.006$). Three more association pairs had $P < 0.05$: *C. nictitans–C. erythrotis*, *C. nictitans–C. pogonias*, and *P. preussi–C. pogonias*. These findings, of course, are subject to the appropriateness of the null model. The more robust BBC test yielded $P$-values of $P < 0.0001$ for general association frequencies and $P = 0.01$ for the drill–mangabey pair. The *C. nictitans–C. erythrotis*, *C. erythrotis–C. pogonias*, and *P. preussi–C. pogonias* pairs also had $P < 0.05$.

For the conservative SBC test, we report here both the median $P$-value (SBC $m$) of $M = 1,000$ samplings and the nonrandomized $P$-value (SBC $d$). The results were $m = 0.004$ and $d = 0.008$ for general associations, whereas the drill–mangabey values $m = 0.03$ and $d = 0.06$ were the lowest of all dyadic associations. For SBC $m$, the null hypothesis of ''no
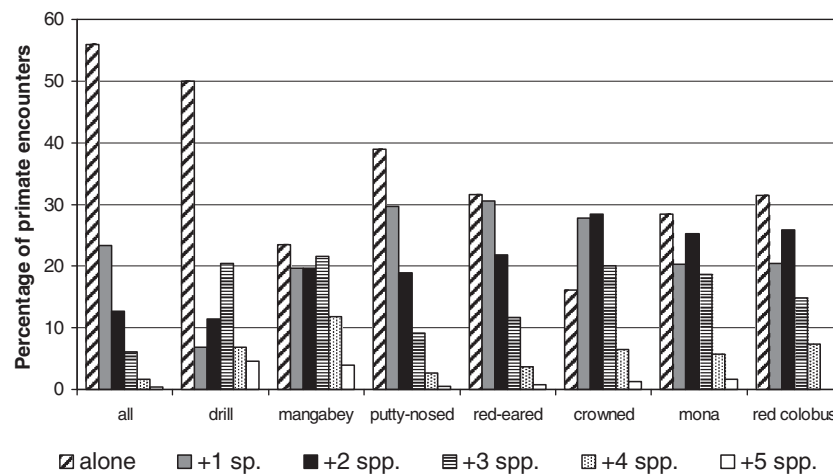


Fig. 2. Proportion of monospecific and polyspecific encounters of nonhominid primates (drill = *Mandrillus leucophaeus*, $N = 44$; mangabey = *Cercocebus torquatus*, $N = 51$; putty-nosed = *Cercopithecus nictitans*, $N = 370$; red-eared = *C. erythrotis*, $N = 267$; crowned = *C. pogonias*, $N = 155$; mona = *C. mona*, $N = 123$; red colobus = *Procolobus preussi*, $N = 54$).

**TABLE I. Summary of Dyadic Association Frequencies Showing the Percentage Presence of Species X (Column) in Total Encounters (N; Both Mono- and Polyspecific) of Species Y (Row)**

| Species (♯ encounters) | C. nictitans | C. erythrotis | C. pogonias | C. mona | P. preussi | C. torquatus | M. leucophaeus |
|---|---|---|---|---|---|---|---|
| *C. nictitans* ($N = 370$) | | 43[a,b,c] | 28[a,c] | 20 | 6 | 8 | 5 |
| *C. erythrotis* ($N = 267$) | 57[a,b,c] | | 28[b] | 21 | 7 | 9 | 5 |
| *C. pogonias* ($N = 155$) | 66[a,c] | 50[b] | | 26 | 15[a,b] | 12 | 7 |
| *C. mona* ($N = 123$) | 59 | 46 | 33 | | 6 | 8 | 5 |
| *P. preussi* ($N = 54$) | 43 | 33 | 43[a,b] | 13 | | 7 | 7 |
| *C. torquatus* ($N = 51$) | 55 | 51 | 35 | 20 | 8 | | 22[a,b,c] |
| *M. leucophaeus* ($N = 44$) | 39 | 30 | 25 | 14 | 9 | 25[a,b,c] | |

[a,b,c]Denotes a dyadic association frequency for which the null hypothesis of ''no association'' is rejected ($P < 0.05$) based on the application of the BC, BBC, and SBC $m$ algorithm, respectively.

