Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds

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Nest-building orangutans must daily build safe and comfortable nest structures in the forest canopy and do this quickly and effectively using the branches that surround them. This study aimed to investigate the mechanical design and architecture of orangutan nests and determine the degree of technical sophistication used in their construction. We measured the whole nest compliance and the thickness of the branches used and recorded the ways in which the branches were fractured. Branch samples were also collected from the nests and subjected to three-point bending tests to determine their mechanical properties. We demonstrated that the center of the nest is more compliant than the edges; this may add extra comfort and safety to the structure. During construction orangutans use the fact that branches only break half-way across in "greenstick" fracture to weave the main nest structure. They choose thicker branches with greater rigidity and strength to build the main structure in this way. They then detach thinner branches by following greenstick fracture with a twisting action to make the lining. These results suggest that orangutans exhibit a degree of technical knowledge and choice in the construction of nests.

biomechanics | intelligence | great apes | wood

Once weaned, all great apes build nests on an almost daily basis. These structures are constructed, in general, for only one night's use or as a place for rest during the day. After use, nests are generally discarded and left to deteriorate, although reuse of nests is occasionally observed (1, 2). Although there is an innate component to nest building in great apes, it is not an entirely instinctive behavior. It has been shown that immature individuals build nests more efficiently and of a higher quality when exposed to nest-building adults (3, 4). This indicates a role for learning and innovation in the building of nests (1–4).

Nest building evinces conserved patterns of construction across the great apes. Nests are usually built in trees, although many gorillas, especially mountain gorillas, often build nests on the ground (1). Animals pull and bend nest material inward and lock it together under the body to build the nest. Because of the conserved nature of nest construction in great apes it is suggested that it evolved in a common great-ape ancestor in the Miocene period (1, 2). Arguably the main function of ape nests is to provide a comfortable sleeping platform to facilitate higher-quality rest and allow greater periods of rapid eye movement sleep, because it reduces disturbances during the night (1, 5, 6). The large body-size of apes implies that the sleeping positions on tree boughs that other primates use may not provide comparable levels of comfort (1, 3, 7). However, other supplementary functions of nests have been proposed, such as an antipredation role, whereby the height of nests and the camouflage they provide may reduce the incidence of night predation (5, 8, 9). Being higher in the canopy may also reduce the risk from airborne parasites, such as mosquitoes (3, 6). Additionally nests may aid thermoregulation by providing a layer of insulation while sleeping (5, 6).

Orangutans generally build their nests in the tree canopy, and hence their height will vary depending on that of the forest canopy itself, which may range from *ca.* 11 m in peat- or disturbed forest to *ca.* 20 m in primary rainforest. Orangutan nest site selection is not random, and certain tree species are preferred over others (3, 10). Most obviously, orangutans avoid building night nests in fruiting trees. This may be a tactic to avoid disturbance and danger from other animals attracted by the fruit of these trees (9). In addition to this more obvious preference, orangutans exhibit a more subtle choice in tree species; they do not use the most common forest tree species but rather demonstrate a preference for certain trees when constructing their night nests (3). It has been suggested (3) that the architecture of trees may play a role in such preference; however, the full reason for these inclinations is still unknown and open to further investigation.

Because they are located in the canopy, orangutan nests must be both comfortable and structurally safe. Construction usually follows a basic pattern (3, 11, 12). After choosing a nest location on a lateral branch, or branches, the orangutan will bend and break branches inward toward a central point, weaving and twisting the branches to lock them into the basic nest structure. Layers are then generally added on top of this basic structure, in the form of smaller branches, bent, broken, and woven, forming a "mattress" or "rim." Leafy branches are detached, usually from the surrounding area, and placed on top of the base structure as a lining. Extra features, such as a roof, "pillow," or "blanket," are then constructed and added if required by the individual (3, 11, 12). Orangutan nests have been described as sturdier, more complex and elaborate, and as lasting longer in the forest canopy, than those of African apes (2, 10).

