RESEARCH ARTICLE

Ground-Nesting by the Chimpanzees of the Nimba Mountains, Guinea: Environmentally or Socially Determined?

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The chimpanzees (*Pan troglodytes verus*) of the Nimba Mountains, Guinea, West Africa, commonly make both elaborate (''night'') and simple (''day'') nests on the ground. In this study we investigated which factors might influence ground-nesting in this population, and tested two ecological hypotheses: 1) climatic conditions, such as high wind speeds at high altitudes, may deter chimpanzees from nesting in trees; and 2) a lack of appropriate arboreal nesting opportunities may drive the chimpanzees to nest on the ground. In addition to testing these two hypotheses, we explored whether ground-nesting is a sex-linked behavior. Data were collected monthly between August 2003 and May 2004 along transects and ad libitum. To identify the sex of ground-nesting individuals, we used DNA extracted from hair samples. The results showed that the occurrence and distribution of ground nests were not affected by climatic conditions or a lack of appropriate nest trees. Support was found for the notion that ground-nesting is a sex-linked behavior, as males were responsible for building all of the elaborate ground nests and most of the simple ground nests sampled. Elaborate ground nests occurred mostly in nest groups associated with tree nests, whereas simple ground nests usually occurred without tree nests in their vicinity. These results suggest that ground-nesting may be socially, rather than ecologically, determined. Am. J. Primatol. 69:407–419, 2007. © 2006 Wiley-Liss, Inc.

Key words: ground-nesting; *Pan troglodytes verus*; Nimba Mountains; DNA analyses

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INTRODUCTION

Nest-building has been found in all chimpanzee populations studied in the wild. Each weaned and healthy member of a community generally makes a new nest to sleep in every night [e.g., Goodall, 1962, 1968]. The chimpanzees build a nest, or sleeping platform, by bending or breaking branches radially, sometimes intertwining adjacent trees, and thus forming a circular frame of about 1 m in diameter. The main branches are then woven together and smaller branches are tucked in to create a sturdy platform [Fruth & Hohmann, 1996]. As a final touch, the nest is often lined with detached leafy twigs [Goodall, 1962, 1968]. In addition to nighttime nests, the chimpanzees sometimes also build nests during the day. These daytime nests usually serve as a place to rest between feeding bouts [Brownlow et al., 2001]. Day nests take less time to make and are usually less complex in structure than night nests (i.e., fewer trees and branches are incorporated and fewer twigs are used for lining) [Brownlow et al., 2001].

Chimpanzees are known to prefer arboreal nests [reviewed by Fruth & Hohmann, 1994, 1996]. Nonetheless, in several study sites across Africa, chimpanzees also make simple cushion-like nests on the ground for daytime resting (Bossou, Guinea [Humle, 2003]; Gombe, Tanzania [Goodall, 1968]; Taï, Côte d'Ivoire [Boesch, 1995]; Budongo, Uganda [Reynolds & Reynolds, 1965]; and Kanyawara, Uganda (Llorente, personal communication). A few instances of chimpanzees sleeping on the ground at night have been observed at Gombe, Tanzania [Goodall, 1968] and Kanyawara, Uganda (Llorente, personal communication), but all of these occurrences involved sick individuals that were too frail to construct an arboreal nest. In the Kalinzu Forest, Uganda [Furuichi & Hashimoto, 2000], and Bwindi Impenetrable National Park, Uganda [Maughan & Stanford, 2001], only a few nests (about 5%) are sited on the ground. Some of these may be night nests, but their status has yet to be established via direct observation. Overall, nesting on the ground is a rare behavior in wild chimpanzees, especially at night.

In contrast to other chimpanzee populations, the unhabituated chimpanzees (*Pan troglodytes verus*) in the Nimba Mountains in Guinea and Côte d'Ivoire, West Africa, commonly make nests on the ground [Humle, 2003; Matsuzawa & Yamakoshi, 1996]. Matsuzawa and Yamakoshi [1996] reported that 35.4% of nests at the Yealé study site on the Côte d'Ivoire side of the Nimba massif were built terrestrially in high-altitude areas during the dry season. At this site, two types of ground nests were distinguishable. The first type consisted mainly of terrestrial herbaceous vegetation (THV) and was structurally similar to the simple cushion-like day nests found elsewhere. The second type of ground nest was more sophisticated and was constructed by bending and breaking a number of small trees or saplings into a circle, yielding a nest similar in appearance to a typical tree nest. Matsuzawa and Yamakoshi [1996] proposed that these more elaborate ground nests may have been used overnight by the chimpanzees, based on their proximity to elaborate arboreal nests that were likely used for resting at night.