**TABLE II. Results of Testing Observed Frequencies of Dyadic Primate Associations in General and Those Involving the Drill (*Mandrillus leucophaeus*) Against the Null Hypothesis of "No Association", Applying Three Variations of the Besag–Clifford Algorithm (Markov Chain Monte Carlo Test)**

| Species dyads | $N$ | BC | BBC | SBC $m$ | SBC $d$ |
|---|---|---|---|---|---|
| | | *P*-values | | | |
| Dyadic associations in general | – | 0.000001 | 0.000009 | 0.004 | 0.008 |
| *M. leucophaeus–C. torquatus* | 11 | 0.006 | 0.01 | 0.03 | 0.06 |
| *M. leucophaeus–P. preussi* | 4 | 0.73 | 0.78 | 0.45 | 0.84 |
| *M. leucophaeus–C. nictitans* | 17 | 0.99 | 0.99 | 0.88 | 1 |
| *M. leucophaeus–C. erythrotis* | 13 | 0.99 | 0.99 | 0.91 | 1 |
| *M. leucophaeus–C. pogonias* | 11 | 0.88 | 0.86 | 0.75 | 1 |
| *M. leucophaeus–C. mona* | 6 | 0.98 | 0.99 | 0.74 | 1 |

BC, a direct, unmodified application of the Besag–Clifford algorithm; BBC, a more robust blocked variant of the Besag–Clifford algorithm; SBC $d$, a novel, conservative application of the Besag–Clifford algorithm, calculated as min(1, $c_M \times m$), where $c_M = 1.846$ for $M = 1,000$, and m is the median of 1,000 *P*-values (reported in column SBC $m$), each computed from one observation per day. The test statistic used is the number of co-occurrences of the drill with a given species, except for the general association test which used the ASSS score for all dyadic combinations of the seven species under consideration.

association'' was also rejected for *C. nictitans–C. erythrotis* and *C. nictitans–C. pogonias*. Table II presents the test results of all three applications of the BC algorithm (BC, BBC, and SBC) for general associations and those involving the drill.

### Nature of Drill Associations

The nature and duration of observed drill associations varied. On five occasions, it seemed that the drills may have encountered another primate cluster by chance. Associations lasted a few minutes, just long enough for the species' travel paths to cross. During three other brief observations, the drills were stationary, feeding in association with other monkeys around fruiting trees (e.g. *Irvingia gabonensis*), which can not exclude the possibility that the involved species were simply attracted to a common food source. The remaining 14 drill associations lasted for hours (up to 6 hr), with all species apparently foraging and moving together. In most cases, we could not determine whether associations were established, maintained, or terminated by actions of all or some of the involved species. Exceptions were two long, late afternoon, encounters during which drills moved on the ground and the associated guenons (*C. pogonias–C. erythrotis*; *C. pogonias–C. nictitans–C. erythrotis*) seemed unilaterally to maintain contact by trailing the drills. We saw a drill group associate with >1 cluster/day only once (3 clusters in a period of 2.5 hr).

We did not see drills physically contact or forage within 5 m of other monkeys. The sole exception occurred when a solitary male crossed the ground through a resting mangabey group, passing within 2 m of juveniles playing on the bank of a creek. When in association, drills were often at the edges of polyspecific clusters, near the upper end of the 50 m limit used to define an association ($N = 6$ confirmed cases). On the contrary, other monkeys

and especially guenons (*Cercopithecus* spp.) often mixed on the same trees with other species.

Drill groups extended over a wide front while foraging on the ground. Depending on the group's size [mean 43; Astaras, 2009], the front ranged from 50 to 100 m. Groups became more compact when having to cross wide trails or streams, with many animals dashing across in line. With the exception of Preuss's red colobus (*P. preussi*) groups, which spread diffusely through the canopy, members of other monkeys typically ranged within a 15 m radius.

We tracked drills to their sleeping sites on five occasions. Group members spread over a few neighboring trees (canopy/emergent) for the night, always apart from other monkeys. Even when a group of *C. pogonias* and *C. erythrotis* remained in association with drills until dusk, the guenons eventually slept >50 m away. On no occasion could we confirm the continuation of a drill group's primate association over an entire day.