Orangutan nests are made exclusively from tree branches and local vegetation (3). The act of breaking and weaving branches together during construction is essential to the success of the structure. However, breaking living, and hence compliant, branches is not as simple as one might think. Branches, when loaded under bending, do not exhibit a uniform mode of fracture and rarely simply break completely across and detach (13, 14). The low-density woods of fast-growing pioneer trees tend to buckle and fail without fracturing (14). Such buckling and failing occurs as a consequence of the low lateral strength of the wood material, which is crushed by the transverse stresses generated during bending. In the denser woods that are characteristic of forest trees, branches placed into bending instead fail in tension on the convex side (13). The branch does not break completely across, however, because the tensile fracture is diverted longitudinally at the midline owing to

ANTHROPOLOGY

the low tangential strength of the wood material. This phenomenon is called "greenstick" fracture. In this process, although fracture has occurred, detachment does not (13, 14), and it can prove extremely hard to completely break off green twigs. Knowledge of the mechanics of branch fracture therefore leads to the consideration that orangutans may be using some experience of the way in which branches break during bending in the construction of their nest structures.

Previous research into orangutan nests can be broadly broken into two major avenues of investigation: one, focusing on nest-building behavior (3, 9–12); and the other, concentrating on the use of nests to predict population numbers and distribution (3, 10, 15, 16). Investigations into nest-building behavior have provided detailed, insightful, and descriptive knowledge of the basic nest-building process. Such data have mostly comprised observations of nest building, such as the frequency and duration of builds, positioning of nests, and preferences within the ritual of nest building (3, 9–12). The study of nests to understand populations of wild orangutans has led to knowledge of nest longevity and geographical distribution (3, 10, 15, 16). However, to date there is still relatively little information about the structural patterns of construction, and almost nothing has been reported on the mechanics of the nest structure itself (3).

The aim of this study was therefore to investigate the mechanical design of orangutan nests and the principles of their construction. By looking at the mechanics of the whole nest structure and the mechanics and form of the nest elements, we aimed to investigate the degree of technical sophistication shown by orangutans in the building of their nests.

Results

Basic Structure and Whole-Nest Mechanics.
Nest observations revealed some basic patterns of construction that were consistent with previous studies of orangutan nest building. Nests were built upon a solid base: usually a larger single or a group of stable branches, a forked branch, or a stable crotch. From this position several branches were bent and half-broken inward from the surrounding area. These branches were then woven together to form the structural base of the nest. From the surrounding area branches were then bent in, or broken off and placed on top of the structure to form the mattress and lining. The nest was then often furnished using leaves and herbaceous ends.

Nests were slightly oval or elliptical in plain view (Fig. 1 A and B), the long axis pointing toward the trunk of the supporting tree, with a central depression that extended on average just over 7 cm below the rim. Nest compliance ranged from 0.0019 to 0.0036 mN^{-1}; the compliance of the middle point where the orangutan would sleep tended to be slightly higher than at the edges of the nest (Fig. 2 A and B). However, a repeated-measure ANOVA showed that this difference was nonsignificant.
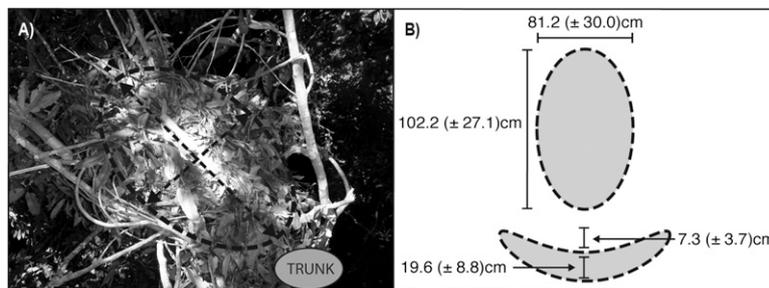
Nest Elements.
The majority of fractures observed in the nest elements were either of the greenstick fracture type (169 of 271) (Fig. 3A), the wood having been broken only halfway across, or showed complete detachment (89 of 271), often with a tail of bark extending from the broken ends (Fig. 3B).