Ground-nesting has been proposed to result from low predation pressure [Furuichi & Hashimoto, 2000; Maughan & Stanford, 2001]. At most sites chimpanzees are vulnerable to large predators, such as leopards [Boesch, 1991] and lions [Tsukahara, 1993]. In the Nimba Mountains, predation pressure seems to be low or even absent, given that no recent sightings or signs of leopards have been reported in the region. However, although low predation pressure may allow the Nimba chimpanzees to nest on the ground, it does not explain what they gain by doing so. Here we address the question as to *why* chimpanzees choose to nest

terrestrially in Nimba. Two ecological hypotheses to explain ground-nesting were considered [Matsuzawa & Yamakoshi, 1996]: 1) Adverse climatic conditions, such as high wind speed at high altitudes, may make it either too dangerous (i.e., risk of falling from a tree) or uncomfortable (i.e., wind chill) to nest in the trees, and may therefore drive the chimpanzees to nest in more sheltered sites on the ground. This effect should be stronger during the dry season due to great seasonal variation in wind speed in the Nimba region. 2) A lack of appropriate nesting trees in areas where the chimpanzees seek to build their nests (e.g., on steep slopes) may lead them to nest terrestrially.

In addition to these ecological hypotheses, we examined whether ground-nesting represents a sex-linked behavior. Given that male chimpanzees have been found to nest lower than females at several study sites (Budongo, Uganda [Brownlow et al., 2001], and Kanyawara, Uganda (Llorente, personal communication)), ground-nesting could be an extreme form of this sex difference. The disparity in nesting height between the sexes may be caused by sexual dimorphism in body weight [Reynolds, 1967]. Heavier males may be more at risk of branches giving way under their weight and may therefore prefer to nest lower or even on the ground. Furthermore, males may be less prone to predation and therefore may be more likely to nest terrestrially [c.f., Brownlow et al., 2001]. Lastly, males may nest on the ground in order to nest below an estrous female as a strategy to minimize mating competition [c.f., Fruth & Hohmann, 1993].

In sum, we aimed to examine the environmental factors that might account for the occurrence and distribution of ground-nesting by chimpanzees in the Nimba Mountains. To test the ecological hypotheses, we examined the effects of season, altitude, slope, nesting tree, and THV availability on the proportion of nests constructed on the ground. In addition, we preliminarily investigated whether ground-nesting is a sex-linked behavior by identifying the sex of ground-nesting individuals based on DNA isolated from hair samples.

MATERIALS AND METHODS

Study Site

The study site was situated in a region of the Nimba Mountains near the village of Seringbara (7° 37′50.0″N, 8° 27′44.7″W) in southeastern Guinea, West Africa. The Seringbara study area covers about 25 km^2 and is 6 km southeast of Bossou, where a community of 12–23 chimpanzees has been studied since 1976 [Sugiyama, 1981, 1984]. The Nimba Mountains form a natural boundary between Guinea, Côte d'Ivoire, and Liberia, and are a protected area (the Réserve Naturelle Intégrale du Mont-Nimba) in Guinea and Côte d'Ivoire. The reserve extends over 12,700 ha on the Guinean side and over 5,000 ha on the Côte d'Ivoire side. Both reserves now form a UNESCO World Heritage Site covering a surface area of approximately 22,000 ha. The Guinean portion of the massif is classified as a Biosphere Reserve, which includes the Bossou hills and the Déré forest.

The Nimba Mountains are characterized by evergreen forest of medium altitude [Guillaumet & Adjanohou, 1971]. The highest (1,752 m) peak of the massif, le Mont Richard Molard, is the second-highest point in West Africa. The landscape below 800 m is covered by primary tropical forest. Above 800 m the slopes become steeper and the vegetation changes into forest interspersed with patches of THV and high-altitude grasslands.

