



LJMU Research Online

Piel, AK

Savanna chimpanzees adjust sleeping nest architecture in response to local weather conditions

<http://researchonline.ljmu.ac.uk/id/eprint/8395/>

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Piel, AK (2018) Savanna chimpanzees adjust sleeping nest architecture in response to local weather conditions. American Journal of Physical Anthropology, 166 (3). pp. 549-562. ISSN 1096-8644

LJMU has developed **LJMU Research Online** for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact researchonline@ljmu.ac.uk

<http://researchonline.ljmu.ac.uk/>

Title: Savanna chimpanzees adjust sleeping nest architecture in response to local weather conditions

Authors: Fiona A. Stewart^{1,2}, Alexander K. Piel¹, Jurgi C. Azkarate³, and Jill D. Pruetz⁴

¹School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, L3 3AF, UK

²Department of Archaeology and Anthropology, University of Cambridge, Cambridge, CB2 3QG, UK

³Hazi Lagun, Arrasate, GI 20500, Spain

⁴Department of Anthropology, Iowa State University, Ames, IA 50011, USA

Number of text pages: 19; plus bibliography: 23; figures: 2; Tables: 6

Abbreviated title: Chimpanzees adjust nest architecture to local weather

Keywords: sleeping-platform, bed, shelter, great-ape

Corresponding author: Fiona A. Stewart

School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, L3 3AF, UK; Email: F.A.Stewart@ljmu.ac.uk; Phone: +447947406953

Grant sponsorship: Carnegie Trust for Universities of Scotland, Harold Hyam Wingate Foundation, L.S.B. Leakey Foundation, International Primatological Society, Wenner-Gren Foundation for Anthropological Research, Iowa State University, National Geographic Society, National Science Foundation, American Society of Primatologists and Primate Conservation Inc., and UCSD/Salk Center for Academic Research and Training in Anthropogeny (CARTA).

ABSTRACT

Objectives

Great ape nests are hypothesized to aid safe, secure sleep via providing thermoregulation or protection from predators and vectors. We aimed to describe and investigate variation in chimpanzee nest architecture across two populations in response to local weather conditions.

Materials and methods

We experimentally tested whether nests provide insulation by measuring heat loss within and outside nests, and took detailed measurements of the number, size, and type of materials used in nest building across two dry-habitat research sites (Fongoli, Senegal, and Issa, Tanzania). We tested application of principal components analysis (PCA) to extract composite quantitative measures of the key components of shape and architecture, before testing how PCs vary across populations with overnight weather conditions that reflect hypothesized thermoregulatory function.

Results

Heat loss is greater and occurs faster outside of nests. PCA allowed meaningful comparison of nests within and between sites. Nest variation at both sites revealed chimpanzees built thicker nests in cooler conditions and used more broken branches and support in moister conditions. Chimpanzees in Fongoli used more lining and mattress material in colder conditions, whilst in Issa nest depth and support branch size were larger in windier conditions.

Discussion

Shape and architectural measures reflected insulation and stability of nest structure. Chimpanzees in Fongoli and Issa may achieve the same functional goals by adjusting nest shape and architecture in different ways. These results suggest that wild chimpanzees show flexible building techniques in response to local, overnight weather conditions in making an insulating and stable, supportive platform for sleep.

INTRODUCTION

For many species of animals, built structures often function as shelters that provide protection against environmental conditions, including climatic extremes and predation threat (Hansell, 2005). Animal constructions most frequently perform shelter functions and through their building behavior, animal architects stabilize their environments, which may allow them to expand their range and be buffered against extinction processes (Hansell, 1993, 2005; Hansell and Ruxton, 2008). For example, the most widely distributed species of ants are weaver ants (*Oecophylla longinoda* and *O. smaragdina*), which sew leaves into a protective shelter (Hansell, 2005), and the evolution of paper nest construction in wasps (Polistinae) allows paper nest-building wasps to attach nests to a greater variety of building sites than mud nest-builders, which may have permitted paper nest-building wasps a greater pantropical range (Hansell, 1993).

Over their post-weaning lives, all great apes build at least one daily shelter; these nests serve for both daytime rest and overnight sleep. This construction is the most pervasive form of technology in the great apes. The four species of great apes make broadly similar nests, despite differences among them in phylogeny and habitat (Fruth and Hohmann, 1996). Such similarity suggests that nest construction evolved in a common great-ape ancestor in the Miocene and may have facilitated the evolution of cognition and technological skill in hominoids (Fruth and Hohmann, 1996). Coolidge and Wynn (2006) suggested that a major jump in cognitive evolution might have occurred during the transition from tree to ground sleeping in *Homo erectus*. Determining the factors involved in nest function in existing hominoids is thus important for modeling the behavior of pre-*erectus* hominins and understanding the evolution of shelter in hominoids.

Nest building is complex, requiring sequential combination of branches into a secure platform in highly variable arboreal substrates. Captive individuals build higher-quality nests more efficiently if they have had exposure to experienced nest-builders early in life, indicating that learning plays an important role in the development of nest-building skills (Bernstein, 1962; Videan, 2006). As an example of problem-solving, nest building may demand as much, or more, cognitive complexity as some forms of tool-use (Hansell and Ruxton, 2008), and study of orangutan nest-building has revealed technical knowledge and choice in ape nest construction (van Casteren et al., 2012).

Research on variation in tools and tool use has extensively shown both functional and cultural variation in tool use across and within populations (Whiten et al., 1999; Humle and

Matsuzawa, 2002; Schöning et al., 2008). Nest building is the most ubiquitous form of ape elementary technology, however, and despite preliminary descriptions of nest architecture (Bolwig, 1959; Goodall, 1962; Schaller, 1963; Mackinnon, 1974; Kano, 1979) few studies have measured and quantified nest shape and architecture beyond classification of nests into types (Tutin et al., 1995). In Fruth's pioneering study, she measured and described the shape and structure of wild bonobo nests (Fruth, 1995). Similar methods have been used more recently to describe orangutan (van Casteren et al., 2012) and chimpanzee nests (Samson, 2012). These studies revealed variation in architectural complexity in ape nests, and, for orangutans, knowledge of the mechanical properties of branches used in their constructions (van Casteren et al., 2012). However, no previous study has quantified how nest architecture varies within or across populations, and if such nuanced variation reflects cultural patterns or functional adaptations of nest building to local environmental conditions.