Greenstick fractures were seen at points where branches were significantly thicker (diameter 14.1 ± 4.6 mm, mean ± SD) than where complete detachments had occurred (diameter 10.5 ± 3.9 mm) ($T_{186.365} = 6.445$, $P < 0.0005$), although there was a good deal of overlap. A logistic regression demonstrated that branch diameter had a significant influence on whether branch was broken or detached ($B = -215.732$, $P < 0.0005$). This indicates that orangutans tended to leave the thicker branches, used in the structural part of the nest, attached and selectively detached thinner ones for the furnishing "lining" of the nest.

Three-point bending tests on the "structural" branches and detached lining branches showed that the rigidity of the structural branches was almost four times higher than that of the lining samples (Fig. 4A), a difference that a Mann-Whitney U test showed was highly significant ($U = 162.5$, $P = 0.007$). Structural branches were also more than four times stronger (Fig. 4B) ($U = 179.5$, $P = 0.031$) than those detached samples taken from the lining. However, the stiffness (E) (structure 2.06 ± 1.80 GPa; lining 2.55 ± 1.95 GPa) and strength (σmax) (structure 20.00 ± 17.88 MPa; lining 19.27 ± 12.71 MPa) of the wood material of which the structural and lining branches were composed were not significantly different. This suggests that the orangutans had selected stronger, more rigid branches for the structural parts of the nest and weaker, flexible ones for the lining on the basis of diameter and structural properties rather than material properties.

Discussion

The nests we studied, resulting from conserved patterns of orangutan nest construction, were strong, safe, and defined structures. They were slightly larger in size than the orangutans that had constructed them and were concave where the weight of the orangutan was situated, both of which would help prevent the orangutan from falling out. Although not significantly so, the central part of the nest, where the orangutan's weight was positioned, was also more compliant than the nest edges, further improving safety and comfort. Assuming an average weight of 38.5 kg (17), a female Sumatran orangutan (*Pongo abelii*) with its weight centered in the middle would depress the whole nest structure an average of 1.08 m and the edges an average of 0.8 m. This leads to the question whether this observed pattern is an artifact of the nest-building process or the result of design.

The relatively high compliance of the middle, despite the fact that the nest is built by an animal resting on a reasonably rigid central branch, may be the result of the nest-making process. As branches are broken inward and locked together, it is reasonable that the area in the middle of the nest might be more compliant

Fig. 1. (*A*) Example of an orangutan's nest. Measurements of length were taken along the long axis pointing toward the tree trunk, whereas the width was measured perpendicular to this (arrows). (*B*) Average dimensions of an orangutan's nest, derived from the nests featured in this study (*n* = 14). Thickness and degree of depression were taken from where the orangutan's weight was situated.

Fig. 2. (A) Recorded compliance for distinct points of the orangutans' nests along the long axis: distal, (n = 10), middle (n = 8), and proximal (n = 9). (B) The recorded compliance along the transverse axis of orangutans' nests: left (n = 11), middle (n = 8), and right (n = 10).

because it is mostly made up of thinner, interwoven branch ends. The high central compliance could therefore be an artifact of the nest construction. However, Mackinnon (11) notes that branches can be used in four main different ways and at different orientations within a nest structure. In "rimming," branches are bent horizontally to form the rim of the nest; "hanging" is a process in which branches are bent down from above and woven in to form part of the bowl; "pillaring" is when a branch from below is bent into the nest to secure the rimming branches, giving support from below; and finally "loose" is when branches are broken off entirely and placed on top of the nest. This being the case, it seems unlikely that the nest-building process alone would be responsible for making the outer rim relatively rigid. Instead, orangutans seem to strengthen the rim by breaking and locking branches together. Many researchers, including authors (A.v.C. and S.K.S.T.) of this article, have observed a step in orangutan nest building, after the completion of the base structure, in which smaller branches are bent from the edge inward to produce a "mattress" or "rim" (1, 3, 6, 12) (Movie S1). This process may actually act to reinforce the edges, lowering their compliance.

