



Nest-Building by Chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: Antipredation, Thermoregulation, and Antivector Hypotheses

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Abstract The construction of nests (or beds) for sleeping is a chimpanzee universal, yet little is known about the adaptive function of nest-building. We present an in-depth study of nest-building by unhabituated chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea, West Africa. We recorded 1520 chimpanzee nests over 28 mo during three study periods between 2003 and 2008. We investigated where chimpanzees built their nests, both across the home range and in nest trees, and assessed how altitude and habitat type affected nest site selectivity. We examined whether or not chimpanzees were selective in nest tree choice regarding physical tree characteristics and tree species and assessed plant species preference for both tree- and ground-nesting. We tested three, nonmutually exclusive, hypotheses for the function of arboreal nest-building. We assessed whether selectivity for nest tree characteristics reflected an antipredator strategy, examined whether nesting patterns (both arboreal and terrestrial) and nesting height were influenced by variation in climatic conditions (temperature, humidity, wind), and measured mosquito densities at ground level and in trees at 10 m and related mosquito densities to nesting patterns. Chimpanzees preferred to nest above 1000 m and nested mainly in primary forest. They preferred relatively large trees with a low first branch, dense canopy, and small leaves and showed preference for particular tree species, which was stable across years, whereas plant choice for ground-nesting was largely based on plant availability. We found no support for the antipredation hypothesis, nor did mosquito densities

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explain arboreal nest-building. The thermoregulation hypothesis was supported, as both nesting patterns and nest-height variation across seasons reflected a humidity-avoidance strategy. Chimpanzees nested higher in trees and at higher altitudes in the wet season. In sum, chimpanzees were selective in their choice of nest sites, locations, and materials, and tree-nesting patterns at Seringbara were best explained by a thermoregulation strategy of humidity avoidance.

Keywords Chimpanzee · Mosquitoes · Nest-building · Predation · Thermoregulation

Introduction

Wild chimpanzees, like other great apes, make nests for rest and sleep almost every day of their lives after being weaned (Fruth and Hohmann 1996). The construction of a nest, also called a sleeping platform or bed (McGrew 1992), takes only a few minutes and entails breaking, bending, and interweaving branches into a circular frame, followed by tucking in of smaller branches to form a sturdy platform (Fruth and Hohmann 1996). These shelters are used daily for sleep at night, and sometimes during the day for rest between foraging episodes (Brownlow *et al.* 2001). Chimpanzees generally nest in trees (Fruth and Hohmann 1994; Goodall 1962), but occasional ground nests have been recorded at several study sites (Boesch 1995; Furuichi and Hashimoto 2000; Goodall 1968; Hicks 2010; Humle 2003; Koops *et al.* 2007; Maughan and Stanford 2001; Pruetz *et al.* 2008; Reynolds and Reynolds 1965). Arboreal nest-building is a chimpanzee universal, but despite its ubiquity, little is known about the actual function of (tree) nest-building (*cf.* Fruth and Hohmann 1996; Pruetz *et al.* 2008; Stewart 2011; Stewart *et al.* 2007). Several, nonmutually exclusive, hypotheses have been proposed to explain why chimpanzees build nests (McGrew 2004).

The hypothesis that has received most attention is the antipredation function of arboreal nest-building (Baldwin *et al.* 1981; Fruth and Hohmann 1993; Kortlandt 1992; Sabater Pi *et al.* 1997; Sugardjito 1983). This hypothesis states that arboreal sleeping is more secure than sleeping on the ground, as sleeping in the trees provides protection from large nocturnal predators (Anderson 1984, 1998, 2000). The location of arboreal nests, especially their height, is suggested to reflect an antipredator strategy, as it reduces accessibility to the sleeping ape (Rayadin and Saitoh 2009; Sugardjito 1983). Nests built higher in the canopy may be more difficult to reach for predators, even for those able to climb trees, and may allow more time to escape in case of attack. Indeed, chimpanzee populations under different levels of predation pressure showed differences in nest height, *i.e.*, higher nests with increased predation pressure (Baldwin *et al.* 1981), which could not be explained by differences in vegetation structure (Pruetz *et al.* 2008). Further, it has been suggested that chimpanzees choose nests with a possible escape route via neighboring trees (Anderson 1984), and that they may increase the functional height of the nest by nesting over gullies or streams (Goodall 1968).

The second hypothesis states that nests may function in thermoregulation (Fruth and Hohmann 1996). Behavioral thermoregulation may help to achieve heat loss and uptake, depending on climatic conditions, and thus reduce metabolic costs of

physiological thermoregulation (Kosheleff and Anderson 2009; Takemoto 2004). For example, a sleeping platform may provide insulation from low ambient temperatures overnight (McGrew 2004). A recent empirical study with a human subject provided support for an insulation function of arboreal nests at a savannah site with low overnight temperatures (Stewart 2011). Western gorillas (*Gorilla gorilla gorilla*) at Mondika, Central African Republic, sometimes slept on bare earth, but as rainfall increased and temperature decreased they more often made nests (Mehlman and Doran 2002). Further, location in the nest tree may ameliorate adverse climatic conditions by taking advantage of the vertical structure of the microclimate. Chimpanzees at Assirik, Senegal, built their nests higher and more open to the sky during the wet season, possibly allowing them to avoid discomfort from dripping vegetation and giving them increased exposure to morning sunshine (Baldwin *et al.* 1981). The relative effects of rainfall, temperature, humidity, and wind speed on nesting height remain to be tested.

The third hypothesis is the antivector hypothesis, which states that by making sleeping platforms up in the trees, disease vectors, i.e., mosquitoes, may be avoided (McGrew 2004). Mosquitoes appear to affect sleeping habits in a number of primate species. In New World monkeys, the use of dense vegetation and tree holes as sleeping sites has been suggested to reduce exposure to mosquitoes of the genus *Anopheles* and thereby decrease malarial infection rates (Heymann 1995). Malaria parasite (*Plasmodium* spp.) infections have been detected in wild chimpanzees (Krief *et al.* 2010; Liu *et al.* 2010; Prugnolle *et al.* 2010), although it is still unknown to what extent these infections are pathogenic. In Bornean orang-utans (*Pongo pygmaeus*), mosquito avoidance appeared to drive selection of nest tree species, as trees with apparent mosquito-repelling properties were chosen more often for nests at times of high mosquito density (Largo *et al.* 2009). No previous study of ape nests has measured mosquito abundance at different heights in the forest, so it is unknown if nesting height by apes is driven by mosquito densities.

In the current study, we examined the function of arboreal nest-building in a population of largely unhabituated chimpanzees (*Pan troglodytes verus*) at the Seringbara study site in the Nimba Mountains, Guinea, West Africa. First, we assessed where and when chimpanzees build their nests, both across the home range, i.e., nest site, *sensu* Fruth and Hohmann (1996), and within nest trees, i.e., nest location, *sensu* Fruth and Hohmann (1996). Second, we examined whether chimpanzees are selective in their choice of nest sites regarding altitude and habitat type and whether chimpanzees are selective in nest tree choice regarding physical tree characteristics. Third, we assessed plant species preference, both for tree and ground nests, across years. We predict that if chimpanzees nest selectively, then this will (in part) reflect the function of nest-building. To investigate the function of arboreal nest-building, we assessed the potential selection pressures, i.e., predators, climatic conditions, disease vectors, and related them to the observed selectivity in nesting patterns and characteristics.

We addressed the antipredation hypothesis by assessing whether selectivity for nest tree characteristics reflects a possible antipredator strategy. Tree characteristics that may be related to predator defense are tree height, tree size, height of lowest branch, and canopy connectivity. If arboreal nesting functions as antipredation strategy, we expect chimpanzees to prefer larger and taller trees with increased height

of the first branch. Also, we expect chimpanzees to be selective regarding connectivity of the canopy to neighboring trees, which may enhance ease of escape from the nest tree. Lastly, we expect chimpanzees to nest at sites that increase functional height of the nest and thus further decrease accessibility.

