

Nest Location Preferences in Zoo-Housed Orangutans

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38 **Abstract**

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

56

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

58

59 **1. Introduction**

60 Great ape nesting, particularly in the wild, has been broadly studied across
61 species. While the principal purpose of nest building is rest (Koops et al., 2012),
62 nest site selection and construction have been suggested to concomitantly support
63 a number of other desirable outcomes, including predator avoidance and
64 thermoregulation (Koops et al., 2012; Samson and Hunt, 2012). In a study of wild
65 bonobos (*Pan paniscus*), Fruth and Hohmann (1993) noted nest utilization in a
66 number of social contexts, including social grooming and play. Other wild-based
67 studies of great ape nests have focused on identifying preferences in tree species
68 (Baldwin et al., 1981; Mulavwa et al., 2010), differences in nest construction
69 between day and night chimpanzee (*Pan troglodytes*) nests (Riss and Goodall,
70 1976), and cultural differences among orangutan (*Pongo spp.*) populations in
71 various innovative behaviors in the nesting context (Bastian et al., 2012; Russon
72 et al., 2007; van Schaik et al., 2003).

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

79 Compared to that of their wild counterparts, the nesting behavior of
80 captive great ape populations has been relatively less studied. As has been
81 advocated for by other researchers (e.g. Anderson, 1998), there is a need to study

82 the sleeping patterns of zoo-housed primates in order to provide knowledge that
83 could lead to improvements in their welfare under human care. Opportunities to
84 study captive ape nesting behavior are likely to reveal insights into their sociality
85 and location preferences, which would aid in making husbandry decisions.
86 Weiche and Anderson (2007) report correlations between social activity and
87 nesting behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*).
88 While room size and other environmental factors influenced sleeping sites, group
89 dynamics also played a role, with associations based on kinship being most
90 evident.

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

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

106 Unlike African apes, wild orangutans do not live in stable social groups.
107 Social nesting (more than one independently ranging orangutan nesting within
108 50m of each other overnight) occurred in less than 4% of all night nests
109 documented in a high-density population of wild Bornean orangutans (Bastian,
110 2008; Bastian, unpublished results). Thus, wild-based studies offer little insight
111 into how orangutan night nest site selection may relate to social associations in
112 captive populations, where group housing is the norm. Observations of zoo-
113 housed orangutan nesting behavior provide an opportunity to note social
114 dynamics that may not be revealed in the study of wild populations.

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

124 This study examines two cases in which anecdotal observations previously
125 suggested that patterns of nesting behavior could be useful to the care and
126 management of a population of zoo-housed orangutans. First, we hypothesized

127 that nearest neighbor associations based on the proximity of night nests could
128 effectively inform decisions about housing options based on orangutan
129 preferences. We also predicted that as in wild orangutan populations, where
130 orangutan nests cluster in specific areas within even extremely homogeneous
131 habitats and night nest site re-visitation is common (Bastian, unpublished results),
132 night nest locations chosen by orangutans at Smithsonian's National Zoological
133 Park (NZP) would show consistent patterns. Our results are analyzed in relation to
134 a survey about zoo-housed orangutan nesting behavior from 31 participating
135 facilities across AZA.

136

137 [INSERT TABLE 1 HERE]

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166 staff the ability to choose from multiple housing configurations depending on
167 which and how many individual orangutans were given access to one another on a
168 particular night. Each room included a water source: a licker (a small metal pipe
169 that when depressed provides a source of drinking water), waterfall, small pool, or
170 combination of these. Artificial trees were found in all but two (rooms 1 and 4) of
171 the six enclosures and all had some sort of elevated platform. Ceiling height
172 varied across rooms, ranging from 2.4m (8ft) in room 1 and 5.2m (17ft) in room 4
173 to 7m (23ft) in rooms 2 and 3 and 7.6m (25ft) in rooms 5 and 6. With the
174 exception of rooms 1 and 4, rooms were visible from the public area.

175 Keepers could easily transfer orangutans to or from outdoor yards and the
176 Orangutan Transit System (or “O-line”) through elevated chutes running from
177 rooms 3, 5 and 6 of GAH and a holding room at TT. Orangutan yards at both
178 GAH and TT consisted of grassy areas with access to a tower leading to the O-
179 line. The O-line, a series of eight 13.7m (45ft) high towers, connected by 16.6m
180 (50ft) high plastic-coated steel cables, allowed the orangutans to travel via the
181 yards and across the cables between buildings, so they could nest at either
182 location if given access by keepers. Only one adult female, Lucy, has never
183 chosen to travel across the O-line since its construction in 1995, so her nests were
184 found only at GAH.