Construction of orangutan nests involves exploitation by orangutans of the natural fracture properties of wood. Within the main structural part of the nest, more rigid and stronger branches are used than those used for the lining. When orangutans bend and break such branches the failure mode is mostly limited to greenstick fracture (Fig. 3A), breaking branches only halfway across and not detaching them. Greenstick fracture is

Fig. 3. (A) Example of a greenstick fracture found within an orangutan nest structure. (B) Detachment from branches surrounding the nests.

Fig. 4. (A) Rigidity (Nm^2) and (B) bending strength (Nm) of structural elements (n = 36) and lining elements (n = 16) of nest structures (means and SEs).

the natural fracture mode expected from the denser wood types typical of canopy tree species (13, 14) and by a considerable margin was the most prevalent fracture type recorded within the nest structures. It could be argued that the predominance of greenstick fracture within the nest structures is because orangutans are not able to completely break and detach the larger, stronger branches used in the structural base of the nest. This seems unlikely, however, not only because orangutans are so strong (18) but also because the greatest amount of intended force required to generate a fracture in bending must be immediately preceding the fracture event (19). Therefore, if fracture has occurred, in the form of greenstick fracture or detachment, the largest force has already been exerted. This suggests that nest-building orangutans avoid detaching the larger, stronger, and more rigid branches used within the nest structure, instead exploiting their natural greenstick fracture to build a stronger nest.

The lining of the nests is made mainly from detached, leafy branches laid on top of the main nest structure. We have shown that these branches are significantly smaller, weaker, and more flexible than those used in the main structure of the nest. Compliant living branches hardly ever break completely across (13, 14), and to detach them takes a degree of skill. Observations of nests revealed that the broken ends of detached branches often had a tail of bark or wood material (Fig. 3B), similar to those reported in the nests of chimpanzees (8). In Movie S2 it is possible to see that the orangutan tends to use two hands to break branches from the tree to make its lining material, breaking the branch with a bending effort before separating it with a twist.

To verify this observation, an experiment was carried out to determine whether we could replicate the observed fractures. Breaking a branch with greenstick fracture and then twisting it (Fig. 5) does indeed create broken ends with the characteristic tails. Therefore, it seems that orangutans detach preferred branches for the lining of their nest structures. The choice of appropriate material from different trees for the purposes of nest lining has previously been described in leaf-carrying behaviors, whereby orangutans select lining materials from other locations and carry them to the nest site (12, 20). Therefore, it is possible that a choice for smaller, weaker, and more flexible branches is being exhibited by nest-building orangutans at Ketambe. The apparent preference for certain tree species by nest-building orangutans (3) may also be influenced by their knowledge of the fracture and mechanical properties of certain trees, although we did not investigate this aspect in this small-scale study. The choice of which branches to half-break, and which to detach, has similarities to results of previous research that indicated that tree architecture may play a role in tree selection (3).

Fig. 5. Steps of an experiment to recreate the way in which orangutans detach smaller branches for their nest structures. (*A*) Branches are first broken in the stereotypical greenstick fracture. (*B*) A twist splits the branch along its length. (*C*) Pulling the two sections separates them to give the two ends. (*D* and *E*) This action generates the wispy tails seen remaining, at points of detachment, in nest-bearing trees. (Scale bar, 5 cm.)

We have demonstrated a distinction in size and mechanical properties of different parts of orangutan nests; but how is such a choice being implemented? A logistic regression demonstrated that branch diameter had an influence on whether the branch was detached or simply left in greenstick fracture. It seems likely that the orangutans chose branches for different purposes according to the diameter of the branch. This could be because branch diameter is a reliable and easily observable indicator of a branch's mechanical properties. Branch diameter has already been shown to be a key influence on the locomotor mode of orangutans (21), and this article indicates that it is used also in their nest-building habits. This could suggest that the orangutan has a degree of technical knowledge concerning likely material properties and behavior, which it can use in the selection and recruitment of nest-building materials.