The primary function of ape nests is likely as a safe, comfortable sleeping platform that permits higher-quality rest and longer periods of REM sleep, through a recumbent posture and fewer disturbances during the night (Fruth and Hohmann, 1996; McGrew, 2004; Stewart et al., 2007; Stewart, 2011a). However, across many species, animal-built structures often act as shelters that provide protection against environmental conditions, including extreme weather and predation threats (Hansell, 2005). Great ape nests are likely no exception and have been proposed to perform other functions that shelter the builder from environmental challenges, such as predation, parasite transmission from biting vectors, and thermal stress (Baldwin et al., 1981; Russon et al., 2007; Pruett et al., 2008; Stewart, 2011a; Koops et al., 2012; Samson and Hunt, 2012; Samson et al., 2012; Stewart and Pruett, 2013). Nest building may permit apes to sleep in higher, more peripheral, and camouflaged sites within the tree canopy, than their large body size otherwise would permit, providing greater protection from possible nighttime predation (Baldwin et al., 1981; Pruett et al., 2008). Height within the canopy and possible phytochemical repelling properties of tree species used for nest building may reduce apes' exposure to biting insects and thus lower potential vector transmission of parasites (Russon et al., 2007; Stewart, 2011a; Koops et al., 2012; Samson et al., 2012). Finally, nests have been proposed to aid thermoregulation by provision of an insulating layer for overnight sleep (Stewart, 2011a) or by enabling apes to select thermally stable sleeping sites (Koops et al., 2012; Samson and Hunt, 2012).

Despite these hypotheses, almost no studies have investigated possible thermoregulatory function in great ape nest-building. Previous studies have described

differences in nest site selection across different conditions; for example chimpanzees at several sites nest higher during the rainy versus the dry season, which may expose the apes to sunshine at dawn, allowing them to dry faster after wet nights (Baldwin et al., 1981; Koops et al., 2012), and gorillas build more arboreal nests during the wet season as well as fuller, more elaborate nests in colder conditions and on nights after rainfall (Remis, 1993; Tutin et al., 1995; Mehlman and Doran, 2002; Sunderland-Groves et al., 2009). Nest structures are thus hypothesized to provide insulation in cold and rainy conditions, yet no studies to date have directly assessed the insulation of nests, nor used detailed climatological data to investigate how nest architecture varies with climatic conditions.

A pre-requisite to examining whether chimpanzee nests serve a thermoregulatory function is determining whether nests provide insulation. We therefore first aim here to test the hypothesis that nests provide insulation by experimentally testing heat loss within and outside of nest structures. We predicted that heat loss would occur less and be slower within a nest than outside of a nest.

Architectural measurements yield many variables for a nest, so measures are often inter-related. We therefore applied a principal components analysis (PCA) to extract the key elements of nest shape and architecture. PCA is frequently used to investigate traits underlying complex behavior, e.g. relationship quality (Fraser et al., 2008), and variation in complex shapes, e.g. primate crania (Fleagle et al., 2010). Such analysis results in composite quantitative measures of shape and architecture across all nests, which we then aimed to compare between sites and nest types.

Thirdly, we aimed to investigate the thermoregulatory hypothesis by testing for a relationship between variation in architecture with climatic conditions. We hypothesized that architectural components associated with characteristics known to improve insulation of structures in other species (Hansell, 2000, 2005) would vary with overnight weather conditions in ways that may provide greater insulation in colder, wetter, and windier conditions. Specifically, we made the following predictions:

- 1) Cooling within nests is less and occurs slower than outside nests
- 2) Nest thickness, amount of mattress material, and additional lining material will increase as temperature decreases, and wetness increases
- 2) Nest depth will increase in colder, wetter, and windier conditions, which may reduce heat loss from convection

We also hypothesized that architectural components associated with characteristics known to improve structural support in other species' constructions (Hansell, 2000, 2005) would vary with overnight conditions in ways that may provide a more stable, safe structure for overnight sleep. Specifically, we predicted that:

- 3) The amount and size of support built and selected will increase in windier conditions.

METHODS

Study sites

The research was done at two study sites: Fongoli (12° 39 N 12° 13 W), in south east Senegal, and Issa (05° 23 S 30° 35 E), in western Tanzania. Both sites have a mosaic of woodland-savanna vegetation, interspersed with small riverine patches of gallery forest, which makes up <2% of the landscape (Pruetz et al., 2008; Stewart et al., 2011). Vegetation types were classed similarly in this study as 'forest', 'woodland', and 'grassland' (*sensu* Pruetz et al., 2008; Stewart et al., 2011).

In Fongoli architectural data were collected during only the dry season from October 2007 to March 2008. In Issa, architectural data were collected during the wet season from January to April 2009 and the dry season from May to September 2009. Nest insulation experiments were conducted at Issa in August to November of 2014.

Nest insulation experiment

In order to measure temperature loss over time within, compared to without nests, we attached sensors of a dual sensor temperature logger (MicroLite II USB Temperature Data Logger with External NTC Sensor) to two Nalgene water bottles. We built ten experimental nests on different occasions and deployed water bottles, one within the nest, and one attached to a branch at the same height and orientation within the same tree. Chimpanzees usually build a fresh nest each night and in a dry, mosaic environment leaves quickly become dry (FS pers. obs.). Freshly-built nests could therefore differ in insulative properties compared to day-old nests, so we chose to use human-built fresh, rather than chimpanzee-built old, nests for this experiment. Although experimental nests were built using known architectural properties described in Table S2, to ensure they were as similar as possible to chimpanzee nests, human-built nests might differ in insulative properties. We filled water bottles with freshly boiled water and deployed for a minimum of three hours with loggers recording temperature each

minute. We calculated the differential temperature for each experiment, plus mean differential temperature and standard deviation across experiments.

Weather conditions

We deployed six assemblages of data loggers within representative vegetation types and topographic levels used for nesting within the study areas; climatic data were averaged across logger assemblages deployed within the same vegetation type or topographic level category (see Table 1). Some data were lost due to rodent-chewed wires, or technical faults. Thus, in Issa, data from wind sensors were averaged across 'open' (woodland plateau, slope and valley) versus 'closed' (forest plateau, slope, valley) vegetation types. All loggers were deployed at known mean nesting height for each vegetation type and study site (Fongoli nest heights from Pruetz et al. (2008) of 7m in forest, 8m in woodland, and 8m in grassland; Issa nest height from Hernandez-Aguilar (2006) of 12m in all vegetation types), in order to represent variable overnight nesting conditions in different vegetation types, as climatic measurements vary with vegetation and deployment height (Koops et al., 2006, 2012; Samson and Hunt, 2012). These data were taken to be representative of microclimate of these vegetation types across the study site. Each assemblage included a Hobo 4-channel micro weather station logger (H21-002) with attached Hobo wind speed smart sensor (S-WSA-M003), and a Hobo temperature and relative humidity logger (H8 Pro series), which recorded data every 30 minutes, including the maximum 2-second wind gust speed, temperature, and percentage relative humidity. In Issa, a Hobo leaf wetness sensor (S-LWA-M003) was also used, which is a flat sensor that uses a capacitive grid to measure percentage surface area (leaf) wetness. In Issa we deployed a Hobo data-logging rain gauge (RG-3) to record overnight rainfall volume. In Fongoli, data were collected during the dry season; none of the nests analyzed were built on the very few rainy nights.

