

Chapter 4

ORANGUTAN NEST-BUILDING BEHAVIORS

Introduction

All mature great apes build sleeping nests, platforms constructed of bent or broken branches and other vegetation that are constructed nearly every night (Fruth and Hohmann, 1996). They sometimes build similar (though usually simpler) nests for resting during the day. While some of this behavior may be innate (as it is displayed even by juvenile apes reared in isolation), there appears to be a learned component to nest building (Lethmate, 1977), and this could lead to cultural variation through social learning. Seventy-five years ago, Yerkes and Yerkes viewed nest-building among great apes as indicative of “increasing dependence on manipulation or modification of environment as a method of behavioral adaptation” (1929 p. 564, reviewed in Fruth and Hohmann, 1996).

While some studies have compared nest building in populations of chimpanzees (*Pan troglodytes*, Baldwin et al., 1981), bonobos (*Pan paniscus*, Fruth and Hohmann, 1993), or gorillas (*Gorilla gorilla*, Tutin et al., 1995), these have mainly focused on physical characteristics of the nests,

and have been unable to discern population differences that could not be accounted for by ecological variation. Orangutan (*Pongo pygmaeus*) researchers found several behavioral variants related to nest-building that could not be attributed to ecological differences and are likely to represent cultural variation (van Schaik et al., 2003).

In this chapter, I will review the data on nest building at Suaq Balimbing as it relates to the context of the **nest raspberries** cultural variant and address its possible function. I will compare some measures from Suaq Balimbing with data on nest building by orangutans at Ketambe, where nest raspberries are completely absent. I will also confirm the difference in frequency of multi-tree nests reported for these two sites, and compare opportunities for social learning during night-nest construction.

Great ape nests

Great apes are the only primates that build nightly sleeping platforms. Some smaller primates in the Lemuriformes and Galaginae build nests for their infants (and sometimes for use by parents), and some small primates in the Lemuriformes and Callitrichidae use tree-holes for sleeping and shelter that may be lined with vegetation, but none of the larger monkeys or Hylobatidae (gibbons and siamangs) construct sleeping platforms or shelters (reviewed in

Kappeler, 1998).

The nests that great ape species build in trees are broadly similar (see Baldwin et al., 1981; Fruth and Hohmann, 1993; Sugardjito, 1983; Tutin et al., 1995). They are constructed by bending or breaking larger branches that are interlaced to achieve a stable platform. This platform is often lined with twigs, leaves and other soft vegetation. Adults and independent adolescent apes generally build a new sleeping nest every night. Dependent infants always occupy their mother's nest, while juveniles often build nests of their own. Nests are also sometimes built in feeding trees during the day (Fruth and Hohmann, 1996).

Nests are often used for census work on unhabituated great ape populations (e.g. Brugiere and Sakom, 2001; Ghiglieri, 1984; Tutin and Fernandez, 1984; van Schaik et al., 1995), because they are large, distinctive structures, easily countable during transect surveys, that are made on a regular basis and decay at a reasonably predictable rate. Consequently, much of the research on nest building in apes has focused on questions that can be answered during such census work or questions that are applicable to census work. Comparisons between sites are generally based on data taken using different methods at each site. When data on nests are taken using census techniques, differences

between individuals (except for what can be determined by the size of the nest or the feces below it) are indistinguishable, and are therefore rarely considered.

Even with these limitations, there is enough information available in the literature to show that nest-building behaviors in the great ape species vary in several ways. The size of nest-groups, the height, location and structure of the nests, and (where known) the duration of nest-building activities varies between and within species.

Gorillas

Gorillas are the only great apes that frequently build nests on the ground (more often than in trees in some populations). For the 35% of nests built in trees at Lopé, the mean height is 10.3m (Tutin et al., 1995); for the 82% built above ground at Ngotto, the average height is only 6.4m (Brugiere and Sakom, 2001). There is some indication of preference or avoidance of certain plant species used for nest material (Tutin et al., 1995). The type of nest constructed is related to habitat type and season (Tutin et al., 1995). Nests are most often built in and around forest clearings (Brugiere and Sakom, 2001).

Gorillas form close-knit bisexual groups, and tend to build their nests in groups; females in a social group will wait for the dominant silverback male to build his nest, then build their own nests nearby (reviewed in Fruth and Hohmann, 1996). Over the course of a four year study of one such group at Lopé, no nest sites had fewer than three recognizable nests (Tutin et al., 1995). At Ngotto, only three out of 27 nest sites had fewer than three individual nests (Brugiere and Sakom, 2001).