To test the thermoregulation hypothesis, we assessed whether the distribution of nests (both arboreal and terrestrial) across altitudes and seasons correlates with variation in climatic conditions, i.e., temperature, humidity, wind, rainfall, on the ground and in the trees. We examined whether nest height varied across seasons, and whether this could be explained by selectivity for optimal climatic conditions for nesting. Further, we examined whether nest position in the tree crown and cover provided by vegetation overhead varied between seasons. If arboreal nests function to avoid dripping vegetation and to increase exposure to the sun, we expect nests to be more open and higher in the tree crown in the wet vs. the dry season. Lastly, we examined whether ground nest structure varied across seasons to test the prediction that sleeping platforms insulate the builder from low temperatures by reducing heat loss or provide protection from wet ground.

We addressed the antivector hypothesis by relating nesting patterns across seasons and altitudes to mosquito densities on the ground and at 10 m height in the trees. If arboreal nest-building is an antivector strategy, we expect chimpanzee nest height to reflect avoidance of mosquitoes, especially of female mosquitoes belonging to species likely to feed on chimpanzee blood and possibly transmit diseases. Further, we expect mosquito densities to be higher close to the forest floor, reflecting the presence of terrestrial host species, such as forest antelopes, buffaloes, and other mammals.

Methods

Study Site

The Seringbara study site (N 07.37°; W 08.28°) is in the Nimba Mountains in the southeastern part of the Republic of Guinea, West Africa. The study site covers *ca.* 25 km² of steep hills and valleys and is 6 km from Bossou, where a community of 12–23 chimpanzees has been studied for >30 yr (Matsuzawa *et al.* 2011). The Nimba region has been surveyed periodically since 1992 (Humble 2003; Humle and Matsuzawa 2001; Matsuzawa and Yamakoshi 1996; Shimada 2000). Since 2003, researchers or field assistants have maintained a near-constant presence at the Seringbara study site. The study population remains largely unhabituated to human observers. (For more information on the study site, see Koops 2011a.)

Data Collection

Data collection took place during three study periods: 1) September 2003–May 2004; 2) April–August and December 2006; 3) November 2007–December 2008. Monthly, we collected data on chimpanzee nests along transects (periods 1, 3), as well as *ad libitum*. We set up two 500-m transects (NS, EW) on each of seven hills in period 1

and on eight hills in period 3, giving total transect lengths of 7 and 8 km, respectively. We established transects according to a stratified random design. We recorded habitat types along transects (period 1): 1) primary forest (excl. riverine forest): undisturbed forest (82%); 2) secondary forest: burned or cultivated in recent past (3%); 3) riverine forest: forest <30 m wide, along permanent water course (1%); 4) terrestrial herbaceous vegetation (THV) dominated forest: dominated by Marantaceae and Zingiberaceae families (14%). In period 3, we established 26.2 km of forest trails, distributed evenly across the study site and selected to represent all altitudes and habitat types. We walked forest trails with a pedometer and altimeter to measure length of trail segments in 100-m altitude categories. We monitored forest trails for evidence of chimpanzee presence, i.e., nest, feeding trace, feces, sighting, once a month for 4 d from January to December 2008. When we found a nest, we searched for other nests of the same age in a 30-m radius, to assess nest group size. The definition of nest group size as “nests of same age ≤ 30 m of any other nest of the nest group” was based on maximum distance between nests of parties in Bossou (Humble 2003).

Nest Sites

For each nest (periods 1–3), we recorded ecological characteristics describing the nest site:

1. Altitude, measured via electronic altimeter
2. Habitat type (see earlier)

Tree Nests

We recorded the following nest characteristics for tree nests (adapted from Baldwin *et al.* 1981; Kano 1983; Tutin and Fernandez 1984; Fruth and Hohmann 1993; Fruth 1995; Hernandez-Aguilar 2006, 2009; Table 1):

1. Nest status: 1) day nest: simple in construction and judged structurally too weak to support a chimpanzee’s weight overnight; 2) night nest: elaborate in construction, often with faeces or urine below or near the nest; 3) unknown status
2. Nest age (*sensu* Tutin and Fernandez 1984): 1) fresh (≤ 2 d): leaves still green and fresh; 2) recent (> 2 d and ≤ 1 wk): leaves still green, but wilted and droopy leaves and branches; 3) old (> 1 wk and ≤ 1 mo): nest mainly made up of dead brown leaves, but still intact.
3. Nest height: Height from base of nest tree trunk directly below nest to base of nest, measured with an electronic clinometer.
4. Nest position in crown: Calculated by dividing distance between nest and lowest branch by height of crown: 1) bottom: 0–0.33; 2) middle: 0.34–0.66; 3) top: 0.67–1.0.
5. Nest cover: Presence of overhanging vegetation in three categories: 1) present: complete vegetation cover above nest; 2) partial: incomplete

vegetation cover above nest, i.e., sky partly visible; 3) absent: no vegetation cover above nest.

Ground Nests

We recorded status and age as described for tree nests, as well as plant species used in ground nest construction (periods 2, 3). To assess seasonal variation in ground nest dimensions, we measured the following variables (period 3):

1. Length: Maximum length crossing nest centrally
2. Width: Perpendicular to length
3. Thickness: Top surface of the nest in center to outer ventral (bottom) surface of nest.

We recorded for each ground nest variables related to complexity and structure (period 3):

1. Number of independently manipulated plants, i.e., woody plants, THV, or plant parts, i.e., branches of small trees, incorporated in a nest
2. Number of manipulations per plant or plant part, i.e., bend, break, detach.
3. Stem diameter of each plant or plant part, measured next to the primary break or bend, or next to the proximal end, in the case of detached twigs

Table I Number of nests recorded during the study periods, by type of nest, and variables recorded

Study period	Nests	Nest groups	Mean no. nests/group ^a	Ground nests	Ground nests (%)	Nest variables	Tree variables
Period 1	994	226	3.8	61	6.1	Status Age (1–3) Nest height	Species DBH Fruit availability
Period 2	293	75	3.1	36	12.3	Status Age (1–3) Nest height	Species DBH Fruit availability
Period 3	233	61	3.8	47	20.2	Status Age (1–2) Nest height Functional nest height Position in crown Nest cover	Species DBH Fruit availability Tree height Lowest branch height Crown height Leaf size Branch architecture Canopy cover Canopy connectivity
Total	1520	362	3.7	144	9.5		

Period 2 (excl. December 2006)

^a Mean no. nests/group (fresh and recent nests only)

Nest Tree Variables

We recorded the following nest tree variables (adapted from Baldwin *et al.* 1981; Fruth 1995; Fruth and Hohmann 1993; Hernandez-Aguilar 2006, 2009; Kano 1983; Tutin and Fernandez 1984; Table I):

1. Tree species used in nest-building. For integrated tree nests, i.e., comprising more than one tree, we recorded all tree species used in nest construction.
2. Stem diameter at breast height, i.e., 1.5 m, DBH, of the trees used in nest-building, measured with DBH tape measure
3. Tree height: Height from base of tree to top of crown, measured with electronic clinometer
4. Lowest branch height: Height from base of tree to lowest branch, measured with an electronic clinometer
5. Crown height: Height of tree crown, calculated by subtracting height of lowest branch from height of tree
6. Leaf size (width \times length): 1) small: $<5.0 \text{ cm}^2$; 2) medium: $5.0\text{--}24.9 \text{ cm}^2$; 3) large: $25.0\text{--}64.9 \text{ cm}^2$; 4) extra-large: $\geq 65.0 \text{ cm}^2$ (*sensu* Fruth 1995).
7. Branch architecture, based on majority of branches: a) horizontal vs. vertically inclined branches; b) opposite vs. alternate branches; c) single vs. multiple canopies; d) single vs. multiple main stems. We considered a stem as main if it branched off below a third of the tree height and supported a large proportion, i.e., $>50\%$, of branches.
8. Canopy connectivity: Level of interconnection (overlap) between tree canopy and neighboring tree canopies, scored as percentage, i.e., 0) none; 1) 1–10%; 2) 11–20%; 3) 21–30%, etc., of canopy's surface area in contact with neighboring tree canopies.
9. Canopy (or leaf) cover: Scored on the proportion of canopy in leaf: 0) leaves absent; 1) 1–25% of canopy covered; 2) 26–50% of canopy covered; 3) 51–75% of canopy covered; 4) 76–100% of canopy covered.
10. Fruit availability: Proportion of canopy containing ripe or unripe fruit: 0) fruit absent; 1) 1–25% of canopy covered; 2) 26–50% of canopy covered; 3) 51–75% of canopy covered; 4) 76–100% of canopy covered.