An overnight period of 12 hrs, from 18:00 to 06:00 hrs, was selected for analyses, following the only study to measure the inactive period of chimpanzees in the wild (Lodwick et al., 2004), and all nests included in this study were built for overnight sleep. For each night, and in each vegetation type, when a nest was built in Fongoli or Issa, we calculated the mean overnight temperature, relative humidity, and gust speed. In Issa, we included mean overnight leaf wetness and total volume of rainfall (mm) overnight. Data from the night each nest was built were used for analyses because chimpanzees may adjust their constructions or move nests during the night (Stewart, 2011b).

Nest location, access, shape and architectural measurements

In Fongoli, habituated focal individuals were followed to the nesting site in the evening and measurements were made the following morning. In Issa, where chimpanzees are unhabituated, fresh nests groups were found opportunistically or after hearing vocalizations at night or in the early morning. Only fresh nests, defined as nests seen built the night before, or with moist feces or urine underneath, were analyzed.

Nest height was measured to the nearest metre from the ground beneath the nest to the centre of the nest using a clinometer and a tape measure. Nest height and height of the tree-crown base were measured in the same way from the base of the tree-trunk and these measurements were used to calculate nest height in the tree crown.

FS accessed 252 freshly-built night nests. Due to time constraints, or if nests sprang apart rapidly, we could not take each measurement for each nest, thus 212 nests for which all variables were recorded were included in a PCA. FS accessed nests by either free-climbing, or using a combination of single-rope technique (SRT) and double-rope technique (DRT) (Houle et al., 2004; Stewart et al., 2011).

Detailed measurements of shape as described in Figure 1 were recorded to the nearest cm, using a meter stick. Depth was recorded a second time with the weight of researcher FS (55kg) within the nest as many nests spring up without an occupant. All diameters were measured to the nearest cm using a metric diameter tape. Detailed measurements of nest architecture were recorded by taking the nest to pieces and recording each step in reverse construction sequence, in order quantify all likely manipulative steps (*sensu* Corp and Byrne, 2002). For each building-step the type of material (grass, liana, shrub, or tree), type of manipulation (bend, <50% broken; break, >50% broken; or detach), and branch diameter (measured at the inside of the bend/break) was recorded. Architectural data were summarized as described in Table 2 to include quantity and size of material. Additional variables measured include the sum of selected support diameter (defined as the sum of the diameters of weight-bearing, but un-modified branches or branch formations on which the nest was built) and the sum of constructed support diameter (defined as the sum of diameters of branches forming initial building-steps that provided structure and support to the nest, but contributed little leafy material). All support diameters were measured at weight-bearing points, where they passed beneath the center of the nest.

Analyses

All statistical analyses were conducted using Predictive Analytics SoftWare PASW Statistics 18, Release Version 18.0.0 (SPSS, Inc., 2009, Chicago, IL, www.spss.com). For the nest insulation experiment, we compared maximum temperature lost within nests and outside nests using a wilcoxon's signed rank test. Within-site differences in microclimate across vegetation types were analyzed with a repeated measures analysis of variance (ANOVA) or the non-parametric equivalent, Friedman's ANOVA, each followed *post hoc* by Bonferroni corrected pairwise comparisons.

Nest height was non-normally distributed and so a series of bivariate Spearman rank correlations was done to investigate how nest height varies with mean overnight temperature, relative humidity, and gust speed. All reported p-values were Bonferroni corrected, to control for Type-1 error.

As a large number of inter-correlated variables were recorded in order to fully describe nest shape and architecture, we used a principal components analyses (PCA) to obtain composite measures of nest shape and architecture. PCA is a statistical technique that can be used to identify clusters of variables, or patterns of correlations within sets of variables, which represent underlying factors, or principal components (Tabachnick and Fidell, 2007). The PCA provides coefficients of correlation between each nest structure variable and each extracted component; correlated variables, which could be measuring aspects of the same underlying factors. PCA reduces these groups of interrelated variables into underlying dimensions or components and the cumulative amount of variance explained by the components. As extracted components are by definition uncorrelated with each other, the total variance explained is the sum of the variance explained by each extracted component. We considered coefficients of correlation greater than 0.5 or less than -0.5 to be high loadings. A varimax rotation was used, which is an orthogonal rotation method that minimizes the number of variables that have high loadings on each component and is most commonly used to simplify the interpretation of the components (Tabachnick and Fidell, 2007). We used a minimum eigenvalue of 1.00, which is standard for PCA using similar sample sizes, in order to determine the number of components extracted from the PCA (Tabachnick and Fidell, 2007).

The 25 variables included in the PCA were determined by the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy (Tabachnick and Fidell, 2007; Table 2). We used a KMO value greater than 0.7, which indicates that the variables are sufficiently inter-correlated to yield distinct and reliable principal components for this sample size (Hutcheson and Sofroniou,

1999). Two measures of nest architecture that did not correlate sufficiently were therefore analyzed separately: sum of selected support branch diameters, and sum of constructed support branch diameter.

The resultant principal components of nest shape and architecture were analyzed individually. A series of backward stepwise multiple linear regression models were generated using dependent variables of each principal component, and independent variables of mean overnight climatic measures, in order to investigate the influence of weather conditions on nest shape and architecture for each study site separately. A Bonferroni correction was applied for all multiple comparisons. When necessary, we applied a negative inverse transformation to the data, to correct for skewness and kurtosis. If data could not be normalized, then non-parametric bivariate correlations were used and a Bonferroni correction applied.

RESULTS

Nest Insulation

All experimental nests built provided insulation with slower temperature loss within nests, than outside of nests (Fig. 2). The maximum temperature difference between inside and outside nests, which we recorded across experiments, was on average 7.32 C (St Dev 3.29 C). The temperature loss after three hours was significantly greater within nests than outside nests (Wilcoxon's signed rank test, $V=0$, $p=0.002$).

Nest Height, Shape and Architecture

Median nest height was greater in Issa (Median=12m, $n=502$) than Fongoli (Median=5m, $n=408$), and no different between seasons. In Fongoli, nests were built higher ($r = 0.15$, $n = 409$, $p = 0.006$), and higher within the tree crown ($r = -0.14$, $n = 336$, $p = 0.036$) in conditions of greater relative humidity. There was no relationship between nest height and wind speed or temperature. In Issa nests were built higher ($r = 0.14$, $n = 470$, $p = 0.010$) and tended to be built higher within the tree crown ($r = 0.12$, $n = 448$, $p = 0.075$), in conditions of greater rainfall. Higher nests were also built in conditions of greater leaf-wetness ($r = 0.13$, $n = 424$, $p = 0.035$), and tended to be built in conditions of greater humidity ($r = 0.11$, $n = 425$, $p = 0.10$). There was no relationship between nest height and wind speed or temperature.

