

Chapter 3

SOCIAL PROXIMITY IN THE ORANGUTANS OF SUAQ BALIMBING AND KETAMBE

Introduction

In Chapter 2: The Content of Orangutan Cultures, consideration of information from eight orangutan study sites revealed that the number of cultural variants exhibited at a given site is independent of the observation intensity at that site. One implication of this finding is that other factors determine the variation in cultural complexity between orangutan populations. Social tolerance has been proposed as a key factor in the social learning that could lead to cultural variation (Coussi-Korbel and Fragaszy, 1995; Fragaszy and Visalberghi, 1990; van Schaik et al., 1999), and by definition social learning can only take place when there is social proximity. Indeed, van Schaik et al. (2003a) showed that time spent in association was correlated with the extent of the local repertoire of cultural behaviors at each site for both orangutans and chimpanzees. Are opportunities for social learning the crucial factor in differential levels of cultural complexity? Given the limitations to field observations, what can we discover about such

opportunities in wild populations? Which aspects of sociality are relevant to the distribution and maintenance of cultural behaviors within a population?

Both chimpanzees and orangutans have behavioral variations that are considered cultural (Whiten et al., 1999, 2001; van Schaik et al., 2003a). Sumatran orangutans (*Pongo pygmaeus abelii*) at Suaq Balimbing have more cultural behavior variants than at Ketambe (van Schaik et al., 2003a; see Chapter 2). Most cultural behaviors that differ between these populations, including two forms of feeding tool-use, may require close proximity for social learning. Within Suaq Balimbing, the southern/central females specialize in tree-hole tool use to a greater extent than the northern females (van Schaik et al 2003b). In this chapter, I will compare several measures of sociality, including mean party size, percent time in parties, cumulative number of partners per day and indices of partner diversity, for the adult females of Suaq Balimbing and Ketambe. Higher scores on these measures of sociality for the orangutans at Suaq Balimbing (particularly the southern/central Suaq Balimbing females) would support an important role for very close observational learning in the spread and maintenance of tool-use behaviors at Suaq Balimbing.

Opportunities for social learning, which allow an innovation to spread and be

maintained throughout a population, are affected by several factors. Mean party size (as used in Fox, 1998; van Schaik et al., 2003b), though easy to calculate, is only a crude indication of sociality. It confounds the time spent in parties (usually defined for orangutans as having at least one conspecific within a 50 meter radius of the focal individual) and the number of possible social partners in one measure. Time spent at $\leq 50\text{m}$ distances may not always correlate with time spent in much closer proximity where details of behavior might be perceived more clearly. A separate look at the percent of time spent in parties clarifies the portion of an orangutan's daily activity which may include opportunities for social learning, but does not address such factors as the diversity or frequency of dyadic interactions. Calculating the number of different social partners observed with a focal individual provides further insight into the opportunities for information exchange within a population.

Another issue of concern is how time spent in parties is distributed between possible social partners. Some researchers have proposed that orangutan sociality is limited by environmental constraints (Mitani et al., 1991; Sugardjito et al., 1987). Orangutans might gain the same benefits that other anthropoid primates apparently receive from higher levels of sociality; they

are generally less social mainly because of the costs of obtaining adequate food and other resources that may be sparse and widely distributed. Sugardjito, te Boekhorst, and van Hooff (1987) found that orangutan social group size is related to fruit availability, and suggest that opportunities for social learning are an important factor promoting orangutan social grouping, particularly for contacts between younger orangutans. If limited resources restrict orangutan's time spent in parties, more even distributions of time with diverse partners would promote the spread of novel behaviors through a population, by allowing innovations and rare behaviors to be observed by more possible learners for a given amount of social time.

The performance of certain cultural behaviors may vary according to social partners within a population. Studies of social transmission in Japanese macaques (*Macaca fuscata*) show that the innovator's most frequent social partners (her peers and matriline) were the first to adopt a novel food-processing behavior (Kawamura 1959, reviewed in Nishida 1987).