Bonobos

For bonobos at Lomako, Fruth and Hohmann (1993) found the mean nest height to be 16m, noting that day nests are on average higher than night nests. Frequency of day nest construction peaks in the late morning. Males build their nests lower in the trees than females. Bonobo females spend an average of less than one minute constructing a day nest, and mean nest-building duration for day nests was even shorter for males.

Bonobos often gather in the evening before building their night nests (Fruth and Hohmann, 1996; Merrill and White, 1996). The loud-calls frequently given by bonobos preparing to build night nests may facilitate this social cohesion (Merrill and White, 1996). Fruth and Hohmann (1996) found the mean nest-building duration for night nests for both sexes at Lomako is 4.2

minutes, with a maximum duration of 7 minutes. Less than 4% of day nests integrate branches of more than one tree, whereas 41% of bonobo night nests incorporate two or more trees (Fruth and Hohmann, 1996).

Fruth and Hohmann (1993) also found that bonobos did not use nests exclusively for resting. Bonobos occupying nests were observed feeding (10%), allo-grooming (5%) or engaging in social play (3%). Nests were built following the approach of a conspecific in 7% of cases, apparently as a way to reduce agonistic interactions over food.

Chimpanzees

Despite the large number of cultural variants reported for chimpanzees, there are no “very likely” (Chapter 2) cultural variants in chimpanzee nest-building (Whiten et al., 2001). The one behavior where chimpanzees were noted to vary (in a comparison of nine long-term study sites) was in building night nests on the ground. More than 10% of night nests were built on the ground at Gombe and Budongo, but ground-night-nests were not common elsewhere; environmental explanations for this difference could not be excluded (Whiten et al., 2001). Earlier comparative studies found differences between sites in nest height, the number of nests per nest-group, the percent of exposed nests built (on the top or periphery of the tree

canopy), the number of nests per tree and the girth of the nest trees for populations in Equatorial Guinea and Senegal, but all of these differences could be attributed to ecological differences in the study sites (Baldwin et al., 1981).

However, there are some suggestions that aspects of nest building might be found to vary culturally with further investigation. For instance, Goodall (1968) describes nest-building in oil nut palms (*Elaeis guineensis*), apparently requiring practice of a special technique for success, that went from absent to widespread among the chimpanzees of Gombe over a period of three months. Boesch (1995) describes the building of day nests (either in trees or, particularly, on the ground) increasing dramatically in frequency and spread amongst individuals in the Taï chimpanzee population. These changes could not be attributed to environmental changes, and are likely to reflect behavioral innovations spread by social learning.

Chimpanzees usually nest in parties (Goodall, 1968; Baldwin et al., 1981; McGrew, 1992). The spacing between nests in the same tree was found to be roughly equal (about 4m) at two ecologically distinct sites (Rio Muni in Equatorial Guinea, and Mt. Assirik in Senegal, Baldwin et al., 1981). At Gombe, nest building duration was 1-5 minutes, and the mean nest height

was about 14m (Goodall, 1968).

Chimpanzees do not regularly build nest covers during rain (though once a chimpanzee built a nest with a “roof” of palm fronds in the 1965 rainy season at Gombe, Goodall, 1968). In fact, one study showed that chimpanzees were more likely to build more exposed nests (at the top or edge of the tree’s canopy as opposed to under the canopy) in the rainy season, which might have an advantage for warming and drying the occupant in the morning sun after a rain (Baldwin et al., 1981).

Orangutan Nests

As the most arboreal of the great apes, orangutans always nest in the trees. Orangutans will sometimes re-use old nests, but for night nests they reconstruct the inner lining (Rijksen, 1978). At Ketambe, the most common nest height was 13-15m (Rijksen, 1978). Day nests are sometimes found in trees where orangutans are feeding, but night nests are rarely built in fruiting trees (Rijksen, 1978; Sugardjito, 1983). The choice of nest sites in different age/sex classes of orangutans (height in the tree, proximity to fruit trees) indicates an important anti-predation function for the nest (Sugardjito, 1983). Orangutans often build their night nest on slopes or at the edge of a gap in vegetation, presumably for a better view of their surroundings (Rijksen,

1978).

Further evidence for orangutan nest-building incorporating a learned component is the lack of skill in nest building exhibited by some ex-captive orangutans during rehabilitation (Rijksen, 1978). Rijksen reports that some of these rehabilitants later “learned to build a proper tree nest, in some cases by imitating others during play sessions” (page 372).

