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Nest Location Preferences in Zoo-Housed Orangutans

Meredith L. Bastian[a], David R. Glendinning[a], Alexandra J. Reddy[a], Elizabeth S. Herrelko[a,b], Melba Brown[a], Elizabeth Renner[b,c], Laurie Thompson[a]

[a] Smithsonian's National Zoo and Conservation Biology Institute
Department of Animal Care Sciences
MRC 5507
Washington, DC 20013-7012

[b] University of Stirling
Psychology
Stirling
FK9 4LA
United Kingdom

[c] Center for the Advanced Study of Human Paleobiology
The George Washington University
800 22nd Street, NW
Suite 6000
Washington, DC 20052

Author email addresses:
M.L. Bastian (Corresponding author): BastianM@si.edu
D.R. Glendinning: GlendinningD@si.edu
A.J. Reddy: ReddyA@si.edu
E.S. Herrelko: HerrelkoE@si.edu
M. Brown: BrownMT@si.edu
E. Renner: lrenner@gwmail.gwu.edu
L. Thompson: ThompsonL@si.edu

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Abstract

Nest building is an advanced and complex activity that wild orangutans engage in, yet they do so on a daily basis and with potential safety consequences. Like their wild counterparts, zoo-housed orangutans also make nests when given adequate materials, yet comparatively little research has documented the nesting habits of captive orangutans, including potential social and environmental influences of nest site selections. We documented the night nesting behavior of six adult orangutans housed at the Smithsonian's National Zoological Park (NZP), identifying preferred nest locations and proximity to conspecifics, comparing observed patterns to those reported in a nest behavior survey of orangutan facilities throughout the Association of Zoos and Aquariums (AZA). Survey results reveal that in addition to several universal patterns of nesting behaviors, as in the wild, the sharing of night nests by captive adult orangutans occurs only rarely (2 of 31 surveyed facilities). Data collected at NZP indicate that night nearest neighbor associations among nesting conspecifics may be a useful proxy for actual nearest neighbor data taken during daytime social interactions and may offer a more feasible alternative for determining social relationships among large groups of socially housed orangutans.

Keywords: orangutan; *Pongo*; nesting behavior; nearest neighbor

1. Introduction

Great ape nesting, particularly in the wild, has been broadly studied across species. While the principal purpose of nest building is rest (Koops et al., 2012), nest site selection and construction have been suggested to concomitantly support a number of other desirable outcomes, including predator avoidance and thermoregulation (Koops et al., 2012; Samson and Hunt, 2012). In a study of wild bonobos (*Pan paniscus*), Fruth and Hohmann (1993) noted nest utilization in a number of social contexts, including social grooming and play. Other wild-based studies of great ape nests have focused on identifying preferences in tree species (Baldwin et al., 1981; Mulavwa et al., 2010), differences in nest construction between day and night chimpanzee (*Pan troglodytes*) nests (Riss and Goodall, 1976), and cultural differences among orangutan (*Pongo spp.)* populations in various innovative behaviors in the nesting context (Bastian et al., 2012; Russon et al., 2007; van Schaik et al., 2003).

Both wild and zoo-housed orangutans routinely build day and night nests (van Casteren et al., 2012). The nesting platforms made by orangutans and other great apes are most often built new each day and are sometimes rebuilt or reused (Fruth and Hohmann, 1996; Prasetyo et al., 2009). Orangutan nests are also complex and technologically sophisticated in structure (Prasetyo et al., 2009; van Casteren et al., 2012).

Compared to that of their wild counterparts, the nesting behavior of captive great ape populations has been relatively less studied. As has been advocated for by other researchers (e.g. Anderson, 1998), there is a need to study the sleeping patterns of zoo-housed primates in order to provide knowledge that could lead to improvements in their welfare under human care. Opportunities to study captive ape nesting behavior are likely to reveal insights into their sociality and location preferences, which would aid in making husbandry decisions. Weiche and Anderson (2007) report correlations between social activity and nesting behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). While room size and other environmental factors influenced sleeping sites, group dynamics also played a role, with associations based on kinship being most evident.