185 The indoor orangutan area at TT consisted of a primary living space - a
186 single room of approximately 67.4m² (725 ft²) with a 5.2m (17ft) ceiling,
187 provisioned with fire hose and other climbing opportunities, shelving at various

188 heights, a holding enclosure, and room designed for public research
189 demonstrations (Figure 2).

190

191 [INSERT FIGURES 1 & 2 HERE]

192

193 *2.3 Data Collection and Analysis*

194 For purposes of this study, we defined a "nest" as an orangutan-made
195 structure formed by manipulating leaves, hay, or other material for use as a
196 platform for resting or sleeping. As the focus of this study was on night nests, data
197 at NKP were recorded twice each day, once in the evening as the building was
198 closed by departing keepers (1630-1830h, depending on season) and again the
199 following morning at first staff arrival (0630-0700h). The study covered the
200 period July 2014 - July 2015. Emphasis was placed on recording night nest
201 location preferences, nest fidelity (as opposed to abandonment in favor of another
202 nest), and the proximity of a nest to the nesting animal's nearest neighbor. From
203 February - July 2015 we collected daytime nearest neighbor data within groups of
204 socially housed NKP orangutans, focusing on individual animals across four time
205 periods spanning the full keeper day (e.g., 0700-0900h, 0900-1100h, 1100-1300h,
206 1300-1500h). Within those periods, data was recorded on the focal animal every
207 five minutes over a 30 min interval. Rotating among focal animals to ensure a
208 balanced distribution of data collection for all orangutans, we collected data
209 between two to three days a week for a total of forty-one hours over 38 days.
210 Both daytime and night nest nearest neighbor data were collected for associations

211 of individuals within 10m (32.8ft) rather than within the 50m distance used in
212 wild studies due to the space restrictions of captive environments. These data
213 were then used to produce proximity matrices based on nearest neighbor data.
214 Due to staffing and schedules, priority was given to nests and activity at GAH,
215 with opportunistic data collected at TT.

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

225 We also disseminated a survey throughout AZA to document generally the
226 nesting habits and location preferences observed among zoo-housed orangutans at
227 30 other facilities. Analysis of nesting behaviors across zoos excluded individual
228 orangutans not yet engaging in nest building behavior.

229 Contrasts of categorical NZP data were analyzed using Chi-square
230 Goodness of Fit tests. SOCPROG Compiled v. 2.7 (Whitehead, 2009) was used to
231 analyze data on the social structure and associations among NZP orangutans. We
232 defined the NZP social "group" on a given evening as all orangutans with access
233 to the same or adjacent enclosures, since individual orangutans in adjacent

234 enclosures with mesh access could choose to spend time in closer proximity to
235 one another than to individuals housed in the same enclosure. Social network
236 analysis statistics were performed on composite matrices within SOCPROG, the
237 output of which were used to generate sociograms using NetDraw 2.160
238 (Borgatti, 2002) in order to visually present social relationships among individual
239 orangutans using each measure of nearest neighbor association.

240 The Dietz R matrix correlation test (Dietz, 1983) using 1000 permutations
241 implemented in SOCPROG 2.7 was used to determine whether we were justified
242 in creating composite matrices based on NZP nearest neighbor and group
243 composition data for day and night nest methods of assessing nearest neighbor
244 associations. A Dietz R-test was also used to analyze matrices generated from
245 day and night nest nearest neighbor methods. Dietz's (1983) R-test is the same as
246 a Mantel test but the Dietz test is analogous to Spearman's rank correlation
247 coefficient with values of the matrices replaced by their ranks, so the Dietz test is
248 much less strongly affected by outlying values than the Mantel test. All tests were
249 two-tailed and alpha was set at 0.05.
250

251 **3. Results**

252 3.1 *Nest Location Preferences*

253 We recorded a total of 851 night nests. Although NZP orangutans were
254 most often found in a *different nest* the next morning, indicating low nest fidelity
255 ($\chi^2 = 41.51$, $df = 1$, $p < 0.001$), the data indicate high room fidelity, as they were
256 most often found in a nest in the *same room* as the last nest recorded the previous
257 day ($\chi^2 = 4.27$, $df = 1$, $p = 0.046$). Chi-square analyses revealed that within GAH,
258 in nights during which multiple rooms were available, Bonnie ($\chi^2 = 58.48$), Kyle
259 ($\chi^2 = 54.24$), and Iris ($\chi^2 = 23.93$) showed a clear preference for off-exhibit room
260 4 ($p < 0.0001$), whereas on-exhibit room 5 was preferred by Batang ($\chi^2 = 81.93$)
261 and Lucy ($\chi^2 = 22.56$) and on-exhibit room 5 was preferred by Kiko ($\chi^2 = 34.37$),
262 $df = 1$, $p < 0.0001$.