Overall nests had basic size, shape and architectural characteristics that were broadly similar across the two study sites, Fongoli and Issa (Table S1-S2). Nests were usually bowl-shaped, oval in shape, with mean length about one fifth longer than width.

All nests were built on a solid base: the ground (Fongoli only), single large branch, group of branches, or stable crotch of branches, over which the first manipulated branches often formed a triangle-shaped framework. Surrounding branches were radially broken or bent into a central structure to form an inter-woven, stable, mattress of overlapping branches (see typical nest in Fig. 1). Manipulated support and mattress branches usually remained attached and pliable. Fully detached branches and twigs were often added as a lining. The median number of building steps was broadly similar between sites (Fongoli, 35; Issa, 36) of which a median of 2 (Fongoli) and 4 steps (Issa) were lining, whilst 4 (Fongoli) and 6 steps (Issa) were support (Table S2).

Thirty five (25%) of the nests analysed in Fongoli were built on the ground, which is greater, and so not representative of the overall proportion of ground nests (12%) built in Fongoli during the study period. We therefore described ground and tree nests separately across-sites. However, ground nesting itself represents a major difference between the two sites. Overall in Fongoli, ground nests are smaller, thinner and more oval in shape (width: $n_1 = 34$, $n_2 = 109$, $t = 2.49$, $p = 0.014$; central thickness: $n_1 = 34$, $n_2 = 108$, $t = 6.99$, $p < 0.001$; mean thickness: $n_1 = 34$, $n_2 = 108$, $t = 5.59$, $p < 0.001$; circularity: $n_1 = 34$, $n_2 = 108$, $t = 2.27$, $p = 0.025$).

Ground nests are likely to differ architecturally from tree nests given these nests are not required to be load-bearing structures. Ground nests were built using trees as the primary source of material in just 35% of nests, whilst shrubs, saplings, lianas or grass were the primary source of material in 65% of nests. Ground nests in Fongoli were built with fewer steps overall, reflected in the number of lining and support steps, whilst the number of mattress building steps was similar ($n_1 = 28$, $n_2 = 85$; total steps: $\bar{x}_1 = 20.9$, $\bar{x}_2 = 34.5$, $t = 3.46$, $p < 0.001$; mattress steps: $\bar{x}_1 = 21.9$, $\bar{x}_2 = 26.9$, $t = 1.63$, $p > 0.05$; lining steps: $M_1 = 0$, $M_2 = 2$, $z = 2.23$, $p = 0.026$; support steps: $M_1 = 0$, $M_2 = 4$, $z = 6.81$, $p < 0.001$).

Tree nests built in Fongoli and Issa in dry and wet seasons differed in sum of constructed support diameter ($df = 2$, 159; $F = 3.15$; $p = 0.045$), and mean constructed support diameter ($df = 2$, 159; $F = 11.49$; $p < 0.001$). Post-hoc comparisons revealed Fongoli nests to be built with greater mean diameter support branches. Post-hoc comparisons of the sum of constructed support diameter were not significant (Table S2). Nests built in Issa in the wet season were built with larger diameter support branches, and had a greater number of support steps, total breaks, bends $>3\text{cm}$ diameter, breaks between 1 and 3cm diameter, and twigs (Table S2).

Principal components of nest shape and architecture

Eight components emerged from a principal components analysis that included 25 variables of nest shape and architecture (Table 3). Together, these components explained 73% of the overall variance in nest shape and architecture. Each variable loaded strongly onto one component, and loadings of over 0.5 were interpreted as high loadings. The compilation of variables that load onto each component allows each component to be interpreted and labeled as a representative part of the nest structure (Table 3).

The first component had high loadings from bends and breaks <1cm diameter, mattress steps and main material, suggesting that the nest mattress is composed of material <1cm in diameter, but that the number of manipulations of such material is also associated with the number of pieces of main material or main branches. Together, these variables represent an overall measure of the amount of material and manipulations of the nest mattress, so we labelled this first extracted component '*mattress*.'

The variables with high loadings on the second component were detachments < 1cm diameter, line steps, and all material. Two types of detached material seem to be used in nest building; small twigs and branches <1cm in diameter which correlate here with lining steps, and larger diameter detached material that is integrated into the nest structure rather than placed on top as lining. We therefore labelled this second component '*lining*'. That the total amount of all material also correlates with lining suggests that lining is an addition to the main nest mattress, rather than a substitute or alternative building technique used to achieve create a similar nest shape and structure.

The third component extracted has the highest loading on bends of 2-3 cm and 1-2 cm in diameter, branches constructed support, and support steps. The fourth component extracted had the highest loading from breaks 2-3 cm in diameter, but also had high loadings from breaks 1-2 cm, and support steps. With the exception of support steps, these variables are all related to the diameter of branches used for building. As larger diameter branches are always manipulated at the beginning of nest building, these branches are necessarily related to the number of support steps. Thus components 3 and 4 may be described as different support types, the first is labelled '*bend support*', as this component is associated more with number of bends than breaks, and the latter '*break support*'.

The fifth component consists of detached branches 1-2 cm, 2-3 cm, and >3 cm in diameter, in addition to large breaks >3cm in diameter. These large detached branches and

breaks do not correlate with 'lining', but rather may be another dimension of nest architecture, so we labelled this component '*fractures*'.

The last three components extracted relate to different dimensions of nest shape. The sixth component is labelled '*thickness*' as the variables of central thickness and mean thickness are strongly loaded. The number of bends >3 cm in diameter is also strongly loaded onto the thickness component, suggesting that large bent branches are most likely to contribute to increased thickness of nests. The seventh component is labelled '*area*', as length, width, and misshapeness are loaded onto this component and reflect two-dimensional measurements, rather than three-dimensional measures of depth or thickness. Lastly, the eighth component extracted is labelled '*depth*', as it had high loadings only from depth and from depth un-sprung.

Cross-site comparison of principal components of nest shape and architecture

The validity of the principal components analysis of shape and architecture was tested through direct comparisons of raw variables of shape and architecture across ground and tree nests in Fongoli and dry and wet season nests in Issa (Table S2). A one-way analysis of variance test revealed no difference in the principal components of mattress ($F_{(3,187)} = 1.08$, $p = 0.36$), lining ($F_{(3,187)} = 0.89$, $p = 0.45$), or depth ($F_{(3,187)} = 1.79$, $p = 0.15$) across study sites, seasons in Issa, or between ground and tree nests in Fongoli. Significant differences emerged across groups in bend support ($F_{(3,187)} = 19.54$, $p < 0.001$), break support ($F_{(3,187)} = 6.20$, $p < 0.001$), thickness ($F_{(3,187)} = 11.78$, $p < 0.001$), and area ($F_{(3,187)} = 5.09$, $p = 0.002$).