The Nimba Mountains harbor several groups of chimpanzees (*Pan troglodytes verus*). Periodic surveys in the Nimba region have been done since 1992 in both the Seringbara area in the Guinean part of the reserve and in the

Yealé region of the Nimba Mountains in Côte d'Ivoire [Humle, 2003; Humle & Matsuzawa, 2001, 2004; Marchesi et al., 1995; Matsuzawa & Yamakoshi, 1996; Shimada, 2000]. However, no permanent research presence in the mountains around Seringbara existed before the present study, and the chimpanzees were largely unhabituated to human presence.

Data Collection

Climate

Data collection took place between August 2003 and May 2004. Two weather stations were set up in the forest: one at low altitude (697 m) and one at high altitude (916 m). Climatic data were collected at 1730 hr each working day. Wind speed measurements (daily maximum) were recorded with a Skywatch 3-D Elite Windmeter to assess differences in wind speed relative to altitude and season. Rainfall was measured using an All-Weather Rain Gauge.

Nesting

We set up two 500-m transects (north–south and east–west) on each of seven different hills, for a total transect distance of 7 km. On the first transect survey, we extensively searched for nests and marked all nests visible from the transect line. During later monthly surveys, we marked all new visible nests using the marked-nest census method [sensu Furuichi et al., 2001a]. Whenever a nest was found, we searched for possible neighboring nests of the same age within a 30-m radius to assess nest party size [sensu Furuichi et al., 2001a]. Any nest less than 1 month old found outside the transect areas was recorded on an ad libitum basis. The following variables were noted for each nest:

1. Location: Arboreal or terrestrial.

2. Number per group: Nests of the same age within 30 m of any other nest in the group.

3. Type: Day nest, night nest, or unknown (night nest: elaborate in construction, often associated with feces below or near the nest and characterized by a strong smell; day nest: simple in construction and thought to be structurally too weak to support a chimpanzee overnight). Nest type was assigned using criteria based on chimpanzee nests observed at Bossou.

4. Age: Three classes [sensu Tutin & Fernandez, 1984]: 1) new (≤ 2 days): leaves still green and healthy; 2) recent (>2 days and <1 week): leaves still green, but droopy and wilted leaves and branches show the nest to be more than a few days old; 3) old (>1 week and <1 month): nest mainly of dead leaves, but is still intact, so most probably is less than 1 month old. Age was assigned using criteria based on chimpanzee nests of known age at Bossou.

5. Species used: For integrated nests (comprising more than one species of woody vegetation) we recorded all species used in nest-making.

6. DBH of the tree(s) used in nest building: Diameter to the nearest cm of nesting tree(s) measured at breast height (i.e., 1.5 m) with a tape measure.

7. Altitude at the base of the tree or on the ground, as determined with a Suunto Escape Electronic Altimeter.

8. Slope of the ground below a nest, as determined with a Haglöf Electronic Clinometer.

Tree availability and THV availability

To measure tree availability around the ground nests, we set up a 20×20 m quadrat around each ground nest with the nest as the middle point. If a nesting

group had more than one ground nest, we set up one single quadrat for all ground nests concerned and took the middle point of the ground nests as the center of the quadrat. We recorded the species of all trees in the quadrat with a diameter of $\geq 5.0\,cm$ and measured their DBH. For each ground-nest quadrat, all trees with a DBH of $\geq 5.0\,cm$ were assigned to one of two categories: ''potential nest trees'' and ''other trees.'' Trees were labeled as ''potential nest trees'' if the tree species had been used as a nest tree by chimpanzees at least once during the study period. Only the ramified, or branched, trees with at least one ramification with a DBH of $\geq 5.0\,cm$ were included. If a tree already contained one or more nests, it was no longer considered a potential nest tree. To quantify the availability of ground-nesting materials, we sampled four $1 \times 1\,m$ THV quadrats within the $20 \times 20\,m$ ground-nest quadrat and counted the stems of terrestrial herbs belonging to the two most common families of THV: Marantaceae and Zingiberaceae. Each $1 \times 1\,m$ THV quadrat was placed in the middle of one of the four $10 \times 10\,m$ subquadrats within the $20 \times 20\,m$ quadrat.