Nest Tree Selectivity

We compared tree variables at nest sites between trees used for nesting and potential nest trees (period 3). We set up $10 \times 10 \text{ m}$ vegetation plots in the middle of a subset of nest groups ($N=11$) across the study site, to represent the different nesting areas in the home range. We aligned the sides of plots north–south and east–west. We considered all trees with a DBH $\geq 5 \text{ cm}$ and without a nest as potential nest trees and measured the same tree variables as for nest trees. We sampled reused nesting areas only once.

Species Preference

To assess tree species preference (periods 1–3), we obtained a measure of habitat-wide tree availability. We recorded the species names of all trees ($N=6287$) with a

DBH ≥ 5 cm and within 5 m each side of the 7-km transect lines (period 1). We estimated the availability of plants for ground nest construction by setting up 1×1 m vegetation plots in the middle of each 5×5 m subquadrant, i.e., NE, SE, NW, SW, of the 10×10 m vegetation plots. We identified and counted all terrestrial herb stems and woody plants, i.e., saplings, shrubs, with height ≤ 2 m and diameter ≤ 2.5 cm in the 1×1 m plots.

Predator Presence

We collected opportunistic data on presence of large mammals for 20 d/mo in period 3. We focused on signs, i.e., footprints, feces, vocalizations, of leopard (*Panthera pardus*), the only potential predator of chimpanzees reported to occur now in the Nimba Reserve (World Conservation Monitoring Centre 1992). The local human population does not hunt chimpanzees, as chimpanzees are the totem of the Manon people (Kortlandt 1986).

Climatic Conditions

We set up three weather stations, one each at low (670 m), medium (920 m), and high (1170 m) altitudes. Stations comprised a HOBO Micro Station data-logger (Onset Computer Corp., Bourne, MA), temperature and relative humidity sensors, and wind speed sensor. Data-loggers recorded temperature ($^{\circ}\text{C}$) and relative humidity (%) every 60 min, with a sensor at ground level and 10 m overhead in the trees. We recorded gust speed, i.e., maximum wind gust, at 5 m every 60 min. The three weather stations were operational from mid-2006 until late 2008, i.e., 529 d, 888 d, 594 d. In 2008, we recorded rainfall daily at 670 m at 17:30 h. In 2006, we recorded rainfall from May to November and in 2007 from November to December. We defined the dry season as months with rainfall < 60 mm and the wet season as months with a rainfall > 60 mm (van Schaik and Pfannes 2005).

Mosquito Collection

We used a CDC miniature light trap (John W. Hock Co., Gainesville, FL) to collect adult mosquitoes. From April to July 2006 (wet season), we trapped mosquitoes at two low-altitude sites (670 m), *ca.* 50 m apart, to assess mosquito species diversity and local differences in mosquito densities. We collected mosquitoes at three heights (1.5, 5, 10 m). Traps operated from 18:30 h to 06:30 h and were installed for 4 d at each sampling point. From November 2007 to June 2008, we measured mosquito densities at two altitudes (670 m, 920 m) in wet and dry seasons. At both altitudes, we collected mosquitoes at 1.5 m and 10 m during two consecutive nights. At 670 m, we collected mosquitoes for 16 nights (wet: $N=12$; dry: $N=4$). At 920 m, we trapped mosquitoes for eight nights (wet: $N=4$; dry: $N=4$). We used lures, i.e., CO_2 , octanol, human skin lure, in addition to a small light attractant. Mosquitoes were killed using ethyl acetate and stored in Petri dishes with silica gel. We sorted mosquitoes by sex and identified to species using CABIKEY (Computer Aided Biological Identification Key, ©CAB International) and keys by Edwards (1941) and Service (1990).

Data Analyses

We tested data for normality using a normal probability plot and a Kolmogorov–Smirnov test and we used parametric or nonparametric tests accordingly. All analyses were 2-tailed and significance levels were set at 0.05. We performed statistical tests in SPSS version 16.0. We corrected for multiple comparisons with a Bonferroni correction.

We employed a backward stepwise logistic regression to investigate which tree variables predicted nest tree selection (period 3). We used the likelihood ratio test of significance as inclusion criterion. We included as tree variables: tree height, principal diameter, lowest branch height, crown height, leaf size, branch architecture type, canopy connectivity, canopy cover, and fruit availability. We entered a score for relative tree abundance as independent variable to the best model, which was based on number of trees per species on transects: 1) 0–50; 2) 51–100; 3) >100. When predictors remained significant, we assumed that tree abundance did not influence nest tree choice. We used Wald statistics (2-tailed) to assess significance of predictors and their coefficients. We assessed the model with a χ^2 statistic and Nagelkerke R^2 and we used a Hosmer–Lemeshow goodness-of-fit test to examine whether the model fit the data, i.e., $P > 0.05$ (Field 2005).

We evaluated tree species preference for nesting by calculating Manly's α for each tree species used for nesting (Brownlow *et al.* 2001; Furuichi and Hashimoto 2004; Krebs 1998; Mulavwa *et al.* 2010). This preference index takes into consideration the prevalence of different tree species and was calculated as follows:

$$\alpha_i = \frac{r_i}{n_i} * \frac{1}{\sum (r_j/n_j)}$$

where

α_i	Manly's α for tree species i
r_i, r_j	proportion of tree species i or j used for nesting (i and $j = 1, 2, 3, \dots, m$)
n_i, n_j	proportion of tree species i or j available in the habitat
m	number of tree species available for nesting, established on the basis of the transect data and nest data

Neutral preference was reflected by a Manly's alpha value of $1/m$, i.e., 0.0046. We considered tree species *preferred* if Manly's α value was $>1/m$ and *not preferred* if values were $<1/m$. We included only the principal nest tree, i.e., tree providing main support for nest frame, in analyses of tree species preference and tree characteristics. We excluded diameters of trees with multiple main stems at breast height. Also, we excluded nest trees with DBH < 5 cm, as we recorded only potential nest trees with DBH ≥ 5 cm.

We compared proportions of nests (period 3) across categories of altitude, height, position in tree crown, and nest cover between seasons using χ^2 tests. We determined the categories in which proportions of nests differed between seasons by inspecting adjusted residuals (adj. res.), which are approximately standard normally distributed, and controlled for multiple testing with the improved Bonferroni procedure (Hochberg 1988).

To assess which ecological factors influenced the mean nest height per nest group (period 3), we used a stepwise linear regression. We included as possible predictors: season, altitude, rainfall, temperature (max., min., mean) at ground level and 10 m high, relative humidity (max., min., mean) at ground level and 10 m high, and gust speed (max., min., mean). We performed the analysis at the level of the nest group because environmental factors should influence all nests in a group similarly. We weighted the linear regression by number of nests per group and included only groups with tree nests ($N=43$). We calculated values per nest group for each of the predictor variables based on when and where the group was found: Rainfall score was rainfall of the month of nest construction; altitude was mean altitude of all nests in the group; temperature, relative humidity, and gust speed was the mean of each nest group, based on 24-h means of 7 d before finding the group. For groups <800 m, we used values from the low-altitude station; for groups between 800 and 1050 m, values from the medium-altitude station; and for groups >1050 m, values from the high-altitude station. Because of occasional failure of weather stations, we had to interpolate missing values for 13 nest groups. As temperature and relative humidity followed a predictable annual pattern (Koops 2011b), we inferred missing values based on 7-d means from previous years. Gust speed followed a less predictable annual pattern, so we inferred missing values by averaging monthly gust speed values for months before and after the missing data.