Orangutans (particularly juveniles) use nests as a component of social play. A pair or group will wrestle on or just above a nest, and one or more members of the play group might add to the nest between wrestling bouts, or the nest might be disassembled during play. Sometimes as many as 12 play nests will be built in a fruiting tree by a play group in one day (Rijksen, 1978). Discussion among orangutan researchers from different long-term sites revealed this behavior to be universal in orangutans (see Chapter 2).

One nest building behavior not reported for chimpanzees (Whiten et al., 2001), rarely seen in bonobos (Kano, 1982), but discovered to be universal in orangutans, is the construction of rain covers (see Chapter 2). Leaves and twigs are arranged loosely over the orangutan in the nest, in a fashion that sheds rain away from the nest and its occupant. The leaves and twigs to be

used for a nest cover may be collected far from where the nest is built (Rijksen, 1978), indicating some planning or forethought in nest cover construction.

No other ape has been reported to have the level of cultural variation in nest-building that has been found in orangutans. In watching the behavior of orangutans during nest building, researchers discovered several cultural variants related to nest building activities, including **bunk nests**, **sun covers**, **shelter under nest**, **nest raspberry** and **twig biting** (van Schaik et al., 2003, see Chapter 2 for details). The Sumatran orangutan populations at Suaq Balimbing and Ketambe showed differences in many of these nest-related behaviors (Table 4.1). While most of these serve apparent functions as weal skills, the functions of the nest raspberry and twig biting are unclear.

The nest raspberry is a forceful expulsion of air between relaxed lips (Chapter 2). The function of this behavior is unclear, and it is not seen in wild orangutans at Ketambe. The sound is similar to the noises orangutans make when spitting wadges of fiber after chewing lianas or stems (C. van Schaik, pers. com.). “Spluttering” noises were made by young, rehabilitant orangutans at Ketambe when they could not get food they saw in the possession of a human or another orangutan, or when another orangutan was

begging for food in their possession (Rijksen, 1978), but these noises were much softer than the nest raspberry (C. van Schaik, pers. com.). As indicated in Chapter 2, nest raspberries generally occur at the end of nest building at Suaq Balimbing. They may be associated with **twig biting**, which in turn seems to be related to lining the nest with small, leafy twigs (C. van Schaik, pers. com.).

When I began my fieldwork in 1999, a difference in performance of the nest raspberry between Suaq Balimbing and Ketambe was suspected but had not been confirmed. I intended to examine the context and possible functions of nest raspberry production in greater detail. I used video to search for other, subtle differences between the sites in nest-building behaviors or techniques. I also looked for differences in learning opportunities during nest building at the two sites.

Methods

Sites

Research was conducted at Suaq Balimbing and Ketambe, two established research sites in Gunung Leuser National Park, on the island of Sumatra (Aceh province, Indonesia – see Table 3.2 and Figure 2.1). Both sites

contained populations of unprovisioned wild Sumatran orangutans, *Pongo pygmaeus abelii*.

Video

Video of orangutan behavior was recorded using a Canon Hi-8 analog camcorder in a water-resistant housing. Fifty instances of nest building or use were at least partially captured on video from April 1999 to April 2000. The cameraperson was always standing on the forest floor, attempting to get the best view of the event available from that vantage. Most of the camera work was done by Nuzuar S. Hut, though video was occasionally taken directly by the author. Whenever orangutans were captured on video, notes were taken immediately afterward about the identity of the individual, the approximate start time, and the tree species or height in the tree. The cameraperson was sometimes accompanied by another observer taking standardized data on datasheets, so it is often possible to compare events recorded on tape with the observer's notes.

Field Datasheets

Ad libitum data were recorded for each nest-building event by a focal animal, using uniform methods and datasheets at each site. Only independent (adolescent, subadult or adult) orangutans were used as focal animals for this

study. For this analysis datasheets from Suaq Balimbing, recorded between 17 April 1999 and 30 August 1999 were used. Datasheets from adult females at Ketambe recorded between 10 May 1999 and 20 October 1999 were used for comparison.