As a measure of general habitat-wide tree availability, we recorded all trees with a DBH of $\geq 5.0\,cm$ within $5\,m$ to each side of the transect lines used for nesting-data collection. To estimate the general density of THV, we placed $2 \times 2\,m$ quadrats [sensu Furuichi et al., 2001b] at 10-m intervals alternatively to the right and left sides of each transect line. In these quadrats we counted the stems of herbs belonging to the Marantaceae and Zingiberaceae families.

DNA analysis

We used DNA analyses to identify the sex of ground-nesting individuals based on DNA extracted from hair samples. We collected hairs from ground nests that were no more than 1 month old. To avoid contamination of the hairs, we used a pair of sterilized forceps to collect the hairs. The hairs were then stored in a plastic bag and kept at room temperature for the rest of the field season. At the end of the field season, the samples were transferred to a refrigerator ($4°C$) or freezer ($–20°C$) at the Kyoto University Primate Research Institute in Inuyama, Japan.

For each ground nest we analyzed one to eight hairs, depending on the number of hairs gathered. Each hair was treated separately and DNA was extracted using the Isohair DNA extraction kit (Nippon Gene, Toyama, Japan). A polymerase chain reaction (PCR) was used to amplify the X-Y homologous gene amelogenin (AMG), which generates different-length products from the X- and Y-chromosomes. These PCR products are distinguishable by gel electrophoresis and can thus be used for sex-assignment purposes [Ensminger & Hoffman, 2002; Sullivan et al., 1993]. To test the reliability of the results obtained from the AMG sexing method, we applied the zinc-finger gene method for DNA-based sex assignment (ZFX/ZFY [Wilson & Erlandsson, 1998]) to samples that yielded clear results for the AMG assay. The ZFX/ZFY method focuses on the loci for the zinc-finger protein. After PCR amplification, the products are digested by restriction enzymes that selectively target either Y- or X-chromosomes. Following digestion with the restriction enzymes, the X- and Y-chromosomes are distinguishable and sex identification is possible.

Data Analysis

The data violated the assumptions of normality, and we therefore used nonparametric statistical tests throughout [Zar, 1999]. All analyses were two-tailed and significance levels were set at 0.05. The statistical tests were performed

in SPSS 10.0. Multiple tests of significance were corrected with an improved Bonferroni correction [Hochberg, 1988]. The results are presented as proportions or as means with standard deviation (SD). In the comparisons of ground-nest proportions between seasons, altitudes, and slopes, we analyzed elaborate ("night") and simple ("day") nests together, since many of the tree nests were of unknown status. In the analyses that concerned ground nests only (i.e., association with tree nests, and sex identification), we analyzed simple and elaborate ground nests separately.

RESULTS

Ground nests accounted for 6.1% (61/994) of all recorded nests. Based on the structure of the ground nests, 32 were classified as elaborate and 29 were classified as simple nests. Most ground nests (73.8%) were made of tree saplings only. Only THV was used for 16.4% of the nests, and 9.8% of the nests were made of both saplings and THV. There was no difference in the materials used for elaborate and simple ground nests ($\chi^2 = 3.483$, df = 2, $P = 0.175$).

Climatic Conditions

The total amount of rainfall between August 2003 and April 2004 was 1,149 mm at the low-altitude weather station and 1,285 mm at the high-altitude weather station. December, January, and February were dry-season months (mean monthly rainfall = < 50 mm) and the other months comprised the wet season (mean monthly rainfall = > 50 mm; Fig. 1).