Post hoc tests revealed that bend support ($p < 0.001$) and break support ($p = 0.045$) values were lower in ground versus tree nests in Fongoli, and in Issa dry versus wet season nests (bend support, $p = 0.007$; break support, $p < 0.001$). Bend support and break support did not differ between tree nests in Fongoli or Issa dry versus wet seasons. Ground nests were thinner than tree nests in Fongoli and Issa ($p < 0.001$). Tree nests in Fongoli tended to be thicker than dry season nests in Issa ($p = 0.093$), but there was no difference in thickness between tree nests in Fongoli versus Issa in the wet season ($p = 0.22$). However, nests built in Issa in the wet season were thicker than those built in the dry season ($p = 0.009$). Fongoli ground and tree nests were similar in area ($p = 1.00$), as were Issa dry and wet season nests ($p = 0.99$), but Fongoli tree nests were larger in area than dry season nests in Issa ($p = 0.002$). The principal component fractures was analyzed using a Kruskal-Wallis test, which revealed no difference in nests across sites or seasons ($H_{(3, 187)} = 6.17$, $n = 191$, $p = 0.10$).

Overnight weather conditions

Mean overnight climatic measurements differed across vegetation types, research sites and seasons (Table 1). Mean overnight temperatures in Fongoli were lowest in forest, followed by woodland and highest in grassland, whilst mean overnight relative humidity was greatest in forest and lowest in grassland (temperature, $F_{(2,173)} = 355.9$, $p < 0.001$; relative humidity, Friedman's two-way analysis of variance, $n = 175$, $df = 2$, $\chi^2 = 334.1$, $p < 0.001$; Bonferroni corrected pairwise comparisons significant to $p < 0.001$). Gust speeds were higher in open than closed habitats (Wilcoxon's matched pairs, $n = 175$, $z = 11.5$, $p < 0.001$; Table 1).

In Issa, mean overnight temperatures were colder in forest than woodland, and on woodland slope than valley, although forest slope and valley did not differ (temperature, $F_{(2,173)} = 355.9$, $p < 0.001$, *post hoc* Bonferroni corrected pairwise comparisons significant to $p < 0.001$; Table 1). Relative humidity was highest in forest valley, followed by forest slope and woodland valley (which did not differ), and lowest in woodland slope (Friedman's two-way analysis of variance, $n = 251$, $df = 3$, $\chi^2 = 390.6$, $p < 0.001$; *post hoc* Bonferroni corrected pairwise comparisons significant to $p < 0.01$). Leaf wetness varies similarly to relative humidity across vegetation types (Forest valley: mean 34.1%, St Dev. 34.0%; Forest slope: mean 13.1%, St Dev. 14.5%; Woodland valley: mean 33.1%, St Dev. 34.2%; Woodland slope: mean 16.4%, St Dev. 23.8%). Mean overnight gust speeds were lowest in forest valley, greater in woodland valley, and greatest in woodland slope, followed by forest slope (Friedman's two-way analysis of variance, $n = 253$, $df = 3$, $\chi^2 = 558.2$, $p < 0.001$; *post hoc* Bonferroni corrected pairwise comparisons significant to $p < 0.01$; Table 1).

As data were collected during the rainy season in Issa, we compared climate also between the dry seasons in Fongoli and Issa. Mean overnight temperatures are greater in Fongoli than in Issa in the dry season (t-test, $n_1 = 175$, $n_2 = 153$, $t = 10.6$, $p < 0.001$), but have a larger range (Fig. S1). Mean overnight relative humidity is greater in Issa in the dry season than in Fongoli (Mann-Whitney test, $n_1 = 175$, $n_2 = 153$, $z = 6.0$, $p < 0.001$), and does not drop as low as in Fongoli (Fig. S2). Mean overnight gust speeds are greater in Issa in the dry season than in Fongoli (Mann-Whitney test, $n_1 = 175$, $n_2 = 153$, $z = 7.8$, $p < 0.001$), but the range in Fongoli is similar (Fig. S3).

Variation in shape and architecture with local weather conditions

Backward stepwise linear regression models revealed more principal components of nest shape and architecture to correlate with mean overnight weather conditions in Fongoli than in Issa (Tables 4, 6, and S3).

In Fongoli, the amount of mattress material increased with greater relative humidity, which explained 9% of the variation in 'mattress'. Nest lining, bend support, thickness, and depth were all greater in colder overnight conditions in Fongoli, although the amount of variance explained by mean overnight temperature was small; 10%, 9%, 11%, and 6% respectively (Table 4). However, thickness also correlated negatively with gust speeds and tended to decrease with greater relative humidity. Thus, nests were thicker in colder conditions, yet thinner in windier conditions. Increased break support correlated with greater gust speeds and relative humidity, which explains more total variance (21%) because gust speed and relative humidity were inversely correlated. Size of the nest area and weather conditions were uncorrelated (Table 4); nor was there a relationship between fractures and weather conditions, although there was a tendency towards more fractures in warmer conditions (temperature: $r = 0.24$, $p = 0.060$, Bonferroni corrected). Greater diameter of constructed support of tree nests also correlated with greater wind speeds, but selected support diameter did not correlate with any weather conditions (Table 4).

Ground nests were included in analysis of nest structural variation with weather conditions, as they are part of the repertoire of typically built nest types in Fongoli (12% of nests in this study). However, materials used for building ground nests are often structurally different from tree nests, e.g. elephant grass (*Pennisetum purpureum*) is weaker, smaller in diameter, and longer than tree branches. If ground nests were excluded from analyses the relationships between weather conditions and principal components of nest architecture and shape remained similar, although a greater amount of variance was explained in mattress (21%), lining (12%), break support (24%) and depth (18%; Table S3). The amount of mattress material was positively correlated also with increased gust speeds. Bend support and thickness were no longer correlated significantly with any weather variables, although thickness approached a tendency to still correlate with decreased temperature, whilst increased lining and nest depth remained correlated with decreased temperature. (Table S3).