For this study, independent individuals were grouped according to five different age/sex classes. Females were either classed as **AF**=Adult (parous) Female or **Adol. F** = Adolescent Female (recently independent, not sexually mature). Males were classified as **AM** = Adult (flanged) Male, **SAM** = Sub-Adult (unflanged, sexually mature) Male or **Adol. M** = Adolescent Male (recently independent, not sexually mature). Adolescents of both sexes were generally smaller than adult females, but sub-adult males were noticeably larger than adult females (see Utami Atmoko, 2000 for a review of bi-maturism in Sumatran orangutans). There were far fewer identified focal animals at Ketambe than at Suaq Balimbing, and relatively fewer focal adult males (Table 4.2).

For each day or night nest built, the beginning and ending times of nest building activities were recorded (to the nearest minute). The presence of nest raspberries or any other vocalization during nest building was noted, and in most instances the number of nest raspberries heard were recorded. For

infants and nearest neighbors of the nest-building focal, distance to the focal was recorded one minute after the nest-building event began, as was the infant's and/or nearest neighbor's probable ability to see the nest-building focal (judged by intervening foliage density and body orientation). The species and diameter at breast height (DBH) were recorded for each nest tree, along with the height of the nest (to the nearest 5m), the distance of the nest from the top of the tree crown, and the position of the nest in the tree (Figure 4.1).

Data Analysis

Nest Raspberries

To investigate the possible functions of the nest raspberry at Suaq Balimbing, several nest-building attributes were compared in the presence or absence of the nest raspberry. For these analyses, I only considered the 11 individuals who were observed building nests both with and without nest raspberries within their observed day nests or night nests (bold in Table 4.3). Samples for most individuals were limited, so in some cases, when differences between individuals were clearly not significant (Chi-square analyses, $P > 0.2$), data were pooled between individuals or between day and night nests to provide larger samples for comparisons. Some have suggested

that Bonferroni adjustments should be applied when a data set is subjected to multiple comparisons (Bland and Altman 1995). However, Perneger (1998) asserts that to do so would lead to excessive type II error, and I will follow his recommendation to instead present each test separately.

Nest building duration. The nest raspberry occurs in the late stages of nest building, and may be connected with adding extra lining to the nests. Considering day nests and night nests separately, I calculated the mean duration of nest building for each individual when nest raspberries were present or absent, then compared these for the whole population using a signed rank test. For the three adult females in this comparison, Mann-Whitney/Wilcoxon tests were used to look for differences in nest building duration whether a nest raspberry was performed for each individual.

Nest positions. Nests in positions 2 (Figure 4.1) are more likely to be exposed and near the edge of a tree canopy, whereas nest positions 1 and 3 are closer to the center of the canopy provided they are not in the top meter or two of the tree, and nests in position 4 are between two tree canopies (usually low). They may also be related to the structure of the tree and therefore the structure of the nest being built. Nest positions were compared for presence or absence of the nest raspberry within day and night nests for

each individual, and for adult females (pooled) and adult males (pooled).

Distance to top of nest tree. The distance to the top of the nest tree is another factor in how exposed the nest is. While it is possible that trees at the edge of a canopy near a clearing or on a hill could be very exposed and still much lower than the top of the next tree, this measure will give some idea of the nest's exposure to the elements and its utility as a vista. For multi-tree nests (position 4, Figure 4.1), the distance to the top of the taller tree was used. Pairs of mean distances (for nests where raspberries were present or absent) were compared with signed rank tests for each age/sex class with multiple individuals.

Nearest neighbor distance and line-of-sight. If the nest raspberry serves a communicative function, its expression should be related to the proximity of conspecifics. Nearest neighbor distance was scored in four classes: >50m (mostly times when no other independent conspecific was detected), 50m->10m, 10m->2m or $\leq 2m$. Chi-square analyses were performed for each individual on nearest neighbor distance class compared with the presence or absence of a nest raspberry, with Yates' correction for individuals with only two nearest neighbor distance classes observed in day nests or night nests. Nearest neighbor line-of-sight was analyzed for all nests built with

independent conspecifics in a 50m radius of the focal.

Infant distance and line-of-sight. Infant distance from the focal adult female was analyzed only for nests when there was no nearest neighbor at 50m. Infant line-of-sight was compared when there was no independent conspecific within 50m, and for all nests regardless of nearest neighbor distance.

Inter-site Comparisons

Multi-tree nests. To clarify the frequency of multi-tree nests at Ketambe, and compare this to Suaq Balimbing, the number of multi-tree nests and their fraction of all nest building incidents observed is reported. The percent of multi-tree nests (position 4, Figure 4.1) was calculated for all positively identified individuals with at least four nests observed at Suaq Balimbing. The mean percent of multi-tree nests for each age/sex class was calculated based on these individual percents.