For a thorough comparison of orangutan populations, it is necessary to use comparable measures of sociality in observations of different sites. This study undertakes an exploration of social learning opportunities, using a uniform methodology for data collection on two wild orangutan populations,

Ketambe (KTB) and Suaq Balimbing (SQB), both on Sumatra. Mean party size for individual female orangutans at Suaq Balimbing correlates with propensity to use tree-hole tools in the same habitat (van Schaik et al., 2003b), and Suaq Balimbing has two distinct social clusters among females (Singleton and van Schaik 2002), so I consider females from these clusters separately for some analyses.

The importance of proximity to social learning

Which behavioral variants can be socially learned may depend on proximity of social partners. Some behavioral variants are easy to observe from a distance, whereas others might require closer scrutiny for successful emulation. Most analyses of orangutan social behavior look only at the broadest possible definition of association, generally proximity between independent conspecifics of 50m or less. By this measure, there is little difference between KTB and SQB. In fact, these two sites represent the upper end for both cultural repertoire and sociality among orangutans (van Schaik et al., 2003a).

Certain behaviors probably require closer observation for successful social transmission. Obviously offspring have opportunities to observe their mothers closely, but a complex behavior would be more likely to spread and

be maintained throughout the population if independent individuals also had the opportunity to observe one another closely while performing the behavior (or infants or juveniles could closely observe the independent social partner of their mothers).

I recorded information for independent orangutans approaching within 50m, 10m and 2m of the focal (see Methods, below). The different proximity classes were selected because of their perceived “value” in social learning. Each proximity class also indicates a different level of social tolerance, in that risk of injury from agonistic interactions is higher if there is less distance between pursuer and pursued.

At 50 meters apart, orangutans are likely to be aware of one another’s presence (this is also about the distance at which a human observer notices another orangutan during a focal follow, pers. obs.). Associations at 50 to 10 meters would be indicative of at least some social tolerance as the orangutans are likely to be aware of the other’s proximity and could attempt to lessen it. The orangutans (and the human observer) may be aware of roughly what the other orangutan is doing, and will probably hear all but the softest vocalizations from the other, but may not be able to see in great detail *how* the other is doing whatever it is doing. This distance was used in previous

party size data at Suaq Balimbing (Fox, 1998; van Schaik et al., 2003b).

At 10 meters the orangutans would be able to see one another fairly well and readily observe one another's behaviors in some detail (provided they are facing one another and the foliage is not obstructing the view too severely). Orangutans less than 10m apart are likely to be in the same tree crown, and the potential for co-feeding (and therefore feeding competition) at this distance indicates greater social tolerance.

At 2 meters or less, orangutans are generally within reach of one another. They should be able to observe one another's behavior quite clearly, distinguishing even very subtle aspects of technique (e.g. what type of grip is used when an object is in the hand). Not only co-feeding, but also food sharing or food "theft" (tolerated or otherwise) is possible. When observers report "play," the participant orangutans are almost always within two meters of one another. Relaxed interactions at this distance are likely to indicate a high degree of social tolerance.

Proximity and social learning opportunities for specific behavior variants

In the Chapter 2, nine very likely cultural behaviors were described which reached customary or habitual frequencies in either the Ketambe (KTB) or

the Suaq Balimbing (SQB) orangutan population, but not in both (summarized in Table 3.1).

Only two of these behavioral variants are clearly observable from more than 10m away. The **symmetric scratch** at SQB is such a large and dramatic movement that it is probably easy to learn observationally up to 50m away. The **sun covers** at KTB are likewise obvious at 50m, particularly because they are only constructed when the orangutan is building a nest in the sun, with limited surrounding foliage.

Three behaviors seen at SQB and two at KTB probably require a distance of no more than 10m for successful observational learning. **Twig biting**, seen only at SQB, involves handling and biting small twigs before placing them in the nest lining. The **nest raspberry** (SQB) is sometimes so quiet that it can be difficult to hear over the shuffling noises that accompany nest building (especially in videotapes, see Chapter 4). The function of the **branch scoop** (SQB) is probably not obvious unless you can see the water coming off the branch's leaves as it is pulled from the tree hole (tree-holes themselves are not generally obvious from a distance). Similarly, the function of an **autoerotic tool** (KTB) would not be obvious unless one could clearly see what part of the body the orangutan was stimulating with a tool. The

function of **leaf padding** (KTB) is only clearly obvious when the thorns or spines being protected against are seen.