Variables of mean overnight temperature, mean overnight relative humidity, and mean overnight gust speed were multi-collinear in Issa, and so could not be used together in multiple

regression analysis without first doing a data-reduction analysis. Nests were also sampled in Issa during the wet season, so it was possible to include the influence of rainfall and dew, using leaf wetness data. Thus, these five variables were entered into a second principal components analysis in order to generate principal components of weather conditions to enter into backward stepwise linear regression models, to investigate the influence of weather conditions on shape and architecture in Issa. Two components were extracted from a PCA that explained 73% of the variance in weather conditions. The first component had high loadings from variables that reflected moisture and so the component was termed '*wetness*', while the second component had strong positive loadings from temperature and gust speed (variables which could then not be differentiated), so this component was termed '*temperature/wind*' for analyses (Table 5).

At Issa, nest thickness correlated negatively with temperature/wind (as wind and temperature were collinear), the influence of each could not be separated, but suggests that nest thickness is influenced by colder conditions, despite slower gust speeds (Table 6). Nest thickness and break support also correlated with wetter conditions. There was a tendency for greater depth with greater temperature/wind. No correlation existed between fractures and wetness or temperature/wind ($r = -0.08$, $p = 0.47$; $r = -0.15$, $p = 0.17$ respectively). There was no relationship between selected or constructed support diameter and weather conditions in Issa.

DISCUSSION

Overall our data support our hypotheses that nests provide insulation, thermoregulation and structural support. Nests were found to insulate and chimpanzees may, by adjusting the architecture of the nests in response to overnight weather conditions, buffer sleep quality against environmental influences. We found a large amount of variation in nest shape and architecture *within* each research site, however, of which only a small part is explained by the apes' flexible building techniques in response to local environmental conditions. In Fongoli, we found support for our predictions that nest thickness, amount of material, and lining would increase in colder conditions. However, without data on wet season nests the influence of rain remains unknown. At Issa, we found thickness to be influenced by wetter and colder conditions, but no relationship with lining or mattress material. Our prediction that depth would increase in windier conditions was not supported in Fongoli, and supported in Issa. In Fongoli, we found nest support to be influenced by wind, whilst at Issa there was no

relationship. Across both sites, we therefore find some support for the hypothesis that chimpanzee nests serve a thermoregulatory function, in addition to providing a secure, safe platform for sleep. However, further research is necessary to understand what factors account for the majority of variation in chimpanzee nest shape and architecture. Despite within site variation, overall the nests built by two chimpanzee communities in such geographically separated populations were similar in shape and architecture. Such similarity may result from conserved building techniques that ensure construction of strong and defined structures for safe, comfortable, and relaxed sleep without risk of injury, e.g. to prevent falling from a tree in the night.

Consistent with previous seasonal comparisons of nest height in chimpanzees (Baldwin et al. 1981; Wrogemann 1992), we found that greater moisture (rainfall, relative humidity), is the main influence on chimpanzee nest height and height within the tree crown in Issa and Fongoli. Correlation between nest height and rainfall is found in Issa, although no difference was found in nest heights in the wet versus dry season in Issa (Stewart, 2011b). Baldwin et al. (1981) suggested that nesting higher in the wet season and so building nests open to the sky may allow individuals to dry out more rapidly after rain stops, or prevent prolonged dripping from overhead vegetation, even after the rain has stopped. This may be especially influential in dry areas like south-eastern Senegal, where showers are usually brief but heavy. That relative humidity also influences nest height in Fongoli during the dry season suggests that higher moisture in the air, or dew, rather than rainfall alone also influences nesting height.

Cross-site differences were observed in nest area, thickness, and the size and amount of support. These differences resemble those seen in pairwise comparisons of each variable of nest shape and architecture (Table S1-S2), showing the utility of PCA as a method to analyze and investigate variation in great ape nest building behavior. Few data on body size are available for wild chimpanzees, but they suggest that eastern chimpanzees (*P. t. schweinfurthii*) are the smallest subspecies, whilst western chimpanzees (*P. t. verus*) are the largest (Morbeck and Zihlman, 1989). Thus, Fongoli chimpanzees may build wider nests due to their larger body size, yielding a larger nest 'area'. Alternatively, nest area may relate to other sources of variation, such as inclusion of more material to make a thicker nest, which also would increase the width of the nest as a by-product.

Some cross-site architectural differences observed were due to the presence of ground nests in Fongoli (12% of observed nests), which are often made of non-woody materials (e.g. grass) and do not require support, or weight-bearing, branch configurations. However, ground

nesting is a significant cross-site difference, and has been proposed to be thermally beneficial (Samson and Hunt, 2012) and made possible theoretically by the absence of predators (Pruetz et al., 2008).

We found ground nests to be structurally thinner and made with fewer large branches than tree nests, which is expected given ground nests are not required to be elevated, secure, load-bearing structures. Ground-nesting occurs primarily during the dry season in Fongoli, and may therefore contribute to observed trends for nests to use fewer branches, less support, and be thinner and less elaborate in dry, warm conditions. Pruetz and colleagues (2008) noted that although more frequent ground-nesting in Fongoli could be due to a lack of predators in the area, the chimpanzees continued to nest arboreally much more often than terrestrially. Thus, although ground-nesting may be proximately influenced by environmental conditions such as predation pressure, raw materials, or climatic factors, it may also be a social custom (Koops et al., 2006, 2012).

Variation in shape or architecture and weather conditions differed across the two study sites, with nests in Issa found to vary less with weather conditions than those in Fongoli. However, both sites provide evidence that nest construction likely serves a thermoregulatory function; at both sites, nests were thicker in cooler conditions and used more broken branches 1-3cm in diameter and support steps (break support) in conditions of greater moisture (relative humidity and 'wetness'). These shape and structural measures reflect greater insulation of nest structure. In Fongoli, results support the hypothesis that nests with greater structural support are built in windier conditions.

All measures of overnight weather conditions influenced components of shape and architecture and, although multi-collinearity of climatic variables in Issa complicates interpretation, the influence of weather conditions in Issa can be inferred. Greater correlation of variation in shape and architecture of Fongoli chimpanzees' nests with weather conditions may reflect the greater variability of climatic conditions in south-eastern Senegal; minimum and maximum mean overnight temperatures in Fongoli differed by a mean annual range of 16.6°C versus 8°C in Issa (Table 1). Yet, minimum mean overnight temperatures and maximum mean overnight gust speeds were similar across the two sites. Chimpanzees in Fongoli and Issa may achieve the same functional goal of thermoregulation or structural stability of the nest by adjusting nest shape and architecture in different ways. For example, in Fongoli the amount of lining added correlated with colder temperatures, but there was no difference overall in the use of lining in nest construction between Fongoli and Issa. In Issa, the amount of lining added

to nests did not correlate with weather conditions. In Fongoli, the amount of mattress material used to construct nests increased with colder conditions, and, similarly to nest lining, there was no difference in mattress material between the two sites, but in Issa the amount of mattress material also does not correlate with weather conditions. Issa chimpanzees may achieve the same functional goal of greater insulation in colder temperatures by increasing the amount of breaks 1-3cm in diameter, which also increases nest support (resulting in a negative correlation with wind speed, as temperature and wind are collinear), whereas Fongoli chimpanzees increase thin (<1cm) mattress material, add more lining, and adjust the depth of the nest.