The traditional method of determining social partner preferences and associations in primates is through the identification of nearest neighbors during daytime activity periods, where social dynamics are evaluated by recording the spatial proximity between each pair of individuals (e.g. Gould, 1997; Taylor & Sussman, 1985;White & Chapman, 1994). Previous studies have analyzed the relationship of daytime associations on sleeping site selections in captive chimpanzees. Riss and Goodall (1976) found that captive chimpanzees maintained sleeping partner preferences that were directly related to early rearing experiences when they were in smaller subgroups, although the social relationships between preferred sleeping partners and others did not differ based on the frequency of affiliative behaviors. In a mixed-sex group of 11 captive chimpanzees, Lock and Anderson (2013) found that neither daytime associations nor the presence of related animals influenced female sleeping site selection.

Among the males, however, they did find a significant correlation between the frequency of daytime associations and shared sleeping locations.

Unlike African apes, wild orangutans do not live in stable social groups. Social nesting (more than one independently ranging orangutan nesting within 50m of each other overnight) occurred in less than 4% of all night nests documented in a high-density population of wild Bornean orangutans (Bastian, 2008; Bastian, unpublished results). Thus, wild-based studies offer little insight into how orangutan night nest site selection may relate to social associations in captive populations, where group housing is the norm. Observations of zoo-housed orangutan nesting behavior provide an opportunity to note social dynamics that may not be revealed in the study of wild populations.

Night nests are of particular interest, as primates spend approximately half of their life at sleeping sites (Anderson, 1998). As one example, using infrared videography to document the sleep architecture of a group of captive orangutans, Samson and Shumaker (2015a, 2015b, 2013) found, in a zoo setting, that a comfortable sleeping environment helped improve orangutan sleep quality, which they identified as being deeper and more efficient than the sleep of baboons (which do not build nests). Aside from these findings, few data are available on the nesting behavior of captive orangutans, a gap that has been identified as a high priority for future research (Samson and Shumaker, 2013).

This study examines two cases in which anecdotal observations previously suggested that patterns of nesting behavior could be useful to the care and management of a population of zoo-housed orangutans. First, we hypothesized that nearest neighbor associations based on the proximity of night nests could effectively inform decisions about housing options based on orangutan preferences. We also predicted that as in wild orangutan populations, where orangutan nests cluster in specific areas within even extremely homogeneous habitats and night nest site re-visitation is common (Bastian, unpublished results), night nest locations chosen by orangutans at Smithsonian's National Zoological Park (NZP) would show consistent patterns. Our results are analyzed in relation to a survey about zoo-housed orangutan nesting behavior from 31 participating facilities across AZA.

[INSERT TABLE 1 HERE]

2. Material and Methods

2.1 *Study Populations*

The primary study population consisted of two Bornean orangutans and four Bornean-Sumatran hybrids, socially housed at the Great Ape House (GAH) and the Think Tank (TT) facilities at NZP: two adult males, Kiko (hybrid, 27yrs at start of data collection) and Kyle (Bornean, 18); and four adult females, Batang (Bornean, 18), Bonnie (hybrid, 38), Iris (hybrid, 28), and Lucy (hybrid, 42). The orangutans were housed using a flexible management protocol based on historical social interactions between each pair of individuals and focused around Batang, who was able to socialize peacefully with all other orangutans and was pregnant during this study (Table 2). The adult males were always separated, as were certain combinations of females, although they were frequently housed in adjacent rooms. Lucy was most usually housed alone when inside, including overnight; thus, she is only listed within social configurations in outside circumstances.

[INSERT TABLE 2 HERE]

2.2 *Orangutan Exhibits*

Indoor orangutan housing at GAH consisted of six rooms with flexibly configured climbing structures, platforms, water features, spools, tubes, and hammocks of various dimensions (Figure 1). This layout allowed for the six rooms to be open or closed to each adjacent room via hydraulic doors, providing staff the ability to choose from multiple housing configurations depending on which and how many individual orangutans were given access to one another on a particular night. Each room included a water source: a licker (a small metal pipe that when depressed provides a source of drinking water), waterfall, small pool, or combination of these. Artificial trees were found in all but two (rooms 1 and 4) of the six enclosures and all had some sort of elevated platform. Ceiling height varied across rooms, ranging from 2.4m (8ft) in room 1 and 5.2m (17ft) in room 4 to 7m (23ft) in rooms 2 and 3 and 7.6m (25ft) in rooms 5 and 6. With the exception of rooms 1 and 4, rooms were visible from the public area.