The mean maximum wind speed was greater at high altitude than at low altitude (high vs. low = 8.2 km/hr, SD = 8.60 vs. 3.4 km/hr, SD = 4.73; Wilcoxon signed-ranks test: n = 113, z = –6.159, $P < 0.0001$). At low altitude the mean maximum wind speed was greater in the dry season than in the wet season (dry vs. wet = 5.3 km/hr, SD = 6.15 vs. 2.4 km/hr, SD = 3.43; Mann-Whitney U-test: $n_1 = 55$, $n_2 = 91$, z = –3.092, $P = 0.002$), whereas at high altitude there was no difference in wind speed between seasons (dry vs. wet = 7.2 km/hr, SD = 9.59 vs.
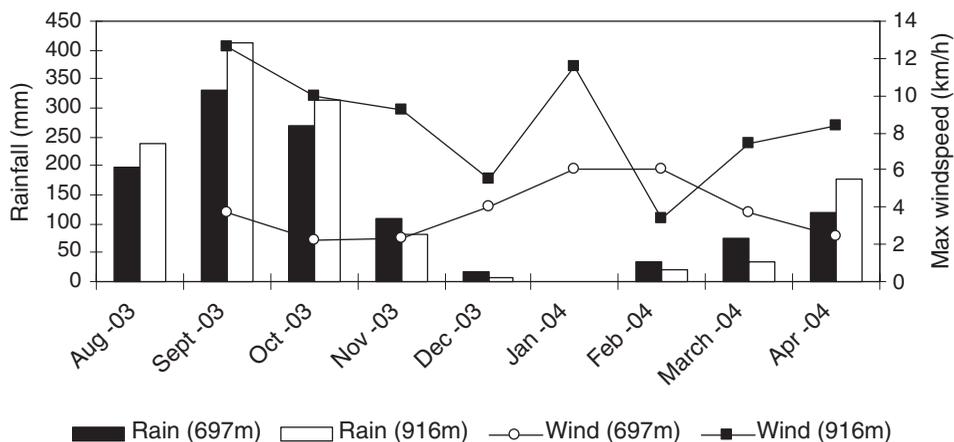

Fig. 1. Monthly rainfall (bars) and mean maximum wind speed (lines) recorded at low (697 m) and high (916 m) altitude weather stations.

8.8 km/hr, SD = 8.05; Mann-Whitney U-test: $n_1 = 39$, $n_2 = 75$, z = –1.574, $P = 0.116$; Fig. 1).

Season and Altitude

The proportion of ground nests did not differ between the dry (5.0%, 19/379) and wet (6.8%, 42/615) seasons ($\chi^2 = 1.343$, df = 1, $P = 0.247$). There was no difference in the proportion of nests built on the ground across three altitude categories ($\chi^2 = 1.409$, df = 2, $P = 0.494$; Table I).

When the altitudinal variation of ground nests during each season was compared, no difference was found during the wet season ($\chi^2 = 1.733$, df = 2, $P = 0.420$), whereas during the dry season there were significantly fewer ground nests below 900 m than at higher altitudes (< 900 m vs. 900–999 m: $\chi^2 = 6.757$, df = 1, $P = 0.009$; < 900 m vs. ≥ 1,000 m $\chi^2 = 5.646$, df = 1, $P = 0.017$; 900–999 m vs. ≥ 1,000 m: $\chi^2 = 0.061$, df = 1, $P = 0.804$; Table I).

Slope

The steepness of the slope did not affect the proportion of nests built on the ground ($\chi^2 = 1.572$, df = 2, $P = 0.456$; Table I). However, there was a *positive* correlation between the steepness of the slope and tree density (Rs = 0.517, n = 26, $P = 0.007$), suggesting a greater (not lower) availability of potential nesting trees on steeper slopes.

Tree Density, Size, and Species

The mean tree density in ground nest quadrats was 0.10 trees/m^2 (n = 26, SD = 0.045) and the mean tree density along transects was 0.09 trees/m^2 (n = 14, SD = 0.016). The mean tree density in ground nest quadrats did not differ from that sampled along the habitat-wide transects (Mann-Whitney U-test: z = –1.299, $P = 0.194$).

The mean DBH of the trees in ground nest quadrats was 16.3 cm (n = 955, SD = 19.5) and the mean DBH of trees on transects was 18.1 cm (n = 6056, SD = 27.4). DBH distributions did not differ between quadrats and transects ($\chi^2 = 19.126$, df = 19, $P = 0.449$; Fig. 2).

Only one of 26 quadrats had no potential nest trees. In the other 25 quadrats, at least 35% of the trees were potential nest trees. The mean percentage of potential nest trees per quadrat was 75.4% (mean = 32 trees/quadrat).