We observed drills with all other monkeys throughout the year. There was no significant difference between wet and dry/transition months in either the frequency of drill associations ($\chi^2 = 0.819$, df $= 1$, 2-tailed $P = 0.36$,) or the number of species with drills (Kolmogorov–Smirnov two-sample test: $Z = 0.453$, 2-tailed $P = 0.07$; see Table III for details).

Drills clearly reacted to the alarm calls of other monkeys by becoming alert and/or fleeing quietly on the ground, but did not join in multispecies alarm calls of agitated polyspecific clusters. In general, drills vocalized rarely. Mean frequency of all drill call types was 3.3 calls/hour, based on data from encounters with >30 min duration [total 101 hr; see Astaras, 2009]. There was no significant difference in the calling frequency of drills when in mono- (mean 5.7/hour) and polyspecific (mean 2.9/hour) clusters (Mann–Whitney test: $U = 94$, $N = 10/23$, 2-tailed $P = 0.43$).

**TABLE III. Summary of Seasonal Research Effort and Drill Encounters**

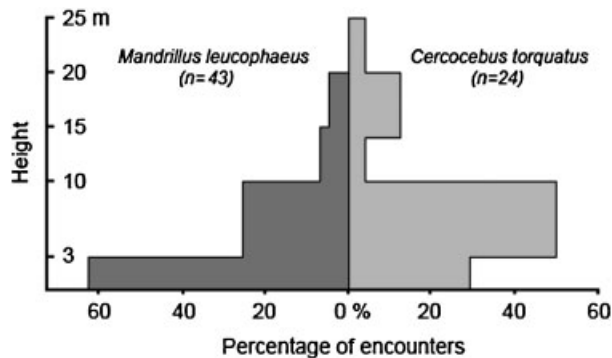| Season | Field effort km/month | Total encounters | Polyspecific encounters (*C. torquatus* present) | Species per encounter (only in polyspecific)[a] |
|---|---|---|---|---|
| Wet (May–October) | 249 ± SD 32 | 21 | 9 (8) | 2.48 (3.6) |
| Dry[b] (November–April) | 308 ± SD 34 | 23 | 10 (3) | 2.35 (4.1) |

[a]Inclusive of drills in both cases.
[b]Inclusive of transition months November, March–April.



Fig. 3. Vertical position of the first observed animal in drill and red-capped mangabey day encounters.

The drill was the most terrestrial monkey species at KNP. The first drill we observed in each group was at <3 m above the ground (e.g. on the forest floor, tree buttresses, small trees, or stilt roots) in 63% of the day encounters where the vertical position of the group could be determined (Fig. 3). Early morning encounters at sleeping sites were excluded from this analysis. Most of the time (88%), the position of the first drill seen was representative of the rest of the group. In the five exceptions, the vertical distribution of the group extended from the ground to <10 m up. Typically, juveniles moving on the periphery of the group were the first to be seen. The red-capped mangabey's day foraging was more arboreal than the drill's and is best described as semi-terrestrial (Fig. 3).

## DISCUSSION

Based on our statistical analysis, we conclude that chance cannot account for the observed frequency of dyadic associations among Korup monkeys in general and is unlikely to account for the drill–mangabey pair specifically, for which rejecting the null hypothesis narrowly failed only for the most conservative SBC *d* test. However, a statistically significant association is not de facto ecologically significant. For instance, the two species could be driven by mutual (but independent) attraction to common food sources. It is, therefore, important to critically examine all possible functional explanations of the drill–mangabey association.

Potential limitations of the data collection process should also be recognized. In the absence of habituated monkeys, our presence may have affected the fission or fusion of associations and consequently the species composition of observed clusters. Moreover, the probability of us detecting a cluster could have been influenced by its size or species composition. For instance, large clusters containing more visible and vocal species could be easier to locate and approach undetected. In such instances, the recorded frequency of some associations would be inflated by their higher detection rate. We are, nevertheless, confident about the quality of our data, because of (a) the training and experience of our field teams in primate identification and tracking (experienced hunters), (b) the dense network of trails which facilitated quiet movement (96% of the distance walked was on trails), (c) the well-established techniques which have been routinely used for primate transect surveys, including in the Korup region [Linder, 2008; Waltert et al., 2002], and (d) the use of a minimum duration for considering an encounter reliable enough to include in analysis. In addition, the encounter rates of monkeys in our study are comparable to those of a primate transect survey by Linder [2008] in the same section of KNP (Spearman rank correlation coefficient: $R = 0.92$, 2-tailed $P < 0.01$), which serves as a control comparison of the detection rate of our methods (Table IV).