Keepers could easily transfer orangutans to or from outdoor yards and the Orangutan Transit System (or "O-line") through elevated chutes running from rooms 3, 5 and 6 of GAH and a holding room at TT. Orangutan yards at both GAH and TT consisted of grassy areas with access to a tower leading to the O-line. The O-line, a series of eight 13.7m (45ft) high towers, connected by 16.6m (50ft) high plastic-coated steel cables, allowed the orangutans to travel via the yards and across the cables between buildings, so they could nest at either location if given access by keepers. Only one adult female, Lucy, has never chosen to travel across the O-line since its construction in 1995, so her nests were found only at GAH.

The indoor orangutan area at TT consisted of a primary living space - a single room of approximately 67.4m^2 (725 ft^2) with a 5.2m (17ft) ceiling, provisioned with fire hose and other climbing opportunities, shelving at various heights, a holding enclosure, and room designed for public research demonstrations (Figure 2).

[INSERT FIGURES 1 & 2 HERE]

2.3 *Data Collection and Analysis*

For purposes of this study, we defined a "nest" as an orangutan-made structure formed by manipulating leaves, hay, or other material for use as a platform for resting or sleeping. As the focus of this study was on night nests, data at NZP were recorded twice each day, once in the evening as the building was closed by departing keepers (1630-1830h, depending on season) and again the following morning at first staff arrival (0630-0700h). The study covered the period July 2014 - July 2015. Emphasis was placed on recording night nest location preferences, nest fidelity (as opposed to abandonment in favor of another nest), and the proximity of a nest to the nesting animal's nearest neighbor. From February - July 2015 we collected daytime nearest neighbor data within groups of socially housed NZP orangutans, focusing on individual animals across four time periods spanning the full keeper day (e.g., 0700-0900h, 0900-1100h, 1100-1300h, 1300-1500h). Within those periods, data was recorded on the focal animal every five minutes over a 30 min interval. Rotating among focal animals to ensure a balanced distribution of data collection for all orangutans, we collected data between two to three days a week for a total of forty-one hours over 38 days. Both daytime and night nest nearest neighbor data were collected for associations of individuals within 10m (32.8ft) rather than within the 50m distance used in wild studies due to the space restrictions of captive environments. These data were then used to produce proximity matrices based on nearest neighbor data. Due to staffing and schedules, priority was given to nests and activity at GAH, with opportunistic data collected at TT.

The closing keeper recorded the location of all occupied orangutan night nests in each building on a facility map containing several fixed landmarks within each enclosure (Figure 1), onto which scaled measurements of distance between rooms were overlaid to determine the proximity of nesting nearest neighbor orangutans in relation to the focal individual and overnight nest fidelity. In the mornings, the first-arriving staff member to walk through the orangutan line recorded the position of each occupied nest on the previous evening's nest location map, indicating the position of any new nests, changes of nest location, and identity of which individual occupied each nest.

We also disseminated a survey throughout AZA to document generally the nesting habits and location preferences observed among zoo-housed orangutans at 30 other facilities. Analysis of nesting behaviors across zoos excluded individual orangutans not yet engaging in nest building behavior.

Contrasts of categorical NZP data were analyzed using Chi-square Goodness of Fit tests. SOCPROG Compiled v. 2.7 (Whitehead, 2009) was used to analyze data on the social structure and associations among NZP orangutans. We defined the NZP social "group" on a given evening as all orangutans with access to the same or adjacent enclosures, since individual orangutans in adjacent enclosures with mesh access could choose to spend time in closer proximity to one another than to individuals housed in the same enclosure. Social network analysis statistics were performed on composite matrices within SOCPROG, the output of which were used to generate sociograms using NetDraw 2.160 (Borgatti, 2002) in order to visually present social relationships among individual orangutans using each measure of nearest neighbor association.

The Dietz R matrix correlation test (Dietz, 1983) using 1000 permutations implemented in SOCPROG 2.7 was used to determine whether we were justified in creating composite matrices based on NZP nearest neighbor and group composition data for day and night nest methods of assessing nearest neighbor associations. A Dietz R-test was also used to analyze matrices generated from day and night nest nearest neighbor methods. Dietz’s (1983) R-test is the same as a Mantel test but the Dietz test is analogous to Spearman’s rank correlation coefficient with values of the matrices replaced by their ranks, so the Dietz test is much less strongly affected by outlying values than the Mantel test. All tests were two-tailed and alpha was set at 0.05.