The two types of feeding-tool use seen only at SQB are likely to require very close observation for successful learning. The insects agitated by **tree-hole tool-use** may be visible at distances of 10m, but the technique of actually getting the tool into the tree hole is hard to see, as the orangutans of SQB generally have the tool in their mouth, with their head and body obscuring most of the tool and the tree-hole itself. **Seed-extraction tool-use** involves the modification of even smaller twigs (Fox et al., 1999) and the seeds thus acquired are only rarely visible to human observers at approximately 10m distance from the orangutans. In video recordings of this behavior, orangutans were sometimes seen to pause in their own foraging activities and closely approach other orangutans who are engaged in **seed-extraction tool-use**, then watch the tool-using orangutan intently (M. Merrill, unpub. data).

The **tree-hole tool-use** behavior is especially noteworthy for two reasons. First, there is no clear ecological reason why orangutans at Ketambe fail to practice this form of tool use (van Schaik et al., 2003a); orangutans at Ketambe do extract insects and honey from tree holes, but they never use probe tools to do so. Second, a previous study at Suaq Balimbing showed

intra-population variation in the degree of specialization on this behavior. This study found that adult females with home ranges focused in the center of the study site had higher mean party size and were more likely to engage in **tree-hole tool-use** than the adult females whose home ranges were toward the north of the study area, even where their home ranges overlapped (van Schaik et al., 2003b). This correlation between degree of **tree-hole tool-use** specialization and mean party size suggests that opportunities for social learning during development are an important factor in **tree-hole tool-use** specialization within the population.

In this chapter, I will compare the opportunities for social learning at Suaq Balimbing and Ketambe, by investigating measures of the time spent in social proximity (within 50m, 10m and 2m of independent conspecifics) and the number of social partners encountered by focal animals at different proximities. Based on the number of cultural variants requiring close proximity for observational learning, the orangutans at Suaq Balimbing are predicted to have more time and more social partners in closer proximity than the orangutans at Ketambe.

Methods

Study sites

Research was conducted at Suaq Balimbing and Ketambe, two established research sites in Mount Leuser National Park, on the island of Sumatra (Aceh province, Indonesia – see Table 3.2, and figure 2.1 from Chapter 2). Both sites contained populations of unprovisioned wild Sumatran orangutans, *Pongo pygmaeus abelii*. Results are reported only for adult females with dependent offspring. Adult females were the most common focals, and they vary less in size and ecological considerations than other age/sex classes, reducing the uncertainty caused by small sample sizes.

Research for this project at Ketambe was conducted from May 1999 to May 2000. Ketambe orangutans were first studied by Rijksen in 1971, and researchers have maintained orangutan observations at Ketambe since that time. Some ex-captive orangutans were introduced to the Ketambe population in the 1970s. One of these, a female named Binjei, successfully raised some offspring, including the now adult female Ans (both of these females are used as focals in this study – see Chapter 5 for more information on these orangutans).

Research for this project at Suaq Balimbing took place from March to September 1999. Carel van Schaik began orangutan research at Suaq Balimbing in 1992, and study there continued until the site was closed in 1999 (at which time research was halted for security reasons due to illegal logging and political turmoil in the region). For certain measures of sociality at 50m and 10m, additional data provided by Carel van Schaik were included, to increase total observation hours for some Suaq Balimbing individuals so they were comparable to those for the Ketambe focal individuals (see Table 2). In these cases, I used the most recent data collected for observation days during or prior to my project. For some analyses, northern and southern/central females from Suaq Balimbing are considered separately, based on the clustering reported by Singleton and van Schaik (2002, see Table 2).

Identical data sheets and methods were used for focal orangutan follows at both sites for the Orangutan Cultures Project. The data sheets and collection procedures for data on social encounters at less than 50m and less than 10m provided by van Schaik were virtually identical to the methods used for this study. Mohammed Isa and Nuzuar S. Hut assisted with data collection at Ketambe. Bakrijas, Nuzuar S. Hut, Abdusamad, Asril, Azhar, Carel van

Schaik, Irma, Ishak, Mukudis, Nur, and Zulkifli assisted with data collection at Suaq Balimbing. The three primary assistants (Mohammed Isa, Nuzuar S. Hut and Bakrijas) were trained by Michelle Merrill, and worked with one another and with the other researchers and assistants to support consistency in data collection procedures.