TABLE I. The Proportion of Ground Nests at Different Altitudes (Overall, Dry and Wet Season) and at Different Slopes*

Altitude	< 900 m	900–999 m	≥ 1,000 m	P
Overall	5.6% (19/339)	7.3% (27/370)	5.3% (15/285)	NS
Dry	0% (0/94)	6.8% (16/234)	5.9% (3/51)	Low < medium** Low < high*
Wet	7.8% (19/245)	8.1% (11/136)	5.1% (12/234)	NS
Slope	0–21 dg	21–40 dg	> 40 dg	P
	7.4% (11/148)	6.5% (37/569)	4.7% (13/277)	NS

*Values in parentheses indicate the number of ground nests/total number of nests.
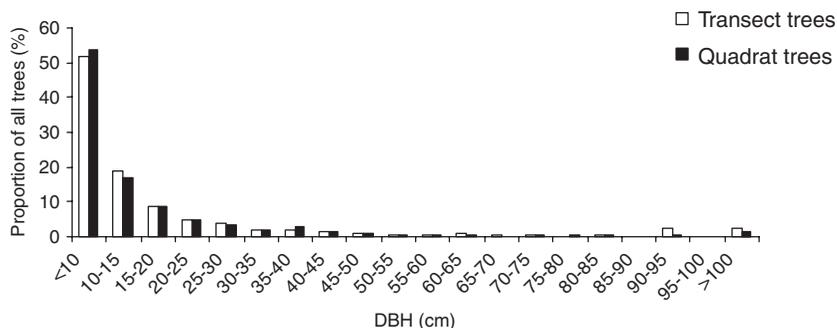NS, not significant.
*$P < 0.05$;**$P < 0.01$.

Fig. 2. Distribution of DBH of trees on transects and trees in ground nest quadrats.

THV Availability

The mean density of Marantaceae stems was $4.5\,\text{stems/m}^2$ (SD = 10.74) in ground-nest quadrats and $1.5\,\text{stems/m}^2$ (SD = 2.02) on transects. These densities did not differ (Mann-Whitney U-test: $n_1 = 26$, $n_2 = 14$, z = –1.809, $P = 0.07$). The mean densities of Zingiberaceae did not differ significantly between ground-nest quadrats and transects (mean = 0.9 vs. mean = 0.2; Mann-Whitney U-test: $n_1 = 26$, $n_2 = 14$, z = –0.457, $P = 0.648$).

Association With Tree Nests

Overall, 16.4% (10/61) of ground nests were solitary nests, while the others were associated with other nests of the same age. Furthermore, 14.0% (31/222) of nest groups contained one or more ground nests (range = 1–5 ground nests/group). Structurally elaborate ground nests were built more often in a nest group with tree nests (87.5%) than in groups lacking tree nests (i.e., alone or with other ground nests), and simple ground nests were more often built in nest groups lacking arboreal nests (69.0%) than in groups with tree nests ($\chi^2 = 20.325$, df = 1, $P < 0.0001$).

Sex of Ground-Nesting Individuals

Based on the sexing results from individual hair samples, we assigned each ground nest to one of five categories: *definitely* male, *definitely* female, *likely* male, *likely* female, and *unknown* sex. Ground nests were labeled as *definitely* male or female if at least two hairs showed clear and consistent results for either the male (X- and Y-band) or female (only X-band) sex in at least two AMG PCRs, as well as a positive result for the ZFX/ZFY method. If at least two hairs yielded clear and consistent results for either male or female in at least one AMG PCR, the nests were labeled as *likely* male or female. Ground nests for which no results were obtained or for which results from different hairs provided contradictory results were placed in the category *unknown* sex. We were able to assign sex to 53% (16/30) of the ground nests, i.e., 13% as *definitely* and 37% as *likely* to have been made by a male chimpanzee, and 3% as *likely* to have been made by a female chimpanzee (see Fig. 3). All of the identified elaborate ground nests (n = 18) were either *definitely* (22%) or *likely* (33%) to have been constructed by a male. None of the simple ground nests (n = 12) could be labeled as *definitely* male or female, since no clear ZFX/ZFY results were obtained for these nests. However, we were
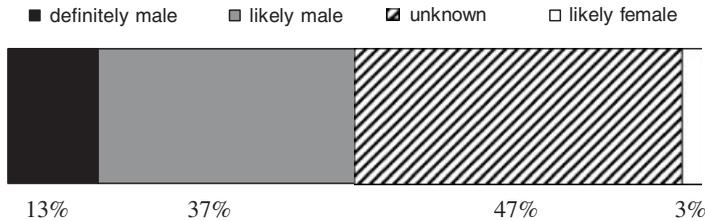
Fig. 3. Percentage of ground nests (n = 30) made by individuals of different sex classes: unknown sex (n = 14), definitely male (n = 4), likely male (n = 11), and likely female (n = 1).