3. Results

3.1 *Nest Location Preferences*

We recorded a total of 851 night nests. Although NZP orangutans were most often found in a *different nest* the next morning, indicating low nest fidelity (χ^2 = 41.51, df = 1, p < 0.001), the data indicate high room fidelity, as they were most often found in a nest in the *same room* as the last nest recorded the previous day (χ^2 = 4.27, df = 1, p = 0.046). Chi-square analyses revealed that within GAH, in nights during which multiple rooms were available, Bonnie (χ^2 = 58.48), Kyle (χ^2 = 54.24), and Iris (χ^2 = 23.93) showed a clear preference for off-exhibit room 4 (p < 0.0001), whereas on-exhibit room 5 was preferred by Batang (χ^2 = 81.93) and Lucy (χ^2 = 22.56) and on-exhibit room 5 was preferred by Kiko (χ^2 = 34.37), df = 1, p < 0.0001.

Significantly more night nests were made on the ground at both GAH (χ^2 = 523.62, df = 1, p < 0.001) and TT (χ^2 = 89.04, df = 1, p < 0.001), although nests on shelves and in hammocks were also occasionally observed and elevated nests were built more frequently at GAH than at TT (χ^2 = 6.37, df = 1, p = 0.012). Of the 31 zoos surveyed, including NZP, 100% reported giving their orangutans opportunities for building elevated nests, 87% of which reported at least occasional nesting above ground, although survey responses indicate that ground nesting is most typical in a zoo setting.

Over time at NZP, we observed all four female orangutans, but no males, partially plug water lickers at one time or another and all orangutans nesting in close proximity to them. Our study observations confirmed that at NZP, all six orangutans showed statistically significant (Chi-square analyses, $p < 0.05$) preferences for nesting in rooms with water lickers over those with alternative water sources but without lickers.

Previous studies have shown that zoo-housed orangutans are known to partially plug water licker mechanisms with a variety of materials to create a constant flow of water (Shumaker et al., 2011). In our nest behavior survey, 28 of 31 AZA facilities reported that one or more individual orangutans regularly partially plug lickers, most individuals also place objects under the water stream, amplifying the sound in many cases.

Of the 28 AZA facilities with individuals known to plug lickers, 17 indicated that at least one orangutan frequently builds nests in close proximity to partially plugged lickers.

3.2. *Night Nest Sharing*

Day nest sharing was observed at four (13%) of the 31 zoos surveyed. Night nest sharing was observed at NZP and only one other of the surveyed facilities (7%). At NZP, adult orangutans (one male-female and one female-female dyad) shared a single night nest in nearly 3% (22 out of 851) of all recorded night nests. We considered incidences of night nest sharing as occurring or not based on nesting associations recorded by keepers as the orangutans settled into their night nests and as they were found the next morning.

3.3. *Orangutan Social Networks*

Dietz R-tests confirmed that for both traditional daytime nearest neighbor (R= 0.625, p = 0.019) and night nest nearest neighbor (R = 0.657, p = 0.05) methods, nearest neighbor and group composition matrices could be combined to form composite matrices in which nearest neighbor data controlled for time individuals were housed in close proximity to one another. Figure 3 presents sociograms to visually represent associations between orangutan dyads using daytime nearest neighbor and night nest nearest neighbor methods. A comparison of composite matrices based on daytime nearest neighbor and night nest nearest neighbor data revealed that the night nest nearest neighbor data reliably predicted daytime nearest neighbor associations (Dietz's R-test: R = 0.692, p = 0.001).

[INSERT FIGURE 3 HERE]

4. Discussion

Although we found relatively high room fidelity in instances where individuals had a choice of rooms in which to nest, nest fidelity within rooms among NZP orangutans was lower. Low nest fidelity within rooms could indicate restless sleep patterns, be influenced by conspecifics (which do not typically nest within close proximity in the wild), or signal the abandonment of nests at the arrival of early morning keeper staff. Individual NZP orangutans also showed significant preferences for particular rooms within buildings and locations within rooms. A preference for an off-exhibit room was detected for some individuals, confirming the importance of offering choice (Herrelko et al., 2015) to orangutans to use off-exhibit space in the late afternoon as they settle into their night nests.

Although a majority of documented night nests were located at ground level, when arboreal nesting did take place, it occurred most frequently in fire hose hammocks where hay and cloth were transported by an orangutan to create a nest. Compared to nearly exclusive arboreal nesting by wild orangutans, which are found at the highest densities in swamp forests (Husson et al., 2009), ground nesting in zoo-housed orangutans could be related to the lack of ground-dwelling predators, convenient access to food and water sources, and the typically dry substrate offered in zoo environments. Furthermore, access doors connecting one room to another are at ground level, as are interactions between orangutans and their caregivers. Another consideration for zoo-housed populations may include a lack of sufficient structures, nesting materials, or open space above them, as perceived by the orangutans, something for which additional study may be warranted.