Foraging advantages and predator avoidance are frequently proposed explanations for the formation of primate associations [e.g. McGraw & Zuberbühler, 2008; Teelen, 2007]. At first glance, the potential foraging advantages of a drill–mangabey association are not obvious. In contrast to the folivorous and frugivorous species that associate together in mixed species groups, drills and mangabeys are likely to have a high dietary overlap. Both genera are omnivores that include a high percentage of fruit in their diet [Astaras et al., 2008; Mitani, 1989; White, 2007] and share morphological adaptations for cracking open hard seeds [Fleagle & McGraw, 1999], a specialization that Korup drills use in the dry season (low fruit abundance) to increase seed predation [Astaras, 2009]. If foraging advantages, such as optimizing of foraging group size [Mitani, 1989; Terborgh, 1983], are to explain the observed drill–mangabey associations, they should exceed the costs of dietary competition. The difference in the terrestriality of drills and mangabeys observed in our study could be a means of reducing food competition

**TABLE IV. Comparison of Species' Encounter Rates During This Study and Those in the Southern Sector of Korup National Park Reported by Linder [2008]**

| Species | This study encounter rates—group/km (3,284 km trail walks) Total visual/audio (only reliable) | Linder, 2008 encounter rates—group/km (243 km transect surveys) Total visual/audio |
|---|---|---|
| M. leucophaeus | 0.02 (0.01) | 0.01 |
| C. torquatus | 0.03 (0.02) | 0.01 |
| P. preussi | 0.03 (0.02) | 0.05 |
| C. nictitans | 0.16 (0.11) | 0.15 |
| C. erythrotis | 0.09 (0.08) | 0.1 |
| C. pogonias | 0.07 (0.06) | 0.08 |
| C. mona | 0.06 (0.04) | 0.03 |

costs between the two species during associations. Reports by Mitani [1989] of a similar semi-terrestrial foraging pattern by red-capped mangabeys in Campo Wildlife Reserve, Cameroon, are consistent with such a proposal. The use of different forest strata is currently thought to explain the association in West and Central Africa of rainforest guenons which share similar feeding mechanisms [Buzzard, 2006; Gartlan & Struhsaker, 1979; Gautier-Hion, 1978; Shreier et al., 2009].

The cost of dietary competition incurred by drills and mangabeys during their associations is probably lower in periods of food abundance. Although the small number of observed drill–mangabey associations precludes safe generalizations, eight (73%) of the observations were made during the rainy season when fruit is plentiful (Table III).

Predator avoidance is a possible functional explanation of the drill–mangabey association. Even though large polyspecific groups may be easier to detect, it is reasonable to assume that their members benefit by having an increased vertical range of sentinels and hence improved predator detection [Gartlan & Struhsaker, 1979]. Indeed, it was noticeably harder for us to approach undetected drills associating with other monkeys, especially guenons, because all species responded to allospecific alarm calls. A study of terrestrial–arboreal primate associations by McGraw and Bshary [2002] in the Taï Forest, Ivory Coast, showed that arboreal species (*Cercopithecus diana* and *Procolobus badius*) benefited from the predator detection services of the terrestrial *Cercocebus atys*, increasing their utilization of lower forest strata. Of course, ecological advantages for involved species do not necessitate long-term associations as they cannot be a priori excluded in chance encounters [Waser, 1982].

The range of species observed to associate with drills is not surprising. Drills in the Southern

Bakundu Forest Reserve, Idenau forest [Gartlan & Struhsaker, 1979], and Bakossi region [Faucher, 1999] of Cameroon were also seen together with all sympatric monkeys, as were mandrills in Equatorial Guinea, Cameroon, and Gabon [Jouventin, 1975; Mitani, 1991; Sabater Pi, 1972].