In Fongoli, nest depth seems to be of greater importance than thickness in cold conditions, or perhaps building a deeper nest may result in a thinner nest as a by-product. Yet in Issa, nest depth is greater in conditions of greater wind speeds, but also greater temperatures; this is most likely influenced by wind speeds, in contrast to Fongoli where temperature influences depth. Although greater wind speeds were recorded in Issa, only in Fongoli did greater wind speeds correlate with greater amount and diameter of support material. Presumably, either depth or amount of material can provide greater structural support and safety in windy conditions. Correlation between support and wind in Fongoli again may be due to greater variability of weather conditions in Fongoli, where overnight wind gust speeds increase suddenly but predictably, in the mid-late dry season from January to March. (Strong winds are an annual phenomenon in southeastern Senegal). In Issa, although wind speeds are higher, they often are high throughout the year and so are more unpredictable. Issa chimpanzees thus may build year-round with sufficient support.

Wetness also appeared to be of greater influence over aspects of nest structure (bend support and thickness) in Issa versus Fongoli. Relative humidity provides a proxy for 'wetness' in Fongoli (as data were collected only in the dry season), and more 1-3cm diameter breaks and mattress material were used in conditions of greater humidity in Fongoli. Further data are needed across wet and dry seasons in Fongoli to address fully these cross-site differences.

Across-site climatic differences are not enough to explain divergent relationships between nest shape and architecture with weather conditions in the two sites; Issa is windier, yet nests are not more supported, Issa has similarly cold nights to Fongoli, yet use of lining does not increase on these nights; such differences in nest shape and architecture suggest cultural variation in nest construction. Previous study of behavioral variation in chimpanzees across Africa did not include nest-building in analyses, as this behavior is universal (Whiten et

al., 1999). However, van Schaik et al. (2003) in a similar analysis of orangutan behavioral variation found vocalizations made at nesting time to be possible cultural variants. Detailed analysis of nest-building techniques may indicate possible socio-cultural variation similar to some tool-using behaviors that are influenced by, but are not explained fully by, environmental conditions (Schöning et al., 2008). Besides differential variation of nest structure with weather conditions, measures of shape and architecture found here to be invariant with weather conditions may be useful for cross-site comparisons. Amount of fractures is also an interesting component of nest architecture: In some cases, nests were made almost entirely of large detached branches, which may result from the brittleness of the tree species used, or an idiosyncratic building style learnt through observation.

It is important to highlight that the variation in shape and architecture described here to correlate with weather conditions actually accounts for a small fraction of the total variation in nest shape and architecture. There are likely to be many other environmental influences including the tree-species, tree-architecture, habitat, and nest height etc. Some variation could also be individual-, age-, or sex-specific. This study has shown that principal components analysis is a useful tool for the study of ape nest architecture, and that detailed analysis of shape and architecture can indicate possible ultimate functions of these ape shelters. Further specific tests are needed to determine causality definitively, for example, the methodology described here to measure nest insulation could be implemented with a greater number of experimentally built nests in order to manipulate and test which variables of nest shape and architecture increase nest insulation properties. However, here we have shown that chimpanzees likely adjust their building effort and techniques in response to local, overnight weather conditions. These adjustments reflect the functions of nest building tested here: thermoregulation and a secure platform for sleep.

Animal construction behaviors may have equally important evolutionary consequences and serve a wider range of ecological roles than tool use (Hansell and Ruxton, 2008). In the great apes, most research into the evolution of both culture and intelligence has focused on tool-use, whereas shelter-construction has been neglected (*c.f.* van Casteren et al., 2012). Flexible building of these complex structures, combined with the fact that nest building is improved through learning (Bernstein, 1962; Videan, 2006), suggests that the behavior requires a degree of cognitive ability.

Similarly, as the climate cooled and habitat dried from the middle to late Miocene (Wynn and Retallack, 2001), great ape nests may have been shelters to buffer apes against

increasingly stressful environmental conditions, including changing climate, habitat loss, and varying predator guilds. These shelters may have ultimately aided the dispersal and survival of a branch of hominoids represented by surviving species of great apes and humans. Nests may have improved type and quantity of sleep through better thermoregulation, and a recumbent posture in a safe and secure location, which may in turn have facilitated the evolution of greater cognitive abilities (Fruth and Hohmann, 1996).

Nest-building has been proposed as part of the behavioral repertoire of several early hominin taxa, but we cannot know what biodegradable structures or tools formed part of their material culture (Sept, 1992; Pi et al., 1997; Stewart, 2011a). Understanding the technological skill and flexibility of great ape nest building may be equally as important as tool-use to reconstructing the evolution of technology and cognition in human ancestors.

ACKNOWLEDGEMENTS

We thank Johnny Dondo Kante, Mboule Camera, Wali Camara, Eladjh Saho, Shedrack Lucas, Busoti Juma, Ndai Sammwely, Moshi Rajabu, Abdalla Said, Abdalla Kanimba, and Mashaka Alimas for their invaluable help and enthusiasm in the field. Special thanks to William McGrew and Jim Moore for their enthusiasm, support, guidance and feedback. We are grateful to the Carnegie Trust for Universities of Scotland, Harold Hyam Wingate Foundation, L.S.B. Leakey Foundation, International Primatological Society, and the Wenner-Gren Foundation for Anthropological Research for financial support to FS, and Iowa State University, National Geographic Society, the Wenner- Gren Foundation, L.S.B Leakey Foundation, National Science Foundation, American Society of Primatologists and Primate Conservation Inc. for financial support to JP. We are grateful to the UCSD/Salk Center for Academic Research and Training in Anthropogeny (CARTA) for support for ongoing research at Issa, Ugalla. We thank the Tanzania Commission for Science and Technology and Tanzania Wildlife Research Institute for permission to work in Issa.

LITERATURE CITED

- Baldwin PJ, Sabater Pi J, McGrew WC, Tutin CEG. 1981. Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates* 22:474–486.
- Bernstein IS. 1962. Responses to nest building materials of wild born and captive born chimpanzees. *Anim Behav* 10:1–6.