able to infer that 42% of the simple nests were *likely* to have been made by a male, and that 8% of the nests were *likely* to have been built by a female chimpanzee.

DISCUSSION

In this study we found that 6.1% of the nests at Seringbara in the Nimba Mountains were built on the ground. This is much less than the 35.4% (164/464) previously observed at nearby Yealé, Côte d'Ivoire [Matsuzawa & Yamakoshi, 1996]. However, a more recent study by Humle [2003] reported that 3.7% (14/378) of nests were built on the ground at Yealé, Côte d'Ivoire, vs. 8.9% (25/281) at Seringbara, Guinea. These apparent contradictions suggest that there may be regional or annual variations in the proportion of nests built on the ground. Thus, the results presented here must be viewed as preliminary.

Environmental Hypotheses

The first hypothesis predicted there would be a greater prevalence of ground nests in high-altitude areas, especially during the dry season, as a result of high wind speeds and the associated risk of nesting in trees. We found higher maximum wind speeds at high altitudes compared to low altitudes, as well as higher maximum wind speeds during the dry season compared to the wet season, albeit at low altitudes only. Contrary to our expectations, we found no seasonal variation in the proportion of nests constructed on the ground. This result is in accordance with the finding that the Nimba chimpanzees showed no seasonal variation in nesting height (Koops et al., unpublished results). High wind speeds did not seem to affect the chimpanzees' choice of nest sites during the dry season.

We found no difference in the proportion of nests made on the ground across different altitude categories, although the maximum wind speed was found to be greater at high altitude compared to low altitude. This result corroborates the finding that the chimpanzees in Nimba showed no variation in nesting height across altitude categories (Koops et al., unpublished results). Contrary to our predictions, the only seasonal difference across altitude categories that emerged was during the dry season when fewer ground nests were constructed below 900 m than during the wet season, while no seasonal differences emerged above 900 m. The occurrence of ground-nesting thus did not depend on variation in wind speed across altitudes. It has to be noted that it would have more accurate to determine the wind speed on the exact day and location of the nest-building. However, we had to generalize the maximum wind speed and proportion of ground nests per season and altitude category because the chimpanzees were unhabituated and therefore nest-building was not directly observed. In addition,

since we had a confidence interval of 1–2 days for establishing the age of fresh nests, we could not reliably carry out a day-by-day analysis of the data.

Based on the second ecological hypothesis, we expected that ground nests would be made in areas with a shortage of appropriate nesting trees (e.g., on steep slopes). However, there was no difference in the proportion of nests built on the ground between areas with varying steepness of slope. Moreover, we failed to support the a priori assumption that steeper slopes had fewer potential nesting trees. On the contrary, there was a significant *positive* correlation between steepness of slope and tree density. To investigate the availability of appropriate nesting trees, we compared the availability of trees in ground nest quadrats vs. the availability on transects. The trees around the ground nests were found to be similar in density, size, and species composition to trees available along transects. In other words, the chimpanzees constructed nests on the ground in areas where there were ample trees available of both the appropriate size and appropriate species for nesting.

The availability of THV was similar between quadrats and transects, which indicates that the chimpanzees did not prefer areas with especially high THV densities for construction of ground nests. However, most ground nests were made of tree saplings–an ecological feature that was not measured in this study. To correctly assess the availability of materials for ground-nesting, we would also have to measure the availability of tree saplings. In summary, we found no effect of environmental factors on the occurrence of ground-nesting, and neither of the two ecological hypotheses tested was supported.