Only independent individuals were followed for focal data (including adolescents, sub-adults and adults of both sexes), but only adult females were included in these analyses (see Table 3.3). For social interactions, observers recorded the start and end of any time when another independent individual was within 50, 10 and 2 meters of the focal individual. The age/sex class and name of the other was recorded whenever it could be determined. For 10 meters and 2 meters, observers also recorded which individual actively approached and which actively left proximity, and often made notes regarding the behavioral context. For details on how inconsistencies or discrepancies in the datasheets were handled, see Appendix I. The different proximity classes were chosen primarily because of their relevance for social learning and the perceived level of social tolerance for each distance (see Introduction, this Chapter).

Measures of sociality

One measure of sociality is **mean party size (MPS)**, computed as follows

$$\text{MPS} = \frac{\sum \mathbf{n}_p}{\mathbf{a}} + 1$$

where **n** is the number of minutes in proximity with an individual, **p** is the number of individuals who were ever recorded at that proximity with the focal, and **a** is the total number of active observation minutes for the focal (Fox, 1998).

The MPS is an efficient way of summarizing the sociality of an individual, and the mean of all MPS scores is a concise measure of the sociality of the population. However, it does eliminate some possibly useful distinctions. For instance, an individual who is in proximity with another independent individual most of the time (but only one at a time) may have a lower MPS than an individual who rarely has any social partners, but the few times she does, she has many others in proximity simultaneously.

For each distance class ($\leq 50\text{m}$, $\leq 10\text{m}$ and $\leq 2\text{m}$), I compare MPS scores for the females at SQB and KTB using the Mann-Whitney (Wilcoxon) test. To compare the females as three populations (KTB, SQB N, and SQB S/C) I use the Kruskal-Wallis test.

Next oldest offspring. These offspring are considered independent individuals, so they were included in the social data. However, social interactions between mother and independent offspring are less likely to produce opportunities to spread and maintain novel behaviors throughout a population. If the bulk of social interactions were between mothers and these offspring, social learning opportunities would be mainly through vertical transmission (leading to uniformity within matriline and variation between matrilines comparable to the variation between populations).

One confounding issue for investigating the role of the next youngest offspring in social measures was the fact that Suaq Balimbing had been a study site for a much shorter duration than Ketambe, so the lineages were not as well known. To accurately compare the two sites, only females whose youngest independent offspring were known were considered.

For each distance class, I compare MPS scores (without the next youngest offspring) for the females at SQB and KTB using the Mann-Whitney (Wilcoxon) test. To compare MPS scores (without the next youngest offspring) for three populations I use the Kruskal-Wallis test.

Percent time in parties is calculated by dividing the number of minutes in

which the focal has one or more social partner within the given distance category (including independent offspring) by the total observation time for that focal. For this measure, I was not able to use the data provided by C. van Schaik. For each distance class, I compare percent time in parties at that distance for the females at SQB and KTB using the Mann-Whitney (Wilcoxon) test; when SQB N and SQB S/C are considered separately, I use the Kruskal-Wallis test to compare percent time in parties for the three populations.

Cumulative number of partners is a calculation of the minimum number of different individuals a focal had encountered (including independent offspring) after a given number of days of focal follows. In determining the cumulative number of social partners, individuals who were not positively identified were assumed to be the same as the next or previous positively identified individual of the same age/sex class.

I took two different approaches to compare the cumulative number of partners for focal females at each site. I used the Mann-Whitney (Wilcoxon) test and the Kruskal-Wallis test to compare the scores for females after a specific number of observation days (day 10 and day 15 for the $\leq 50\text{m}$ and $\leq 10\text{m}$ distance classes, day 6 for the $\leq 2\text{m}$ distance class). I also used a

signed-rank test (with continuity correction applied) to compare the mean cumulative number of partners by day for each possible pair of sites (KTB vs. SQB, KTB vs. SQB N, SQB N vs. SQB S/C, and KTB vs. SQB S/C).