For other statistical comparisons between Suaq Balimbing and Ketambe, only adult females with more than four observation days were considered.

Frequency of day-nest building. Adult females from each site were compared in the number of day-nests built per hour of observation while

active with a Mann-Whitney (Wilcoxon) test.

Nest building duration. To investigate whether the difference in nest raspberry production between the two sites was linked to a difference in nest building duration, the mean duration for building day and night nests was compared between Suaq Balimbing and Ketambe females.

Nearest neighbor distance. I compared the percent of night nests with neighbors at each distance class ($>50\text{m}$, $\leq 50\text{m}$, $\leq 10\text{m}$ or $\leq 2\text{m}$) for individual females at Ketambe and Suaq Balimbing (with more than 4 night nests observed), using Mann-Whitney (Wilcoxon) tests. I also calculated nesting dispersion tendency for each site: the time spent alone (nearest neighbor $>50\text{m}$) when building night nests minus the time spent alone throughout the day (based on percent time in parties data presented in Chapter 3), and compared this with expected (0) using a signed rank test. I compared dispersion tendency between sites with a Mann-Whitney (Wilcoxon) test.

Results

Video of Nest Building at Suaq Balimbing and Ketambe

Of the fifty nest-building events captured on video, the majority showed only the movement of foliage with an occasional glimpse of an orangutan's hand or leg. Four video clips from Suaq Balimbing and three clips from Ketambe were captured at an angle where the orangutan's behaviors were more clearly discernable. Even in the best of these, there are portions of the video where the activities of the nest building orangutan are not visible due to camera angle, the orientation of the orangutan or intervening vegetation.

With those caveats, in one of the night nests with clear video from Suaq Balimbing, the orangutan (an adult male) is clearly **twig biting**. In three night nests and one day nest video from Suaq Balimbing, the orangutans appear to be using an exaggerated shoulder sweep, arcing a leafy twig over a shoulder and across the torso before tucking it into the nest lining. In the day nest, one can see that this is accomplished via a twist or flick of the wrist. One night nest for Ketambe also appears to include a shoulder sweep. In no case was the **nest raspberry** visible or audible over other noises on the video, though the night nest with **twig biting** is recorded in field notes as having included a **nest raspberry**. Based on these few usable video clips,

there were no obvious differences between the nests built by orangutans in Suaq Balimbing and Ketambe.

Nest Raspberry Correlates at Suaq Balimbing

Of the 27 identified individuals at Suaq Balimbing whose focal follow observations included at least one nest building incident, only three individuals were not observed performing the nest raspberry, and these three had only 1-3 nest observations each (Table 4.3). A more extensive data set for five years of research at Suaq Balimbing found nest raspberries produced by all well-habituated orangutans there (M. van Noordwijk, pers. com.).

The nest raspberry was more common with night nests than day nests. Across all age/sex classes at Suaq Balimbing, nest raspberries were confirmed for 11% of all day nests and 73% of all night nests.

Nest building duration. The overall average time spent building a day nest at Suaq Balimbing was approximately 2.7 minutes (range 1-8 minutes, N = 137). The overall average time spent building a night nest was approximately 8.5 minutes (range 2-15 minutes, N = 83). Table 4.4 shows the mean nest building duration for each age/sex class for day and night nests, and comparisons of day and night nest building duration within each

class (averages for each individual were averaged among age/sex classes). All age/sex classes spent longer building day nests than night nests; the results were highly significant for adult males and adult females. Differences between the age/sex classes were not significant (Kruskal-Wallis $H = 2.92$, $P = 0.081$ for day nests, $H = 2.92$, $P = 0.232$ for night nests; AF, AM and SAM only).

Figure 4.2 shows the average nest building duration for day and night nests, with or without nest raspberries for each age/sex class observed at Suaq Balimbing. When the mean for each individual who was observed building nests both with and without nest raspberries is considered, there is no significant difference in building duration between day nests with or without raspberries (signed rank test = 0.0, $P=0.999$), but the difference in building duration for night nests with and without nest raspberries is significant (signed rank test = 2.25, $P=0.0242$). Adults always spent longer building night nests with raspberries than they did building nests without raspberries, but the adolescent female did not (Figure 4.3). For day nests, adults always spent the same amount of time or longer building nests with raspberries, but the adolescent female and a subadult male spent longer building nests without nest raspberries (Figure 4.4).