- Bolwig N. 1959. A study of nests built by mountain gorilla and chimpanzee. *S Afr J Sci* 55:286–291.
- van Casteren A, Sellers WI, Thorpe SKS, Coward S, Crompton RH, Myatt JP, Ennos AR. 2012. Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proc Natl Acad Sci U S A* 109:6873–6877.
- Coolidge F, Wynn T. 2006. The effects of the tree-to-ground sleep transition in the evolution of cognition in early *Homo*. *Before Farming Anthropol Archaeol Hunters-Gatherers* 2:1–18.
- Corp N, Byrne RW. 2002. Leaf processing by wild chimpanzees: Physically defended leaves reveal complex manual skills. *Ethology* 108:673–696.
- Fleagle JG, Gilbert CC, Baden AL. 2010. Primate cranial diversity. *Am J Phys Anthropol* 142:565–578.
- Fraser ON, Schino G, Aureli F. 2008. Components of relationship quality in chimpanzees. *Ethology* 114:834–843.
- Fruth B. 1995. Nest and nest groups in wild bonobos (*Pan pansicus*): Ecological and behavioral correlates. Aachen: Shaker: Ph.D, Ludwig-Maximilians-Universität München.
- Fruth B, Hohmann G. 1996. Nest building behavior in the great apes: the great leap forward? In: McGrew WC, Marchant LF, Nishida T, editors. *Great Ape Societies*. Cambridge: Cambridge University Press. p 225–240.
- Goodall JM. 1962. Nest building behavior in free-ranging chimpanzee. *Ann N Y Acad Sci* 102:455–467.
- Hansell MH. 1993. The ecological impact of animal nests and burrows. *Funct Ecol* 7:5–12.
- Hansell MH. 2000. *Bird nests and construction behaviour*. Cambridge: Cambridge University Press.
- Hansell MH. 2005. *Animal Architecture*. Oxford: Oxford University Press.
- Hansell MH, Ruxton GD. 2008. Setting tool use within the context of animal construction behaviour. *Trends Ecol Evol* 23:73–78.
- Houle A, Chapman CA, Vickery WL. 2004. Tree climbing strategies for primate ecological studies. *Int J Primatol* 25:237–260.
- Humle T, Matsuzawa T. 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am J Primatol* 58:133–148.

- Hutcheson G, Sofroniou N. 1999. *The Multivariate Social Scientist*. London: SAGE publications Ltd.
- Kano T. 1979. A pilot study of the ecology of pygmy chimpanzees, *Pan paniscus*. In: Hamburg DA, McCown ER, editors. *The Great Apes*. Menlo Park, CA: Benjamin/Cummings. p 123–135.
- Koops K, Humle T, Sterck E, Matsuzawa T. 2006. Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: environmentally or socially determined? *Am J Primatol* 69:1–13.
- Koops K, McGrew WC, de Vries H, Matsuzawa T. 2012. Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: Antipredation, thermoregulation, and antivector hypotheses. *Int J Primatol* 33:356–380.
- Lodwick JL, Borries C, Pusey AE, Goodall J, McGrew WC. 2004. From nest to nest - influence of ecology and reproduction on the active period of adult Gombe chimpanzees. *Am J Primatol* 64:249–260.
- Mackinnon J. 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim Behav* 22:3–74.
- McGrew WC. 2004. *The Cultured Chimpanzee: Reflections on Cultural Primatology*. Cambridge: Cambridge University Press.
- Mehlman PT, Doran DM. 2002. Influencing western gorilla nest construction at Mondika Research Center. *Int J Primatol* 23:1257–1285.
- Morbeck M, Zihlman A. 1989. Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. *Primates* 30:369–382.
- Pi JS, Veà J, Serrallonga J. 1997. Did the first hominids build nests? *Curr Anthropol* 38:914–916.
- Pruetz JD, Fulton SJ, Marchant LF, McGrew WC, Schiel M, Waller M. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 70:393–401.
- Remis MJ. 1993. Nesting behavior of lowland gorillas in the Dzanga-Sangha Reserve, Central African Republic: Implications for population estimates and understandings of group dynamics. *Tropics* 2:245–255.

- Russon AE, Handayani DP, Kuncoro P, Ferisa A. 2007. Orangutan leaf-carrying for nest-building: toward unraveling cultural processes. *Anim Cogn* 10:189–202.
- Samson DR. 2012. The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda. *Primates* 53:357–364.
- Samson DR, Hunt KD. 2012. A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *Am J Primatol* 74:811–818.
- Samson DR, Muehlenbein MP, Hunt KD. 2012. Do chimpanzees (*Pan troglodytes schweinfurthii*) exhibit sleep related behaviors that minimize exposure to parasitic arthropods? A preliminary report on the possible anti-vector function of chimpanzee sleeping platforms. *Primates* 54:73–80.
- van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M. 2003. Orangutan cultures and the evolution of material culture. *Science* (80-) 299:102–105.
- Schaller GB. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.
- Schöning C, Humle T, Möbius Y, McGrew WC. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *J Hum Evol* 55:48–59.
- Sept J. 1992. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Curr Anthropol* 33:187–207.
- Stewart FA. 2011a. Brief communication: why sleep in a nest? Empirical testing of the function of simple shelters made by wild chimpanzees. *Am J Phys Anthropol* 146:313–8.
- Stewart FA. 2011b. *The evolution of shelter: ecology and ethology of chimpanzee nest building*. Cambridge, UK: PhD dissertation, University of Cambridge.
- Stewart FA, Piel AK, McGrew WC. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. *J Hum Evol* 61:388–95.
- Stewart FA, Pruettz JD. 2013. Do Chimpanzee Nests Serve an Anti-Predatory Function? *Am J Primatol* 75:593–604.
- Stewart FA, Pruettz JD, Hansell MH. 2007. Do chimpanzees build comfortable nests? *Am J*

Primatol 69:930–939.

Sunderland-Groves JL, Ekinde A, Mboh H. 2009. Nesting behavior of *Gorilla gorilla diehli* at Kagwene Mountain, Cameroon: Implications for assessing group size and density. Int J Primatol 30:253–266.

Tabachnick BG, Fidell LS. 2007. Using Multivariate Statistics. Boston: Pearson/Allyn & Bacon.

Tutin C, Parnell R, White LJT, Fernandez M. 1995. Nest building by lowland gorillas in the Lopé Reserve, Gabon: environmental influences and implications for censusing. Int J Primatol 16:53–76.

Videan E. 2006. Bed-building in captive chimpanzees (*Pan troglodytes*): the importance of early rearing. Am J Primatol 68:745–751.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. Nature 399:15–18.

Wrogemann D. 1992. Wild chimpanzees in Lope, Gabon: Census method and habitat use
Bremen: PhD dissertation, Bremen University

Wynn JG, Retallack GJ. 2001. Paleoenvironmental reconstruction of middle Miocene paleosols bearing *Kenyapithecus* and *Victoriapithecus*, Nyakach Formation, southwestern Kenya. J Hum Evol 40:263–88.