Nest building in orangutans and other great apes is a good example of animal construction (22, 23). The daily construction of structurally sound nests demonstrates a regular and complex manipulation of greatly variable arboreal substrates to perform the uniform tasks of support and shelter during rest periods. The complexity of nests and the fact that construction is improved by learning (3, 4) suggests a degree of cognitive ability, but is this different from that shown by those other nest builders, the birds? Birds construct varied and sometimes even more elaborate nests, which range from simple shallow depressions to sophisticated constructions (24). It has long been a topic of contention as to whether birds' nests are the products of innate construction rules or whether birds show a degree of cognitive processing in their construction (24). Through field observations, recent research into the woven nests of African weaver birds has demonstrated that, although there may be evidence for a genetic element of nest building, there is also evidence for improved constructions and construction behavior through nest-building experience. This suggests that nest building in birds and primates both require a degree of cognitive ability, but certainly no less than that needed for tool construction and use (25, 26). The importance of nest building should not therefore be overlooked when investigating the evolution of intelligence; its cognitive and technical requirements may be comparable to that of tool use, and continued research into nest building highlights the technical abilities of great apes and other animal architects (8, 23–27).

In this context, Byrne (27) proposed the technical intelligence hypothesis, in which it is suggested that the difference seen between ape and monkey intelligence can be accounted for by their representational understanding of the world. He proposed that one of the evolutionary selection pressures that led to the evolution of representational minds in apes is that of construction skills. In this study we have shown that orangutans do choose specific branches for certain nest functions and that branch diameter does have an influence on the function the orangutan assigns to the branch. This could suggest that orangutans have knowledge or experience of the nest building materials available locally and use it during nest construction to plan the use of material to construct a safe and comfortable nest. Another suggestion put forward by Povinelli and Cant (28) is that ape intelligence is linked to the difficulties and dangers that such large-bodied animals face when clambering among narrow branches. They must be able to understand and predict their mechanical environment.

According to both of these theories, branch diameter and strength will both be highly salient (29), so the ability to learn how they are related may have been important in the evolution not only of intelligence but also of cognition and creativity. Certainly, Rumbaugh and Washburn (29) found that orangutans, which are the most arboreal apes, have a particular need for environmental stimulation in captivity to fully develop their cognitive abilities.

Our findings about the sophistication of the choices that orangutans make in their nest construction also cast light on the likely technological abilities of our early hominin ancestors, although there can never be certainty with regard to their material culture. It has been speculated that nest building may have provided an evolutionary foundation for higher levels of tool use in hominoids by promoting exploratory branch and twig use and nurturing increased cognition and technological skills (1, 8). In demonstrating patterning in construction and material selection, this study illustrates a degree of technical know-how in nest-building orangutans, which may aid in the reconstruction of the evolution of tool use and technology in human ancestors.

Methods

Nest Location and Access. Nests were located during follows of habituated orangutans during an 11-mo field season at Ketambe research center in the Gunung Leuser National Park. Once a suitable nest was located, all observations and testing were conducted within 1 wk because aging of the nest would affect the results. A total of 14 nests were accessed using double- and single-rope canopy access techniques (8, 30). This enabled general measurements and photographs of nests to be taken, compliance measurements to be made, and allowed nest deconstruction. Some nests, because of their challenging positions, were inaccessible using safe climbing techniques and therefore unavailable for testing, introducing a degree of unavoidable bias to nest selection.

Basic Structure and Whole-Nest Mechanics. First, and while the nest was in pristine condition, general nest measurements were taken by hand using a tape measure. The length was measured along the long axis pointing toward the tree-trunk, whereas the width was measured perpendicular to this. The thickness and degree of vertical indent were measured from the point where the orangutan's weight would be centered.