Table 4.5 presents information on the construction duration of day and night nests built by Suaq Balimbing adult females with or without the nest raspberry, considering the nests for each individual separately. Only three adult females (Ani, Beki and Hanes) were observed performing a nest raspberry while building a day nest. For Beki and Hanes, the nests built when performing a nest raspberry took longer to build, and for Ani the mean building duration was slightly shorter, but in no case was the difference significant (Mann-Whitney/Wilcoxon). These three females were also the only ones observed building night nests both with and without a nest raspberry. For all three females, the night nest building duration without a nest raspberry was shorter than those with a raspberry, but the differences were not significant.

Nest position. There was only one significant difference in nest position whether nest raspberries were or were not given when considered by individual for day nests (for the adult female Hanes, $X^2=8.0$, $P=0.046$), and no significant differences for night nests (Table 4.6). As there were no significant differences in nest position between individuals within age sex classes, the nests for adult females and for adult males were pooled to see if any significant differences would appear; there were no significant

differences even with these larger samples for whether a nest raspberry was given (Table 4.7). Given the small samples of other age/sex classes, these were not pooled for further comparison. As there were significant differences in night nest position between adult males and adult females ($X^2=10.75$, $P=0.0143$), the age/sex classes could not be pooled further.

Distance to top of nest tree. The distance between the nest and the top of the tree was not significantly different for nests with and without the nest raspberry for day or night nests in any age/sex class (paired-sample signed rank tests, Table 4.8).

Nearest neighbor distance and line-of-sight. The distance to the nearest neighbor (in classes of $>50\text{m}$, $\leq 50\text{m}$, $\leq 10\text{m}$ or $\leq 2\text{m}$) was not significantly associated with whether a nest raspberry was given by most individuals (X^2 tests, Table 4.9). The only exceptions were for two of the adult females when building day nests (note that one had only one nest raspberry during a day nest and the other had three). However, these females had different patterns for which distance a nest raspberry was more likely to be given (Figures 4.5). When nest raspberries were not considered, there was a highly significant difference between the three females in the pattern of nearest neighbor distance when building a nest ($X^2 = 29.1$, $P = 0.0001$). There were

no significant relationships between the nearest neighbor's line-of-sight and the production of a nest raspberry for day nests or night nests (X^2 and Fisher's Exact Test, Table 4.10).

Infant distance and line-of-sight. The distance between focal females and their offspring was not significantly related to the presence or absence of nest raspberries in those cases where there was no independent conspecific within 50m of the nest-building focal (Table 4.11). There was no variation in infant line-of-sight when there was no independent conspecific within 50m of the focal (when nests were built by females who varied in nest raspberry production during day nest or night nest building); infants were always able to see their mother build the nest in those cases. The one time when Ani built a day nest and her infant was not able to see her, an adult female and a subadult male were less than 50m away (Ani did not give a raspberry); the one time her infant did not have a line-of-sight when Ani built a night nest, there were no independent conspecifics within 50m (Ani did give a raspberry).

Comparison of Ketambe and Suaq Balimbing

During 1999 and 2000, in nest data taken for this study, **nest raspberries** or other vocalization were never observed at Ketambe, despite active searching

and systematic notations of any vocalizations produced during nest building by researchers who were familiar with the phenomenon at Suaq Balimbing.

Nest position and multi-tree nests. Only one observation of nest building at Ketambe (out of 28 day nests and 73 night nests) was a multi-tree nest (position 4): an adult female's night nest. It was one of 10 night nests recorded for Elisa.

At Suaq Balimbing, multi-tree nests accounted for 14% of all nests observed in this study. Among individuals with at least four nest-building incidents observed for day nests, multi-tree nests accounted for 11% of day nests in adult females, 20% of day nests for adult males. Among individuals with at least four nest-building incidents observed for night nests, multi-tree nests accounted for 7.5% of adult females' night nests and 39% of adult males' night nests. Differences between adult males and females within day or night nests or between day or night nests within those sex classes were not significant (Mann-Whitney/Wilcoxon, NS, see Table 4.12 for results). None of the nests built by the adolescent female or subadult males were multi-tree nests.

Frequency of day-nest building. Adult females at Suaq Balimbing built

about three times more day nests per observation hour (0.166) than those at Ketambe (0.055), but the difference did not reach statistical significance ($W=26.0$, $P=0.055$). This came out to a mean of 1.3 day nests per observation day at SQB, compared to only 0.57 per day at KTB.