We analyzed mosquito densities in three ways: 1) overall number of adult mosquitoes per night; 2) number of female mosquitoes per night, as only females take blood meals; and 3) number of female mosquitoes belonging to known human-biting genera per night. Given the close genetic relatedness of chimpanzee and human, we considered mosquitoes to be potential biters of chimpanzees, as well as potential disease vectors (Hayakawa *et al.* 2009), if the species' feeding habits included human blood.

Results

We recorded 1520 nests in 362 nest groups (Table 1). Mean (\pm SD) nest group size (fresh and recent nests only) was 3.7 ± 3.96 nests per group ($N=280$, median=2). Nest group size did not differ between study periods (Kruskal–Wallis test: $N_1=180$, $N_2=39$, $N_3=61$, $H=0.98$, $df=2$, $P=0.61$). Proportion of ground nests varied across study periods ($\chi^2=46.7$, $df=2$, $P<0.0001$). We classified 45% (65/144) of ground nests as night, 53% (76) as day and 2% (3) as unknown status. Tree nests were 94% (290/1376) night, 4% (55) day, and 2% (31) unknown. Given the small number of arboreal day nests and the difficulty of assigning status to ground nests, we analyzed day and night nests together.

Nest Site Selectivity

Chimpanzee nested between 681 and 1169 m ($N=1520$, median=933 m). The altitudinal distribution of nests on forest trails ($N=139$) differed from chance ($\chi^2=83.9$, $df=3$, $P<0.0001$; Fig. 1). Chimpanzees nested less below 800 m (binomial test: $P<0.0001$) and more above 1000 m ($P<0.0001$). The distribution of

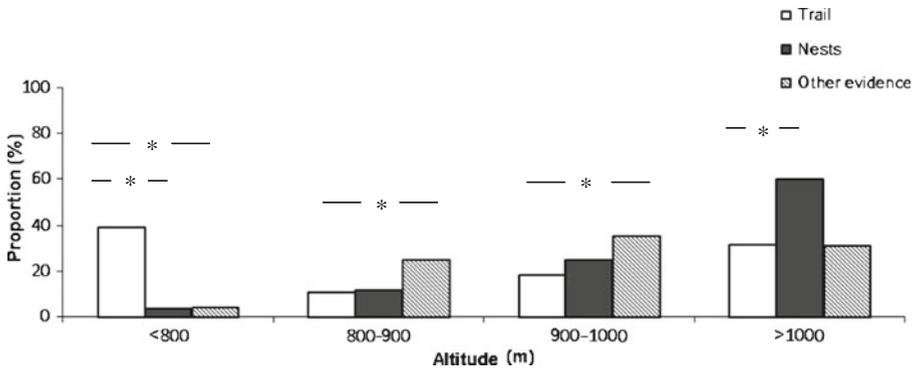


Fig. 1 Proportions of forest trail length (26.2 km), nests ($N=139$), and other evidence of chimpanzee presence ($N=46$) across altitude categories on forest trails. *Binomial test: $P<0.01$.

other (independent) chimpanzee signs ($N=46$) also differed from chance ($\chi^2=32.9$, $df=3$, $P<0.0001$) with fewer signs below 800 m (binomial test: $P<0.0001$) and more signs between 800 and 900 m ($P=0.003$) and 900–1000 m ($P=0.002$). Thus, chimpanzees used areas below 800 m relatively little for nesting and feeding. They preferred altitudes between 800 and 1000 m for feeding and areas above 1000 m were preferred for nesting. Nest distribution across habitat types differed from chance ($\chi^2=736.2$, $df=3$, $P<0.0001$). Most nests (79%; $N=1202$) were in primary forest, but this was used less than expected (binomial test: $P=0.001$). THV-dominated forest (4%, $N=58$) was also used less than expected ($P<0.001$) while secondary (11%, $N=174$) and riverine (6%, $N=86$) forest were used more than expected (both $P<0.001$).

Nest Location Selectivity

Mean height (\pm SD) of tree nests was 11.3 ± 6.3 m ($N=1376$, median=10.5 m). Nest height did not differ across study periods (Kruskal–Wallis test: $N_1=933$, $N_2=257$, $N_3=186$; $H=0.26$, $df=2$, $P=0.88$). Most nests (58%; 885/1520) were built between 5 and 15 m and only 2% (33) of nests were above 25 m. In period 3, most nests (50%; 92/183) were located in the middle third of the crown, 27% (49) in the lower third, and 23% (42) in the top third. Mean height (\pm SD) to the base of the tree was 11.0 ± 5.1 m (median=10.7, $N=185$) and to the ground 11.3 ± 5.1 m (median=10.9, $N=185$). This was a small but significant difference (Wilcoxon signed-ranks test: $z=-5.1$, $P<0.0001$).

Tree Characteristics Preferred for Nest-Building

Four factors significantly predicted nest tree selection (model $\chi^2=55.5$, $df=8$, $P<0.0001$): principal diameter, lowest branch height, canopy cover, and leaf size (Table II). Nagelkerke R^2 for the best model was 0.255 and the Hosmer–Lemeshow goodness of fit test confirmed a good fit of the model ($\chi^2=10.6$, $df=8$, $P=0.22$). Increasing principal diameter and decreasing lowest branch height and leaf size improved the likelihood of use as a nest tree. Canopy cover categories 2 and 3 had the highest likelihood and category 1 had the lowest likelihood of being used for

Table II Factors determining the use of trees ($N=265$) as nest trees ($N=159$)

	Wald	df	P	Category	No. of trees	No. of trees with nest	% trees with nest	β	Wald	P
					265	159	60.0			
Principal diameter	17.97	1	<0.001					0.067		
LBH	9.48	1	0.002					-0.125		
Canopy cover	11.46	3	0.009							
				1 (0–25%)	16	2	12.5	-1.548	6.71	0.01
				2 (26–50%)	61	39	63.9	0.887	8.50	0.004
				3 (51–75%)	107	70	64.4	0.616	5.08	0.02
				4 (76–100%)	81	48	59.3	0.046	0.02	0.88
Leaf size	9.03	3	0.03							
				1 (<5.0 cm ²)	9	8	88.9	1.306	2.50	0.11
				2 (5.0–24.9 cm ²)	75	50	66.7	-0.184	0.27	0.60
				3 (25.0–64.9 cm ²)	62	42	67.7	-0.216	0.36	0.55
				4 (\geq 65.0 cm ²)	119	59	49.6	-0.905	7.63	0.006

Significant variables of the best model are presented with Wald statistics (Wald), degrees of freedom (df), estimated coefficients (β), and P -values.

nesting. When multiple nests in the same tree were included as independent data points, the same best model was found. Lastly, when relative tree abundance was added as an independent variable to the best model, the same predictors remained significant.

Nest Tree Species Selectivity

The chimpanzees used 115 of 216 available tree species for nesting ($N=1468$ nests). The 10 most used species contained 56% ($N=816$) of nests and the 50 most used species contained 90% ($N=1321$) of nests. Tree species preference was found in all study periods, as well as similarities in preference across years (Table III, bold). Of 115 tree species used, 32% (37/115) provided fruit eaten by chimpanzees. Overall, 37% (542/1468) of nests were in food trees, but chimpanzees rarely nested in food trees with ripe fruit. Only 3% (5/186) of nests (period 3) were built in food trees with ripe fruit. On average, 3% (31/1141) of food trees on transects had ripe fruit per month (period 3) and this was not different from the proportion of nests in food trees with ripe fruit ($\chi^2=0.001$, $df=1$, $P=0.98$).