263 Significantly more night nests were made on the ground at both GAH (χ^2
264 $= 523.62$, $df = 1$, $p < 0.001$) and TT ($\chi^2 = 89.04$, $df = 1$, $p < 0.001$), although nests
265 on shelves and in hammocks were also occasionally observed and elevated nests
266 were built more frequently at GAH than at TT ($\chi^2 = 6.37$, $df = 1$, $p = 0.012$). Of
267 the 31 zoos surveyed, including NZP, 100% reported giving their orangutans
268 opportunities for building elevated nests, 87% of which reported at least
269 occasional nesting above ground, although survey responses indicate that ground
270 nesting is most typical in a zoo setting.

271 Over time at NZP, we observed all four female orangutans, but no males,
272 partially plug water lickers at one time or another and all orangutans nesting in
273 close proximity to them. Our study observations confirmed that at NZP, all six

274 orangutans showed statistically significant (Chi-square analyses, $p < 0.05$)
275 preferences for nesting in rooms with water lickers over those with alternative
276 water sources but without lickers.

277 Previous studies have shown that zoo-housed orangutans are known to
278 partially plug water licker mechanisms with a variety of materials to create a
279 constant flow of water (Shumaker et al., 2011). In our nest behavior survey, 28 of
280 31 AZA facilities reported that one or more individual orangutans regularly
281 partially plug lickers, most individuals also place objects under the water stream,
282 amplifying the sound in many cases.

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

286

287 3.2. *Night Nest Sharing*

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

295

296 3.3. *Orangutan Social Networks*

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

307

308 [INSERT FIGURE 3 HERE]

309 4. Discussion

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

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

331 perceived by the orangutans, something for which additional study may be
332 warranted.

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

340 Of potential importance to captive group management strategies, our
341 comparison of daytime nearest neighbor data with observations of night nesting
342 proximity among members of the NZP group reveals that overall, nesting
343 information accurately predicted preferential social relationships. The few visual
344 differences in the relative strength of dyadic associations between the sociograms
345 in Figure 3 can be explained based on differences in daytime vs. nighttime
346 orangutan housing arrangements. For example, the stronger relationship indicated
347 between Lucy and Batang at night may be explained by the fact that Lucy had
348 more frequent opportunities to associate with Batang at night at GAH than during
349 the day when Batang had more physical location opportunities. Batang was a
350 frequent O-line traveler when given the opportunity, while Lucy never traveled,
351 giving Batang and others in her group access to areas (including TT) where Lucy
352 would not go. Further, the weaker relationship between Iris and Batang at night is
353 consistent with the authors' observations, recorded for another study, that Iris is

354 primarily responsible for maintaining close proximity to Batang when the pair is
355 housed together during the day. At times when they were housed together at
356 night, it could be that for Iris, rest is prioritized over social interaction with
357 Batang, giving Batang the opportunity to select a nest site away from Iris without
358 being pursued. This specific social dynamic and the differences noted between
359 daytime and nighttime relationships present the opportunity for further study.
360 Nesting nearest neighbor data may therefore be a highly valuable, yet overlooked
361 predictive tool.

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

371 Although observations of approach-leave interactions can be used to
372 calculate the Hinde Index, a calculation determining which member of a particular
373 dyad is most responsible for maintaining proximity (Hinde & Atkinson, 1970),
374 collection of approach-leave data can be cumbersome and requires considerable
375 time outside normal staff activities. We therefore propose that the night nest
376 nearest neighbor method for detecting social relationships described in this paper

377 is a viable proxy for traditional daytime nearest neighbor data, and perhaps a
378 superior method of identifying preferred dyadic social relationships in zoos,
379 where observations of night nest nearest neighbors can be recorded by staff during
380 the course of their normal husbandry routine.

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

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

396

397 **5. Conclusions**

398 Our study of the night nesting behavior of six adult orangutans at NZP,
399 together with results of a survey of 30 additional AZA member zoos, revealed

400 insights into nest location preferences, sociality, and innovative behavior in the
401 nesting context. Night nest room location preferences followed consistent
402 patterns, including a strong preference for ground nesting. Orangutans at a
403 majority of AZA facilities surveyed, including NZP, have at least one orangutan
404 who nests in close proximity to plugged water lickers.

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

410

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418 zoos from across the AZA.

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