As a matter of husbandry, tracking orangutan night nest location preferences can help primate keepers identify the few preferred arboreal nesting locations, which can be targeted to encourage nesting off the ground to more closely approximate typical wild orangutan nesting behavior. Consideration for orangutan facility design should maximize arboreal elements whenever possible, enhancing opportunities for public education relating to species-typical behavior and to learn more about orangutan preferences when given options.

Of potential importance to captive group management strategies, our comparison of daytime nearest neighbor data with observations of night nesting proximity among members of the NZP group reveals that overall, nesting information accurately predicted preferential social relationships. The few visual differences in the relative strength of dyadic associations between the sociograms in Figure 3 can be explained based on differences in daytime vs. nighttime orangutan housing arrangements. For example, the stronger relationship indicated between Lucy and Batang at night may be explained by the fact that Lucy had more frequent opportunities to associate with Batang at night at GAH than during the day when Batang had more physical location opportunities. Batang was a frequent O-line traveler when given the opportunity, while Lucy never traveled, giving Batang and others in her group access to areas (including TT) where Lucy would not go. Further, the weaker relationship between Iris and Batang at night is consistent with the authors' observations, recorded for another study, that Iris is primarily responsible for maintaining close proximity to Batang when the pair is housed together during the day. At times when they were housed together at night, it could be that for Iris, rest is prioritized over social interaction with Batang, giving Batang the opportunity to select a nest site away from Iris without being pursued. This specific social dynamic and the differences noted between daytime and nighttime relationships present the opportunity for further study. Nesting nearest neighbor data may therefore be a highly valuable, yet overlooked predictive tool.

In the case of both the Lucy-Batang and Iris-Batang female dyads, we found night nest nearest neighbor data to more closely reflect subtle social dynamics between individuals than daytime nearest neighbor calculations. Although Iris often followed Batang closely during the day when the two were housed together, maintaining close proximity, their night nests were rarely observed in the same room, which was consistent with our subjective observations. Relying solely on daytime nearest neighbor data may result in a bias towards more dominant individuals, whereas night nest site proximity data may more accurately reflect the preferred social dynamics of particular dyads.

Although observations of approach-leave interactions can be used to calculate the Hinde Index, a calculation determining which member of a particular dyad is most responsible for maintaining proximity (Hinde & Atkinson, 1970), collection of approach-leave data can be cumbersome and requires considerable time outside normal staff activities. We therefore propose that the night nest nearest neighbor method for detecting social relationships described in this paper is a viable proxy for traditional daytime nearest neighbor data, and perhaps a superior method of identifying preferred dyadic social relationships in zoos, where observations of night nest nearest neighbors can be recorded by staff during the course of their normal husbandry routine.

Somewhat surprisingly, considering the close proximity with which many zoo-housed orangutans nest, nest sharing between two adult orangutans during overnight periods is relatively rare across AZA institutions, reported at only one facility besides NZP. This observation is consistent with wild data, however, which indicate that nest sharing at night is rare among dyads of all age-sex classes besides mother-infant (Groves and Pi, 1985) and identify night nest sharing between a sexually mature adult male and female as a cultural behavior, occurring in only two wild populations (Bastian et al., 2012).

Nearly all reporting AZA facilities, including NZP, have orangutans who regularly plug water lickers, with 60% of those facilities stating that at least one orangutan nests in close proximity to them, warranting further investigation. The recent installation of cameras in the orangutan area at NZP presents an opportunity for future investigation of orangutan nighttime activities, which may help determine when and why individuals move from their nests within preferred rooms overnight.

5. Conclusions

Our study of the night nesting behavior of six adult orangutans at NZP, together with results of a survey of 30 additional AZA member zoos, revealed insights into nest location preferences, sociality, and innovative behavior in the nesting context. Night nest room location preferences followed consistent patterns, including a strong preference for ground nesting. Orangutans at a majority of AZA facilities surveyed, including NZP, have at least one orangutan who nests in close proximity to plugged water lickers.

We conclude that nearest neighbor associations based on the proximity of night nests could reliably predict preferred daytime associations, a finding that may offer animal care staff a practical and efficient method to determine associations among socially housed orangutans and support population care and management decisions in a zoo setting.

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