Ground Nest Plant Selectivity

Most ground nests, 83% (39/47), consisted of woody plants, 11% (5/47) of THV, and 6% (3/47) of both woody plants and THV. Chimpanzees used 48 plant species for ground nest construction in period 2 and 55 species in period 3. There was a bias for

Table III Preference for the 10 most used tree species for nesting over three study periods

Period	Nesting tree species	Family	Obs. nests (N)	Nests (%)	Transect trees (N)	Transect trees (%)	Exp. nests (N)	Manley's α	P^a	Pref.
1 (N=927)	<i>Chidlowia sanguinea</i>	Leguminosae	99	10.7	184	2.9	27	0.0180	<0.0001	+
	<i>Rinorea</i> sp.	Violaceae	87	9.4	540	8.6	80	0.0054	0.21	ns
	<i>Chrysophyllum africanum</i> ^b	Sapotaceae	65	7.0	171	2.7	25	0.0127	<0.0001	+
	<i>Amanoa bracteosa</i>	Euphorbiaceae	63	6.8	26	0.4	4	0.0811	<0.0001	+
	<i>Santiria trimer</i> ^d	Burseraceae	58	6.3	238	3.8	35	0.0082	<0.0001	+
	<i>Iuridendron bequaertii</i> ^b	Sapotaceae	34	3.7	65	1.0	10	0.0175	<0.0001	+
	<i>Bussea occidentalis</i>	Leguminosae	32	3.5	79	1.3	12	0.0136	<0.0001	+
	<i>Synsepalum</i> sp. ^b	Sapotaceae	30	3.2	74	1.2	11	0.0136	<0.0001	+
	<i>Manilkara obovata</i> ^b	Sapotaceae	29	3.1	15	0.2	2	0.0647	<0.0001	+
	<i>Drypetes afzelii</i>	Euphorbiaceae	27	2.9	155	2.5	23	0.0058	0.24	ns
2 (N=356)	<i>Amanoa bracteosa</i>	Euphorbiaceae	46	12.9	26	0.4	1	0.1093	<0.0001	+
	<i>Chidlowia sagguinea</i>	Leguminosae	44	12.4	184	2.9	10	0.0148	<0.0001	+
	<i>Drypetes afzelii</i>	Euphorbiaceae	24	6.7	155	2.5	9	0.0096	<0.0001	+
	<i>Chrysophyllum africanum</i> ^b	Sapotaceae	24	6.7	171	2.6	10	0.0087	<0.0001	+
	<i>Rinorea</i> sp.	Violaceae	17	4.8	540	8.6	31	0.0019	0.004	-
	<i>Pouteria altissima</i> ^b	Sapotaceae	15	4.2	99	1.6	6	0.0094	0.001	+
	<i>Iuridendron bequaertii</i> ^b	Sapotaceae	11	3.1	65	1.0	4	0.0105	0.001	+
	<i>Memecylon</i> sp. ^b	Melastomataceae	11	3.1	34	0.5	2	0.0200	0.0001	+
	<i>Octonema borealis</i>	Olaceae	11	3.1	96	1.5	5	0.0071	0.02	+
	<i>Santiria trimer</i> ^d	Burseraceae	10	2.8	238	3.8	13	0.0026	0.20	ns
3 (N=185)	<i>Amanoa bracteosa</i>	Euphorbiaceae	20	10.8	26	0.4	1	0.0558	<0.0001	+
	<i>Iuridendron bequaertii</i> ^b	Sapotaceae	18	9.7	65	1.0	2	0.0201	<0.0001	+
	<i>Diospyros heudelottii</i>	Ebenaceae	14	7.6	2	0.03	0.06	0.5080	<0.0001	+

Table III (continued)

Period	Nesting tree species	Family	Obs. nests (N)	Nests (%)	Transect trees (N)	Transect trees (%)	Exp. nests (N)	Manley's α	P^a	Pref.
	<i>Chidlowia sanguinea</i>	Leguminosae	13	7.0	184	2.9	5	0.0051	0.003	+
	<i>Rinorea</i> sp.	Violaceae	12	6.5	540	8.6	16	0.0016	0.19	ns
	<i>Synsepalum</i> sp. ^b	Sapotaceae	10	5.4	74	1.2	2	0.0098	<0.0001	+
	<i>Chrysophyllum africanum</i> ^b	Sapotaceae	9	4.9	171	2.7	5	0.0038	0.07	ns
	<i>Drypetes afzelii</i>	Euphorbiaceae	8	4.3	155	2.5	5	0.0037	0.10	ns
	<i>Caviera macroura</i> ^b	Rubiaceae	6	3.2	29	0.5	1	0.0150	<0.0001	+
	<i>Octonema borealis</i>	Oleaceae	6	3.2	96	1.5	3	0.0045	0.06	ns

Manley's α = preference index per tree species. Value for neutral preference was 0.0046 (+ = positive preference; - = negative preference; ns = neutral preference). Obs. = observed, Exp. = expected.

In bold: one of 10 most used species for nesting during three study periods (period 2 incl. December 2006).

^a Binomial test of the difference between observed and expected numbers of trees used for nesting.

^b Tree species with fruit eaten by chimpanzees.

Alchornea hirtella, which was used in 44% (40/90) of nests and was the most used species in both periods (Table IV). Plant density and frequency of use in ground nests correlate positively ($N=27$, Kendall's $\tau=0.51$, $P=0.001$). This correlation is even stronger for the 15 most used plant species ($N=8$, Kendall's $\tau=0.74$, $P=0.01$). Chimpanzees thus largely selected plants for ground nest construction according to availability and not preference.

Predator Presence

During 14 mo (period 3), we heard no vocalizations of leopards, nor found any leopard footprints or feces. This agrees with previous findings (Koops *et al.* 2007). However, we cannot exclude leopard presence in high-altitude grasslands, as we rarely visited these areas.

Climatic Conditions

Rainfall was 3244 mm in 2008 and the dry season lasted 3 mo (November–January). Mean daily temperature was higher and mean relative humidity lower at 10 m

Table IV The most used plant species in ground nests in periods 2 (2006) and 3 (2007–2008)

Period	Nesting plant species	Family	Obs. nests (N)	Nests (%)	Density (plants/m ²)
2 ($N=43$)	<i>Alchornea hirtella</i>	Euphorbiaceae	17	39.5	0.32
	<i>Drypetes afzelii</i>	Euphorbiaceae	10	23.3	0.09
	<i>Drypetes chevalieri</i>	Euphorbiaceae	8	18.6	?
	<i>Tarennia vignei</i>	Rubiaceae	8	18.6	0.41
	<i>Chrysophyllum africanum</i>	Sapotaceae	7	16.3	0.16
	<i>Tricalysia sp.</i>	Rubiaceae	7	16.3	?
	<i>Rinorea sp.</i>	Violaceae	5	11.6	0.11
	<i>Amanoa bracteosa</i>	Euphorbiaceae	4	9.3	?
	<i>Chidlowia sanguinea</i>	Leguminosae	4	9.3	?
	<i>Diospyros heudelotti</i>	Ebenaceae	4	9.3	0.02
	<i>Memecylon sp.</i>	Melastomataceae	4	9.3	?
	3 ($N=47$)	<i>Alchornea hirtella</i>	Euphorbiaceae	23	48.9
<i>Tarennia vignei</i>		Rubiaceae	10	21.3	0.41
<i>Chrysophyllum africana</i>		Sapotaceae	7	14.9	0.16
<i>Rinorea sp.</i>		Violaceae	5	10.6	0.11
<i>Amanoa bracteosa</i>		Euphorbiaceae	4	8.5	?
<i>Brillantaisia nitens</i>		Acanthaceae	4	8.5	?
<i>Manilkara obovata</i>		Sapotaceae	4	8.5	0.07
<i>Mareya micrantha</i>		Euphorbiaceae	4	8.5	?
<i>Tricalysia sp.</i>		Rubiaceae	4	8.5	?
<i>Whitfieldia lataritia</i>		Acanthaceae	4	8.5	0.14
<i>Aframomum spp.</i>		Zingiberaceae	4	8.5	?