Overall, the fragmentary knowledge of drill and red-capped mangabey ecology limits our interpretation of the statistically nonrandom association frequency between the two species. Nevertheless, we consider Gartlan and Struhsaker's [1972] characterization of drill associations as "insignificant" and "infrequent" to be overly simplistic and inaccurate. Our analysis also identified significant dyadic association frequencies between *Cercopithecus* species which had previously been reported in southwest Cameroon [Gartlan & Struhsaker, 1972, 1979], further supporting their ecological relevance. Methodologically, we believe that our novel approach to analyzing dyadic association patterns merits consideration, as a statistically sound method of testing for nonrandom associations where subjects are not habituated. Finally, our study brings attention to the complexity of interspecific interactions within the rich primate community of Korup National Park, identifying its value as a site for further studies. However, only with sustained commitment to the effective conservation of Korup and other remaining lowland Guinean forests will these complex biotic relationships be secured for the future.

## REFERENCES

Astaras C. 2009. Ecology and status of the drill (*Mandrillus leucophaeus*) in Korup National Park, Southwest Cameroon: implications for conservation [Dissertation]. Göttingen: Georg-August-Universität Göttingen. 267p.

Astaras C, Mühlenberg M, Waltert M. 2008. Note on drill (*Mandrillus leucophaeus*) ecology and conservation status in Korup National Park, southwest Cameroon. American Journal of Primatology 70:306–310.

Besag J, Clifford P. 1989. Generalized Monte Carlo significance tests. Biometrika 76:633–642.

Buzzard PJ. 2006. Ecological partitioning of *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* in the Taï Forest. International Journal of Primatology 27:529–558.

Chapman CA, Chapman LJ. 1996. Mixed-species primate groups in the Kibale forest: ecological constraints on association. International Journal of Primatology 17:31–50.

Chapman CA, Chapman LJ. 2000. Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. Behavioral Ecology and Sociobiology 47:129–139.

Chuyong GB, Condit R, Kenfack D, Losos E, Sainge M, Songwe NC, Thomas DW. 2004. Korup forest dynamics plot, Cameroon. In: Losos EC, Leigh Jr EG, editors. Forest diversity and dynamism: findings from a network of large-scale tropical forest plots. Chicago: University of Chicago Press. p 506–516.

Cords M. 1987. Mixed-species association of Cercopithecus monkeys in the Kakamega forest, Kenya. Berkeley: University of California. 109p.

Cords M. 1990. Mixed-species association of East African guenons: general patterns or specific examples? American Journal of Primatology 21:101–114.

Disotell TR, Honeycutt RL, Ruvolo M. 1992. Mitochondrial DNA phylogeny of the Old World monkey tribe Papionini. Molecular Biology and Evolution 9:1–13.

Faucher I. 1999. Natural history of the Bakossi mountains, Cameroon with special reference to diurnal primates. [M.Phil./Ph.D. upgrading proposal]. London: University College London. 42p.

Fleagle JG, McGraw SW. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. Proceedings of the National Academy of Sciences 96: 1157–1161.

Gartlan JS, Struhsaker TT. 1972. Polyspecific associations and niche separation of rainforest anthropoids in Cameroon, West Africa. Journal of Zoology 168:221–266.

Gartlan JS, Struhsaker TT. 1979. Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. In: Sussman RW, editor. Primate ecology: problem-oriented field studies. New York: Wiley. p 155–164.

Gautier-Hion A. 1978. Food niches and coexistence in sympatric primates in Gabon. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, Vol. 1 behaviour. London: Academic Press. p 269–286.

Gautier-Hion A, Gautier JP. 1974. Les associations polyspecifiques de plateau de M'passa, Gabon. Folia primatologica 22:134–177.

Gautier-Hion A, Quris R, Gautier JP. 1983. Monospecific vs. polyspecific life: a comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys. Behavioral Ecology and Sociobiology 12:325–335.

Höner OP, Leumann L, Noë R. 1997. Dyadic associations of red colobus and Diana monkey groups in the Taï National Park, Ivory Coast. Primates 38:281–291.

Hutchinson JMC, Waser PM. 2007. Use, misuse and extensions of ''ideal gas'' models of animal encounter. Biological Reviews of the Cambridge Philosophical Society 82:335–339.