To test the compliance of different parts of the nest, low-stretch testing rope was looped (by hand or using a thin stick) through distinct areas of the nest and anchored sequentially to five main points of the nests in relation to the trunk: proximal, distal, left, right, and center. The nest positions were defined as follows. The distal point was the area of the nest that was furthest away from the front of the tree trunk, the proximal point was the area of the nest closest to the trunk, and the left and right were the areas to the left and right, looking away from the trunk. The middle of the nest was not necessarily the measured midpoint of the nest but the area where the orangutan's weight had been situated, as indicated by a clear indentation. During this process care was taken to disrupt as little as possible of the nest's structure.

The testing rope was then lowered to the ground for compliance measurements to be made. On the ground a force gauge [Mecmesin Advanced Force Gauge (AFG1000N)] was mounted on a stand and anchored by the weight of a field assistant. A series of knots, on a single piece of rope, a known distance apart were then attached to the testing rope via a tensile steel ring. The rope was then pulled down in increments by looping the knots

sequentially onto the probe of the force gauge, and the force generated was measured. This gave a force/displacement curve. This procedure was carried out for each of the distinct areas around the nests, giving five measurements of compliance around the nest. To prevent overestimation of compliance, we allowed for the compliance of the testing rope. A series of stretch experiments was therefore run, allowing us to calculate rope compliance at different lengths. The compliance of the length of rope that equaled the height of each nest was finally calculated and subtracted from the recorded compliances, to give the nest's true compliances.

Nest Elements. Once nest compliance had been recorded, the nest was carefully dismantled branch by branch. The mode of failure at each fracture point (Fig. 3) was recorded, and the diameter of the branch directly below the fracture was measured. In total 271 fractures were recorded.

From three nests, samples were taken, from both structural parts of the nest ($n = 36$) and from the detached lining that furnished the nest ($n = 16$). These samples were returned to the research camp, where three-point bending tests were performed to measure their mechanical properties. Tests were performed on a portable apparatus that consisted of a T-shaped frame constructed out of 2-cm U-shaped aluminum bars. The sample was placed on top of adjustable supports on the cross-bar of the T structure. Attached to the cross-bar via a screw attachment and a piece of threaded stud bar and some modified attachments was a Mecmesin Advanced Force Gauge (AFG1000N), which could measure both tensile and compressive forces. The head of the force gauge was hooked over the sample, and by turning the threaded stud bar the force gauge was moved down the mid-bar of the apparatus while measuring the force generated. The displacement of the sample was measured using a Mitutoyo Dial Indicator, which accurately measures small linear distances. This allowed the simultaneous measurement of force and displacement during bending. The three-point bending apparatus had a maximum bending span of 60 cm. In three-point bending tests, to limit the effects of shear on the results, there has to be span-to-depth ratio of 20 (31, 32). This meant that no sample could have a diameter of >3 cm.

From the force/displacement curve generated it is possible to calculate both bending strength and rigidity of the branch. The bending strength, M_{max}, of each sample was given by the expression (Eq. **1**)

$$M_{max} = \frac{WL}{4}, \qquad [1]$$

where W is the maximum force, and L is the length between the supports (33).

To calculate the rigidity it is first necessary to correct for machine compliance. This was measured by performing a three-point bending test on a steel rod that has a negligible compliance. The slope of the initial linear region of the force deflection graph generated during this test gives the stiffness of the machine (104,242.6 Nm^{-1}). The apparent stiffness [$(dF/dy)_{app}$] is the slope of the initial linear region of the force displacement graph generated during testing of branches. Using Eq. **2** it is then possible to calculate the corrected stiffness [$(dF/dy)_{cor}$] from the two previous values.

$$(dF/dy)_{cor} = \frac{(dF/dy)_{app}}{(1 - [(dF/dy)_{app}/(dF/dy)_{mach}])}. \qquad [2]$$

Once the stiffness was corrected, the rigidity of the branch, EI, was calculated using the following equation (Eq. **3**; 32, 33).

$$EI = \frac{(dF/dy)_{cor}L^3}{48}. \qquad [3]$$

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ANTHROPOLOGY