In bold: plant species belonging to the 11 most used species for ground-nesting during both study periods.

compared to ground level across altitudes in both seasons (Table V). Mean temperatures and mean relative humidity also differed across altitudes (Table VIa,b). In wet seasons, temperatures were highest at low altitude and lowest at high altitude. The pattern was reversed in dry seasons, with highest temperatures at high altitude and lowest temperatures at low altitude. Mean relative humidity was highest at low altitude across seasons. In wet seasons, high altitude had slightly higher humidity than medium altitude and in dry seasons humidity was slightly lower at high vs. medium altitude (Table VIb). Gust speed increased with altitude in both wet and dry seasons (Table VIc).

The distribution of nests across altitudes differed between seasons ($\chi^2=19.5$, $df=2$, $P<0.001$). In the wet season, more nests were found above 1000 m (adj. res.=4.0, $P<0.0001$), whereas in the dry season more nests were found between 900 and 1000 m (adj. res.=3.3, $P<0.001$) and below 900 m (adj. res.=2.0, $P<0.05$; Fig. 2). The distribution of nest groups could not be analyzed owing to a small number of groups on forest trails ($N=27$). Nest group size did not differ between seasons (Mann–Whitney U test: $N_1=43$, $N_2=18$, $z=-1.4$, $P=0.17$), suggesting that nest distribution was not biased by seasonal group size differences.

Nest height differed between seasons (Mann–Whitney U test: wet vs. dry: $N_1=146$, $N_2=39$, $z=-2.5$, $P=0.01$). In period 3, mean height of tree nests was 11.5 ± 5.1 m ($N=146$, median=11.0 m) in the wet season vs. 9.1 ± 4.8 m ($N=39$, median=8.9 m) in the dry season. Height distribution of nests also differed seasonally ($\chi^2=8.8$, $df=3$, $P=0.03$). In the wet season fewer nests were built below 5 m (adj. res.=2.7, $P<0.01$; Fig. 3). The most influential factor affecting mean nest height was maximum relative humidity in the trees ($R^2=0.16$, $F_{1, 41}=7.82$, standardized $\beta=0.40$, $P=0.008$). Mean nest height increased as maximum relative humidity in trees increased. Proportion of tree nests covered by vegetation, either fully or partially, did not differ between seasons ($\chi^2=1.0$, $df=2$, $P=0.62$). In the wet season, 29% (42/146) of nests were fully covered,

Table V Mean temperature (a) and relative humidity (b) in the trees (10 m) and on the ground (mean \pm SD) year-round and during wet and dry seasons separately

	Low altitude (670 m)	Medium altitude (920 m)	High altitude (1170 m)
a. Temp ($^{\circ}$ C)	Tree > Ground (22.1 \pm 1.5) (21.4 \pm 1.5)	Tree > Ground (21.5 \pm 1.2) (21.0 \pm 1.1)	Tree > Ground (21.2 \pm 1.6) (20.6 \pm 1.4)
	Wet: Tree > Ground (22.5 \pm 1.1) (21.9 \pm 0.82)	Wet: Tree > Ground (21.4 \pm 1.2) (21.0 \pm 0.99)	Wet: Tree > Ground (20.9 \pm 1.6) (20.4 \pm 1.4)
	Dry: Tree > Ground (20.7 \pm 1.9) (19.8 \pm 2.1)	Dry: Tree > Ground (22.0 \pm 1.1) (20.8 \pm 1.8)	Dry: Tree > Ground (22.3 \pm 1.0) (21.5 \pm 1.1)
b. RH (%)	Tree < Ground (90.2 \pm 11.5) (95.5 \pm 9.3)	Tree < Ground (73.8 \pm 24.7) (89.1 \pm 17.3)	Tree < Ground (76.2 \pm 24.8) (80.6 \pm 23.2)
	Wet: Tree < Ground (94.9 \pm 6.2) (98.3 \pm 4.3)	Wet: Tree < Ground (82.2 \pm 16.9) (94.9 \pm 9.5)	Wet: Tree < Ground (85.6 \pm 15.1) (89.5 \pm 13.4)
	Dry: Tree < Ground (74.5 \pm 11.4) (86.0 \pm 14.1)	Dry: Tree < Ground (46.2 \pm 26.0) (70.1 \pm 22.6)	Dry: Tree < Ground (41.7 \pm 23.3) (47.7 \pm 22.1)

Wilcoxon signed-ranks tests were significant for all comparisons between tree and ground ($-24.6\leq z\leq -8.7$, $P<0.0001$).

Temp = temperature; RH = relative humidity.

Table VI Mean (\pm SD) temperature (a), relative humidity (b), and gust speed (c) across altitude categories in wet and dry seasons

	Low altitude (670 m)	Medium altitude (920 m)	High altitude (1170 m)
a. Temperature ($^{\circ}$ C)	Wet (22.3 \pm 0.98) Dry (20.2 \pm 2.0)	> Wet (21.7 \pm 1.2) < Dry (21.5 \pm 1.4)	> Wet (21.0 \pm 1.5) < Dry (22.0 \pm 1.0)
b. Relative humidity (%)	Wet (96.3 \pm 5.8) Dry (80.1 \pm 12.2)	> Wet (83.8 \pm 13.6) > Dry (46.5 \pm 20.6)	< Wet (85.8 \pm 13.7) > Dry (45.2 \pm 23.2)
c. Gust speed (m/s)	Wet (0.19 \pm 0.20) Dry (0.39 \pm 0.29)	< Wet (0.49 \pm 0.44) < Dry (1.1 \pm 0.40)	< Wet (0.98 \pm 0.79) < Dry (1.5 \pm 0.97)

Friedman ANOVAs were significant for all comparisons across altitude categories ($77.6 \leq \chi^2 \leq 468.5$, $P < 0.0001$); Wilcoxon signed-ranks tests were significant for all *post hoc* comparisons ($-15.0 \leq z \leq -3.17$, $P < 0.0001$).

52% (76) partially, and 19% (28) had no cover. In the dry season, 23% (9/40) of nests were covered completely, 53% (21) partially, and 25% (10) had no cover. Nest position in tree crowns did not differ between seasons ($\chi^2 = 1.2$, $df = 2$, $P = 0.56$).

In the wet season, 19% (34/180) of nests were ground nests vs. 25% (13/53) in the dry season. This was not significantly different ($\chi^2 = 0.8$, $df = 1$, $P = 0.44$). Further, neither ground nest length (Mann–Whitney *U* test: $N_1 = 33$, $N_2 = 13$, $z = -0.6$, $P = 0.57$), width ($N_1 = 33$, $N_2 = 13$, $z = -0.7$, $P = 0.514$) nor thickness ($N_1 = 25$, $N_2 = 12$, $z = -1.3$, $P = 0.18$) differed seasonally. Also, number of plants used did not differ ($N_1 = 34$, $N_2 = 13$; $z = -0.6$, $P = 0.53$), nor did the number of manipulations per plant ($N_1 = 268$, $N_2 = 81$; $z = -1.1$, $P = 0.29$). However, stem diameters of plants used differed ($N_1 = 268$, $N_2 = 81$; $z = -2.3$, $P = 0.02$) with slightly thicker plant stems used in the dry season (mean \pm SD: wet: 0.9 ± 0.47 vs. dry: 1.1 ± 0.50).