Nest building duration. Females at Ketambe and Suaq Balimbing spent about the same amount of time building their day nests (2.5 minutes and 2.7 minutes, respectively); the difference was not significant ($W=22.0$, $P=0.231$). Ketambe females significantly spent less time building their night nests (6.9 minutes) than Suaq Balimbing females (9.2 minutes; $W=28.0$, $P=0.022$).

Nearest neighbor distance. The average percent of night nests built with a conspecific in a 50m radius by Ketambe females was 17%, compared to 41% at Suaq Balimbing, but the difference did not reach significance ($W=4.0$, $P=0.106$). Females at Suaq Balimbing had a higher percent of night nests with neighbors at 50m-10m (29% compared to 6% at Ketambe, $W=19.0$, $P=0.138$), but 10-2m were nearly identical (10.1% at SQB compared to 10.7% at Ketambe, $W=15.0$, $P=0.570$). Ketambe females never built a night nest with a neighbor less than 2m away, but one female at Suaq Balimbing (Ani) built one night nest (out of 18) with a nearest neighbor at less than 2m (Figure 4.6). Nesting dispersion tendency (tendency to be more than 50m

from independent conspecifics when building night nests than through the rest of the day) did not reach significance at either site, though both were positive when averaged across females (Table 4.13). Ketambe had a higher dispersion tendency than Suaq Balimbing, but the difference between the two sites was not significant ($W=9.0$, $P=0.594$).

Discussion

The only feature of nest building that showed any significant relationship to the production of the nest raspberry was the duration of nest building (and that was only true for night nests). This was expected, because the nest raspberry generally occurs during the final stages of nest building, when the orangutan is adding supplemental lining to cushion the nest. Day nests at Suaq Balimbing were built in significantly less time than night nests, presumably because they lack this lining and are of simpler construction most of the time.

The nest raspberry did not show any relationship to nest position or distance to the top of the nest tree. Nest raspberries do not appear to have any function related to nest exposure, and probably do not have anything to do with tree structure, both of which would have some impact on nest position

or distance to the top of the tree canopy.

Nest raspberries do not appear to serve any function as a signal. They are not related to the distance to independent conspecifics or dependent offspring, nor to whether these others had opportunity to observe the nest builder in progress (their line-of-sight). Nest raspberries are fairly quiet, perhaps audible up to 50m away, but less audible than the breaking and rustling of branches over that distance (at least, to listeners near ground level). Where the loud-calls made by bonobos around the time of nest building function over long distances and alert others who could not hear the bonobos movements, an orangutan's nest raspberries, at best, serve only reinforce the orangutan's intention. The noises associated with manipulating vegetation during nest building might be mistaken for the noises of a moving orangutan, but the nest raspberry occurs only when a nest is being built.

The distance between an infant or juvenile orangutan and its mother did not appear to have any effect on whether she gave a raspberry during nest building. This was true even when there was no other independent orangutan within 50m. This would seem to indicate that mothers do not use the nest raspberry as a signal to their dependent young that they are building a nest. Distance from the mother is related to the age of the infant or juvenile (Fruth

and Hohmann, 1996; van Schaik and Knott, 2001). When the mother of an infant is building a nest, the infant is usually less than 2m from her, and is often sitting in the nest with her, playing with twigs as she lines the nest (pers. obs.). Older infants sometimes build their own nests, even if the mother is not building a nest during the day (pers. obs.). Infants approaching weaning will build their own night nests a few meters away from their mothers, but often are seen emerging from their mother's nest the next morning (pers. obs., D. Agee, pers. com., van Noordjwick and van Schaik, in press).

The lack of associated nest-building or social features with nest raspberry production makes this behavior a candidate for classification as a cultural “convention.” A convention would be a behavior that is widespread in a population due to social transmission, but that does not serve any adaptive or social function. Such behaviors may be a by-product of the propensity to mimic behaviors of others. As such, they might represent the ideal behaviors for more detailed field research into non-human culture, as their very “functionless-ness” indicates that they are unlikely to be innovated and maintained by individuals attempting to solve adaptive problems, and that ecological explanations for behavioral variation are highly implausible.