Sex-Linked Behavior

Our preliminary sexing results appear to support the idea that ground-nesting is a sex-linked behavior. Males were responsible for making most nests on the ground, including all elaborate nests. Only one out of 30 ground nests tested was likely to have been used by a female chimpanzee. This particular nest was rudimentarily constructed and was most likely used during the day. It was also part of a nest group containing another ground nest. The bias toward males is unlikely to be a consequence of an extremely skewed sex ratio in the Nimba population. At two long-term study sites of West African chimpanzees, the sex ratios are approximately one male to three females (Bossou, Guinea [Sugiyama, 1984], and Taï, Côte d'Ivoire [Boesch & Boesch-Achermann, 2000]).

The explanation that ground-nesting is done only by individuals in poor health, as was previously observed in chimpanzees at Gombe, Tanzania [Goodall, 1968], seems highly unlikely based on our results. First, ground-nesting occurred regularly throughout the year, and nest groups sometimes had more than one ground nest, with up to five ground nests found in one nest group. It seems improbable that all of these ground-nesting individuals were physically too sick to climb a tree. Second, ground nests were made almost exclusively by male chimpanzees. Such a continuous sex bias in illness also seems unlikely. Furthermore, it seems unlikely that ground-nesting would be simply more comfortable than tree-nesting. If this were the case, we would expect both sexes to nest on the ground much more frequently.

The question remains as to *why* ground-nesting might be a sex-linked behavior. Sexual dimorphism in body weight, and therefore in the risk of tree-nesting, may explain why males are more prone to nest on the ground, but it does not explain the difference between simple and elaborate ground nests in their association with tree nests. Whereas most elaborate ground nests were made in

nest groups with tree nests, simple ground nests were mostly built in groups without adjacent arboreal nests, indicating that elaborate and simple nests may be functionally different. Simple nests on the ground may provide a more comfortable rest in the daytime, while elaborate night nests on the ground may function as a male social strategy. One possibility is that males nest on the ground to guard an estrous female in the trees above. However, the underlying assumptions–that elaborate ground nests reflect nighttime use, and simple ground nests are used during the day–remain to be verified.

To further investigate a possible mate-guarding function of ground-nesting, we need to determine the sex of individuals that construct tree nests above associated ground nests. We would expect that all tree nests found above ground nests are used by females. Furthermore, hormonal analyses of fecal samples collected below tree nests may shed light on the reproductive state of the nest-builders, and especially cycling females.

Lastly, it remains unclear whether only some individuals in the community make ground nests or it is a community-wide behavioral pattern. Individual genotyping could clarify the number of different individuals that habitually nest on the ground [McGrew et al., 2004].

For almost half of the ground nests, sex assignment was unsuccessful. These limited results were mainly due to low PCR success rates and the problem of both X- and Y-allele nonamplification. The occasional failure to amplify the Y-allele (also known as allelic dropout) complicates sex allocation because it can cause the misidentification of males as females. Also, spurious amplification of the Y-allele in DNA from a female can occur as a result of either contamination or ''false allele'' artifacts of PCR [Ensminger & Hoffman, 2002; Taberlet et al., 1996]. The presence of false second bands in amplifications from females may lead to the incorrect assignment of the male sex [Bradley et al., 2001]. Such erroneous amplifications make it necessary to obtain multiple extractions from each hair sample and to set up PCR reactions at least in triplicate, in order to lower the chance of errors in sex assignment [Taberlet et al., 1996]. As a consequence of these methodological questions, our conclusions regarding the sex of ground-nesting individuals should be considered preliminary.

In conclusion, our data corroborate earlier reports of ground-nesting by the chimpanzees of the Nimba Mountains, and show that it is an integral part of chimpanzee behavior in Nimba. Ground-nesting in Nimba may be enabled by the lack of predation in the region; however, the occurrence and distribution of ground nests cannot be explained by basic environmental factors. Social or cultural factors may provide a more likely explanation for ground-nesting behavior in the Nimba chimpanzees.

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