Mosquito Densities

We collected 1025 mosquitoes, from 23 species and 7 genera (Table VII). *Culex* was most common ($N = 824$ mosquitoes), followed by *Coquillettidia* ($N = 77$), *Uranotaenia* ($N = 65$), *Aedes* ($N = 23$), *Mimomyia* ($N = 14$), and *Mansonia* ($N = 13$). Females of

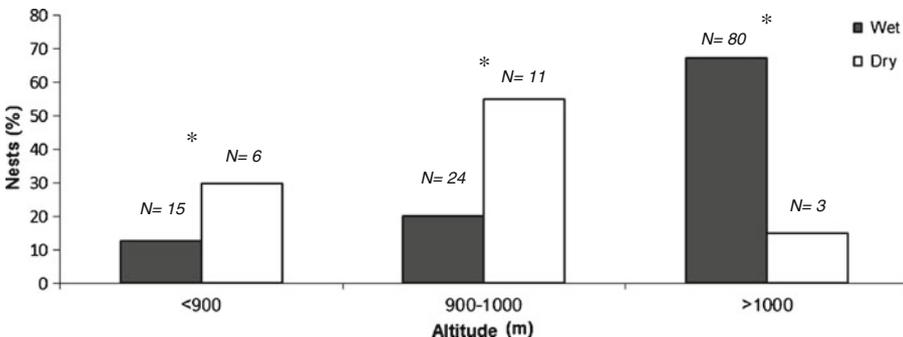


Fig. 2 Seasonality of nests ($N = 139$) across altitude categories on forest trails ($N =$ number of nests). $*P < 0.05$.

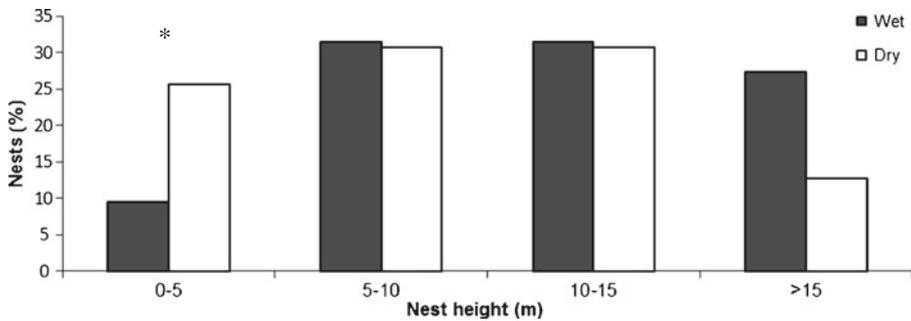


Fig. 3 Seasonality of nest heights for the wet and the dry seasons. * $P < 0.01$.

Aedes, *Coquillettidia*, *Culex*, and *Mansonia* bite humans and include disease vectors. No mosquitoes of the genus *Anopheles* were collected, so malaria vectors were absent from the study site.

Mosquito densities differed between two nearby low-altitude sites (Mann–Whitney U test: $N_1 = 12$, $N_2 = 12$, $z = -3.6$, $P < 0.0001$). The mean number of mosquitoes (\pm SD) per night was 4.2 ± 4.5 ($N = 12$, median = 2, range = 0–14) at site 1 and 70.7 ± 105 ($N = 12$, median = 32, range = 5–379) at site 2. We found no differences between 1.5 and 10 m in nightly catches (Table VIII) of mosquitoes (Wilcoxon signed-ranks test: $N = 12$, $z = -0.2$, $P = 0.87$), females ($z = -0.0$, $P = 1.00$), or potential biters ($z = -0.5$, $P = 0.61$). We found no altitudinal difference in the number of mosquitoes caught per night (Mann–Whitney U test: $N_1 = 16$, $N_2 = 8$, $z = -0.5$, $P = 0.65$), nor in number of females ($z = -0.3$, $P = 0.76$), nor in number of potential biters ($z = -0.1$, $P = 0.96$). We found no seasonal difference in nightly catches of mosquitoes (Mann–Whitney U test: $N_1 = 16$, $N_2 = 8$, $z = -1.0$, $P = 0.34$), females ($z = -1.0$, $P = 0.36$), or potential biters ($z = -0.9$, $P = 0.40$).

Discussion

Nest-Building Selectivity

Nimba chimpanzees showed selectivity for nest height and nested mostly in the middle layer of the canopy. Nest height at Nimba (mean = 11.3 m, median = 10.5 m) resembled that at other sites, e.g., median height of 10 m in Equatorial Guinea (Baldwin *et al.* 1981); 12 m in Sapo, Liberia (Anderson *et al.* 1983); 10 m in Lopé, Gabon (Wrogemann 1992, in Fruth and Hohmann 1994); and mean height of 10 m in Kahuzi-Biega, DRC (Basabose and Yamagiwa 2002) and 13.6 m in Assirik, Senegal (Pruetz *et al.* 2008). Chimpanzees in Nimba preferred larger trees, lower first branches, denser canopy, and smaller leaves. Selectivity for larger trees may reflect the need for trees with strong branches. However, tree size, i.e., DBH, and height correlate strongly ($r_s = 0.84$, $N = 284$, $P < 0.0001$) and larger trees were also taller. The observed preference for dense leaf cover and small leaves may be linked to nesting comfort (Stewart *et al.* 2007), as it may increase softness of the nest (Fruth and Hohmann 1993). Bonobos at Lomako, DRC (Fruth and Hohmann 1993), and chimpanzees at Ugalla, Tanzania (Hernandez-Aguilar 2009), also preferred smaller leaves.

Table VII Mosquito species collected at the Seringbara study site

Species	Human biting	Disease vectors
	<i>Aedes</i>	
<i>Ae. (Aedimorphus) apicoannulatus</i>	Yes ^a	—
<i>Ae. (Albuginosus) stokes</i>	Yes ^a	Yellow fever ^{a,c}
<i>Ae. (Stegomyia) spp.</i>	Yes ^a	Yellow fever ^a (some spp.)
	<i>Coquillettidia</i>	
<i>Cq. (Coquillettidia) annettii</i>	Yes ^b	—
<i>Cq. (Coquillettidia) aurea</i>	Yes ^b	—
<i>Cq. (Coquillettidia) chrysosoma</i>	Yes ^b	—
<i>Cq. (Coquillettidia) fuscopennata</i>	Yes ^b	Rift Valley fever ^f
<i>Cq. (Coquillettidia) maculipennis</i>	Yes ^b	—
<i>Cq. (Coquillettidia) metallica</i>	Yes ^b	West Nile virus ^g
	<i>Culex</i>	
<i>Cx. (Culex) invidiosus</i>	Yes ^a	West Nile virus ^h
<i>Cx. (Culex) perfuscus</i>	Yes ^a	West Nile virus ^g
<i>Cx. (Culiciomyia) sp.</i>	No ^a	—
<i>Cx. (Eumelanomyia) albiventris</i>	No ^a	—
<i>Cx. (Neoculex) spp.</i>	No ^a	—
	<i>Lutzia</i>	
<i>Lt. (Metaluzia) tigripes</i>	No ^a	—
	<i>Mansonia</i>	
<i>Mansonia spp.</i>	Yes ^b	Rift Valley fever ⁱ (some spp.)
	<i>Mimomyia</i>	
<i>Mi. (Mimomyia) hispida</i>	No ^{a,b,c}	—
<i>Mi. (Mimomyia) lacustris</i>	No ^{a,b}	—
<i>Mi. (Mimomyia) pallida</i>	No ^{a,b,d}	—
	<i>Uranotaenia</i>	
<i>Ur. (Pseudoficalbia) mashonaensis</i>	No ^{a,b,d}	—
<i>Ur. (Pseudoficalbia) pseudohenrardi</i>	No ^b	—
<i>Ur. (Uranotaenia) alboabdominalis</i>	Yes ^d	—
<i>Ur. (Uranotaenia) pallidocephala</i>	No ^{a,b}	—

References: ^a Edwards 1941; ^b Service 1990; ^c Boreham *et al.* 1975; ^d Haddow and Ssenkubuge 1962; ^e Reinert 1987; ^f Gillet 1946; ^g Hubalek and Halouzka 1999; ^h Snow and Boreham 1978; ⁱ Meegan and Bailey 1988.