Jouventin P. 1975. Observations sur la soci-ecologie du mandrills. Review of Ecology–Terre Vie 29:493–532.

Krause S, Mattner L, James R, Guttridge T, Corcoran MJ, Gruber SH, Krause J. 2009. Social network analysis and valid Markov chain Monte Carlo tests of null models. Behavioral Ecology and Sociobiology 63:1089–1096.

Letouzey R. 1968. Études phytogéographiques du Cameroun. Paris, France: Éditions Paul Lechevallier.

Linder JM. 2008. The impact of hunting on primates in Korup National Park, Cameroon: implications for primate conservation [Dissertation]. New York: The City University of New York. 376p.

McGraw WS, Bshary R. 2002. Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. International Journal of Primatology 23: 311–325.

McGraw WS, Fleagle JG. 2006. Biogeography and evolution of the *Cercocebus-Mandrillus* clade: evidence from the face. In: Lehman SM, Fleagle JG, editors. Primate biogeography: progress and prospects. New York: Springer. p 201–227.

McGraw WS, Zuberbühler K. 2008. Socioecology, predation, and cognition in a community of west African monkeys. Evolutionary Anthropology 17:254–266.

Mattner L. 2010. Combining individually valid and conditionally i.i.d. *P*-variables. arXiv:1008.5143v1.

Mitani M. 1989. *Cercocebus torquatus*: adaptive feeding and ranging behaviors related to seasonal fluctuations of food resources in the tropical rain forest of south-western Cameroon. Primates 30:307–323.

Mitani M. 1991. Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. Primates 32:137–151.

Moreno-Black G, Maples WR. 1977. Differential habitat utilization of four cercopithecidae in a Kenyan forest. Folia Primatologica 27:85–107.

Noë R, Bshary R. 1997. The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. Proceedings of the Royal Society of London B: Biological Sciences 264:253–259.

Oates JF, Whitesides GH. 1990. Association between Olive Colobus (*Procolobus verus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. American Journal of Primatology 21:129–146.

Oates JF, Gartlan JS, Struhsaker TT. 1987. A framework for African rain forest primate conservation. In: Marsch CW, Mittermeier RA, editors. Primate conservation in the tropical rain forest. New York: Alan R. Liss, Inc. p 321–327.

Oates JF, Bergl RA, Linder JM. 2004. Africa's Gulf of Guinea forests: biodiversity patterns and conservation priorities. Advances in applied biodiversity science No. 6. Washington, DC: Conservation International. 90p.

Sabater Pi J. 1972. Contribution to the ecology of *Mandrillus sphinx*, Linnaeus 1758, of Rio Muni (Republic of Equatorial Guinea). Folia Primatologica 17:304–319.

Shreier BM, Harcourt AH, Coppeto SA, Somi MF. 2009. Interspecic competition and niche separation in primates: a global analysis. Biotropica 41:283–291.

Struhsaker TT. 1978. Food habits of five monkey species in Kibale forest, Uganda. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, Vol. 1 behaviour. London: Academic Press. p 225–248.

Sundaresan SR, Fischhoff IR, Dushoff J. 2009. Avoiding spurious findings of nonrandom social structure in association data. Animal Behaviour 77:1381–1385.

Teelen S. 2007. Influence of chimpanzee predation on associations between red colobus and red-tailed monkeys at Ngogo, Kibale National Park, Uganda. International Journal of Primatology 28:593–606.

Terborgh JW. 1983. Five New World primates: a study in comparative ecology. Princeton: Princeton University Press. 280p.

Waltert M, Lien, Faber K, Mühlenberg M. 2002. Further declines of threatened primates in the Korup project area, south-west Cameroon. Oryx 36:257–265.

Waser PM. 1982. Primate polyspecific associations: do they occur by chance? Animal Behaviour 30:1–8.

Waser PM. 1984. ''Chance'' and mixed-species associations. Behavioral Ecology and Sociobiology 15:197–202.

White EC. 2007. Ecology of *Mandrillus sphinx*: ranging, diet and social structure of a mandrill horde in Lopé National Park, Gabon [Dissertation]. Exeter: University of Exeter. p 354.

Whitesides G. 1989. Interspecic associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: biological significance or chance? Animal Behaviour 37: 760–776.