There is a clear difference between Ketambe and Suaq Balimbing in tendency toward building multi-tree nests. As multi-tree nests occurred in less than 1% of all observed nests at Ketambe, and in only 1 of 10 nests built by only one individual in this study, I would classify this as a rare behavior at Ketambe. The distribution of multi-tree nest observations among individuals at Suaq Balimbing makes this a customary behavior there. The difference between sites may be due to habitat differences; the forest structure at the two sites is quite different (see Table 3.2), which might make the trees at Suaq Balimbing more suitable for multi-tree nests, or the need for multi-tree nests lower in the larger boughs of Ketambe's trees. Interestingly, it was only observed in adult females and adult (flanged) males at Suaq Balimbing. This may support a role for learning in this behavior, in that only the older individuals had opportunities to develop the skill necessary to build multi-tree nests. However, it might also be considered a function of body size in this habitat; sub-adult (unflanged) males are generally as large as or larger than adult females, but adult female nests also have to support the weight of their dependent offspring. So an ecological explanation for the variation in this behavior between the sites cannot be dismissed.

Orangutan females at Suaq Balimbing built more day nests than those at Ketambe. It has been suggested (van Schaik and Knott, 2001) that feeding tool use at Suaq Balimbing (particularly when *Neesia* sp. fruit are available) could provide a richer diet than found in other orangutan populations, allowing for higher population density. This could also provide more energy for orangutans at Suaq Balimbing to devote to preparing for extended rest during their active day by building a nest, and spending more time constructing a nest at night (adding more twigs and leaves to the nest lining for improved comfort during sleep).

Most nests built by orangutans at Ketambe, and nearly half of those at Suaq Balimbing were built when there were no conspecifics within 50m of the focal. This is quite different from the situation for other apes. In lowland gorillas, less than 8% of 27 nests in one survey were built with no others nearby (Brugiere and Sakom, 2001), and no lone nests were found in 137 nest sites observed in another (Tutin et al., 1995).

Ape nests are a way of manipulating the environment that demands some energy and intelligence on the part of the builder. Fruth and Hohmann (1996) suggest that nest building may have been a contributing factor in the evolution of ape intelligence, providing more secure and comfortable

sleeping sites to facilitate the types of sleep (Rapid Eye Movement and Slow Wave Sleep) that promote learning and memory. Nests may serve important functions beyond simply providing a stable platform for rest. The use of nests as a social tool to de-fuse potential agonistic interactions has been suggested for bonobos (Fruth and Hohmann, 1993) and orangutans (see **sneaky nest approach**, Chapter 2). Orangutan females may also build a nest to prevent forced copulation with males (van Schaik, in press). Like home base in a children's game of tag, an ape's nest might be "safe" from competitors or aggressors.

Much of what is known about great ape nests comes from the perspective of censusing, with a focus on the nest itself rather than the activities of the builder. These studies are critical for determining where unhabituated apes can be found, and at what density they are present. But this approach overlooks important variations in aspects of nest-building behavior, because the end result (the structure and location of the nest itself) is roughly identical. When researchers rely only on nest counts for statistics on various nest conditions, multiple nests from the same individual are counted as independent data points (e.g. Baldwin et al., 1981; Brugiere and Sakom, 2001; Fruth and Hohmann, 1993; but see Sugardjito, 1983; Tutin et al.,

1995), masking potentially interesting variation in nest location and structure within populations that could account for apparent variation between populations when multiple sites are compared. While such work makes an interesting starting point for investigating great ape nests, it should by no means be the end.

Nest building appears to be a cognitively complex task, with abundant opportunities for cultural variation. Clearly, more detailed investigation of nest building behaviors in other orangutan populations would be beneficial. It would particularly be helpful to investigate further possible behavioral correlates with the nest raspberry at other sites (Soraya, Lower Kinabatangan, see Chapter 2). The intriguing nest raspberry cultural variant, with its apparent lack of adaptive or social function, could be an excellent test case for looking at the innovation and spread of socially learned behaviors. Methods of research that allow more detailed observation from a better vantage-point (such as aurally deployable video recording devices) might reveal a wealth of subtle and complex behavioral diversity. Interpopulation distinctions in day-nest frequency and night-nest-building duration, the use of multiple trees for nest building, and the production of nest raspberries were clear from what limited data were available for this

comparison.

Aside from some brief fashions and variations that could be due to differences in habitat for chimpanzee populations, cultural variation in nest-building behaviors has only been reported in orangutans, the one species shown to disperse instead of gathering (chimpanzees and bonobos) or remaining together (gorillas) to build night nests. I suspect that the absence of nest-building variations reported in those species has more to do with how nest building is (or more often, is not) observed than with the actual behaviors. For a behavior that was considered so important 75 years ago (see Fruth and Hohmann, 1996), there is still a lot to be learned about nest-building in the great apes.