Nimba chimpanzees were also selective regarding tree species, which was largely consistent across years. Similarly, chimpanzees in Bwindi preferentially nested in the same four most used species across years (Stanford and O'Malley 2008). At Nimba, selective use was not restricted to a few species, as 50 species were used for 90% of nests, vs. 14 species for 91% of nests in Kalinzu, Uganda (Furuichi and Hashimoto 2004), 12 species for 90% of nests in Bwindi (Stanford and O'Malley 2008), 17 species for 90% of nests in Kahuzi-Biega (Basabose and Yamagiwa 2002), and 10

Table VIII Number of mosquitoes, female mosquitoes, and potentially biting female mosquitoes collected in 2007–2008 per night at two heights (1.5 m, 10 m), two altitudes (670 m, 920 m), and in wet and dry seasons

	1.5 m vs. 10 m	670 m vs. 920 m	Wet vs. dry
Mosquitoes	4.1±9.3 (M=0, N=12) 5.9±11.7 (M=1, N=12)	6.5±12.3 (M=0, N=16) 2.0±3.7 (M=0, N=8)	2.7±6.3 (M=0, N=16) 9.6±15.3 (M=1, N=8)
Females	2.7±5.1 (M=1, N=12) 2.4±4.7 (M=1, N=12)	2.9±5.4 (M=0, N=16) 1.9±3.4 (M=0, N=8)	1.6±3.1 (M=0, N=16) 4.4±6.9 (M=1, N=8)
Biting females	2.3±3.9 (M=0, N=12) 1.4±2.3 (M=1, N=12)	1.8±3.2 (M=0, N=16) 1.9±3.4 (M=0, N=8)	1.4±2.6 (M=0, N=16) 2.8±4.1 (M=1, N=8)

Results are mean ± SD. M = median; N = trapping nights.

species for 76% of nests in Goulougo (Sanz *et al.* 2007). It remains to be established whether “steepness” in tree species selectivity is determined by forest structure and species diversity, or whether it reflects nest-building “cultures.” Tree species preference was not explained by fruit availability, nor linked to tree characteristics, as preferred species varied greatly in tree size, height, and leaf size. Preferred species may have relatively more trees with suitable characteristics, but choice for specific species could not be explained solely based on physical properties. Species selectivity may depend on properties related to comfort (Stewart *et al.* 2007) and quality of nest-building material, such as flexibility, leaf arrangement, and insect repellent properties.

Antipredation Hypothesis

Predation pressure in Nimba was low or absent. Current tree-nesting may reflect a recent extermination of large ground predators. The observed preference for bigger and taller trees could reflect a strategy to reduce accessibility from ground predators. However, chimpanzees nested mostly in the middle layer of the tree crown and thus did not maximize nest height. Further, preference for a low first branch increased, rather than reduced, accessibility to the nest tree. The chimpanzees increased their functional nest height, possibly by orienting nests in the direction of the slope, but the height difference was small and unlikely to be functional. Also, chimpanzees showed no preference for either more or less isolated tree canopies. In sum, our findings provide no support for the antipredation hypothesis. We cannot exclude the possibility that arboreal nests functioned (partly) as an antipredator strategy in the past, but current tree-nesting does not reflect predator avoidance adaptations.

Thermoregulation Hypothesis

Preferential use of altitudes above 1000 m for nesting was not explained by the general ranging pattern of the chimpanzees. Moreover, previous research showed that altitude use for nesting did not reflect ripe fruit availability (Koops 2005). What seems to drive altitude use for nesting is the avoidance of humid conditions. First,

chimpanzees nested at less humid high altitudes when overall humidity was highest in the wet season. Second, chimpanzees avoided nesting below 800 m year-round, which was consistently more humid than high altitudes. Third, chimpanzees nested higher up in trees, i.e., warmer and less humid, in the wet vs. the dry season. Increased nesting height in the wet season has been reported for chimpanzees elsewhere (Assirik, Senegal: Baldwin *et al.* 1981; Lopé, Gabon: Wrogemann 1992, in Fruth and Hohmann 1994; Fongoli, Senegal: Pruetz *et al.* 2008), as well as for bonobos (Lomako, DRC: Fruth and Hohmann 1994).

The main climatic factor affecting nest height was maximum relative humidity in the trees so that when humidity increased, chimpanzees increased their nest height. High humidity reduces heat loss in high ambient temperatures and increases heat loss in low ambient temperatures and thus has a significant effect on thermoregulatory processes (Bell and Greene 1982). Humidity avoidance thus provides evidence for a thermoregulation function of arboreal nest-building. At a rain forest site, humidity avoidance may be an important factor influencing chimpanzee nesting, but avoiding heat loss may be more crucial for chimpanzees at a savannah site with low overnight temperatures (Stewart 2011). Our linear regression had a low R^2 (0.16), which suggests that factors besides humidity, e.g., social influences, played an additional role in nest height selection. Further, interpolation of climatic data and possible errors in assigning nests to nest groups may have caused some inaccuracy in our data. We found no support for the suggestion that chimpanzees make more open nests to avoid dripping vegetation or increase exposure to morning sun in the wet season (Baldwin *et al.* 1981).

The proportion of nests on the ground did not vary seasonally. Further, dimensions and complexity of ground nests showed no seasonal differences, except for slightly thicker plant stems used in the dry season. Ground nests thus did not seem to function in insulating nest-builders from low ambient temperatures during dry season nights, nor from wet ground in the rainy season. Our results suggest that ground-nesting was not influenced by climatic conditions, corroborating previous research (Koops *et al.* 2007), and thus did not function in thermoregulation. However, a possible difference between day and night nests on the ground remains to be addressed. Plant choice for ground nest construction was based mainly on availability of plants, rather than on preference. Ground-nesting is done predominantly by males and may be best explained by social factors (Koops *et al.* 2007). When nesting on the ground, (male) chimpanzees were seemingly less selective with regard to both climatic conditions and plant material used as compared to when they nested in the trees.

Antivector Hypothesis

Year-round mosquito catches were low, except for one of the low-altitude sites in the wet season. Mosquito catches were zero on many nights, even when using several attractants, such as human skin lures. In addition, no systematic differences in mosquito densities were found between altitudes or seasons, and no possible link with chimpanzee nesting patterns could thus be established. Further, no differences in overall mosquito densities, or in densities of potentially biting species, were found between heights in the forest. These findings suggest that mosquito densities in Nimba are not a significant selection pressure influencing nest-building. Our results

have to be considered as preliminary because of a limited number of trapping nights and more intensive sampling is necessary to establish differences in mosquito species composition across heights, altitudes, and seasons.

Conclusions

Our findings provided no support for either the antipredation or the antivector hypothesis for arboreal nest-building. The thermoregulation hypothesis seemed to best explain current tree-nesting patterns and nest height variation across seasons. Chimpanzees avoided making nests in humid conditions, i.e., by nesting at higher altitude and higher up in the trees in the wet season. Ground-nesting could not be explained based on climatic conditions and may thus function in the social domain. Nest height variation within nest groups remains to be explored, and is likely influenced by social relationships and sex differences. The adaptive value of nest-building may lie in the connection between nest-building and improved quality of sleep leading to increased fitness (Fruth and Hohmann 1996). How chimpanzees improve sleep quality may vary from site to site, depending on the ecological conditions the apes face. Predation pressure may be an important factor for some populations, but our results highlight the importance of thermoregulation in arboreal nest-building.

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