Partner diversity or “evenness” I calculated the Shannon-Weaver index of diversity (H' , Zar 1999) for each focal, at each site, in each proximity class, to determine how evenly the focal divided her time among identified social partners (instances where the social partner was not positively identified were not included in this analysis). Zar (1999) indicates that H' is influenced by the number of categories. As there were more identified possible partners at Suaq Balimbing than Ketambe, I also computed an evenness score for each focal (J' , also known as “relative diversity”) that factors out the number of categories. J' is often an overestimate of population evenness (Zar 1999). I used the same population-wide number of categories at Suaq Balimbing when calculating the J' scores for northern and southern/central Suaq Balimbing females. For each distance class, I compare H' and J' at that distance for the females at SQB and KTB using the Mann-Whitney (Wilcoxon) test; when SQB N and SQB S/C are considered separately, I use the Kruskal-Wallis test to compare H' and J' for the three populations.

Results

Mean party size

Results for mean party size analysis are presented in Table 3.4-3.7. Comparison of MPS at Ketambe and Suaq Balimbing showed significant differences at $\leq 2\text{m}$ distances. When the northern and southern/central females were considered separately, the SQB S/C females had significantly higher MPS than the SQB N or KTB females at $\leq 50\text{m}$ distances. The KTB females had significantly lower MPS at $\leq 2\text{m}$ distances than the SQB S/C females. The pattern of significant results was the same whether the next youngest offspring was included (Table 3.4 and 3.5) or not (Tables 3.6 and 3.7).

Percent time in parties

Figure 3.1 shows the mean percent time spent in parties, by nearest neighbor distance, for Ketambe, the combined Suaq Balimbing population and the separate northern and southern/central Suaq Balimbing females. All percent-time-in-parties data is based on data from this study without additional data provided by van Schaik. Suaq Balimbing females spent significantly more time with partners at $\leq 2\text{m}$ distances than Ketambe females, and southern/central Suaq Balimbing females spent significantly more time with

partners at $\leq 10\text{m}$ and $\leq 2\text{m}$ distances than Ketambe or Suaq Balimbing northern females (Tables 3.8 and 3.9).

Cumulative number of partners

The cumulative minimum number of partners for each focal by observation day (at $\leq 50\text{m}$, $\leq 10\text{m}$ and $\leq 2\text{m}$ distances) are shown in Figures 3.2a-f. The cumulative minimum number of partners for each focal on days 10 and 15 (for the $\leq 50\text{m}$ and $\leq 10\text{m}$ distances) and day 6 (for the $\leq 2\text{m}$ distances) were compared between sites (Table 3.10). The southern females at Suaq Balimbing had a higher mean number of partners for those days in all distance classes. Differences were significant only on day 15 for the $\leq 10\text{m}$ distances (for KTB, SQB N, and SQB S/C) and on day 6 for the $\leq 2\text{m}$ distances.

The mean cumulative number of partners by observation day for Ketambe and Suaq Balimbing females were compared in a signed rank test (with continuity correction applied, Table 3.11, Figures 3.3a-c). For the $\leq 50\text{m}$ and $\leq 10\text{m}$ distance classes, the difference between means was compared for the first 14 days of observation. Pluis from KTB and Tevi from SQB were excluded from these means because they did not have sufficient observation days. For the $\leq 2\text{m}$ distance class, the means for the first 6 observation days

were compared. Pelet was excluded from these means, as she had insufficient days based on data from this study without the additional data from van Schaik.

The three possible pairs of Ketambe, Suaq Balimbing northern and Suaq Balimbing southern/central females mean cumulative number of partners by observation days were likewise compared (Table 3.12, Figures 3.4a-c). All comparisons showed significant differences except for KTB – SQB N at $\leq 2m$.

Partner diversity

For every distance class the Suaq Balimbing population had higher average indices of diversity and evenness than the Ketambe population. In all but one case (H' at 10m) this difference was not significant (Wilcoxon, Table 3.13). In these diversity scores, northern Suaq Balimbing females often scored lower than the Ketambe females, with southern/central Suaq Balimbing females scoring much higher. In all but one case (J' at 50m) this difference was significant (Kruskal-Wallis, Table 3.14).

Discussion

Of the cultural variants that differ between Suaq Balimbing and Ketambe,

Suaq Balimbing has more requiring an estimated minimum learning distance of 10m or 2m (Table 3.1). In every measure of sociality, the combined Suaq Balimbing score was higher than Ketambe. These differences were significant in almost all cases at the $\leq 2\text{m}$ distances, except for the diversity measures. This strongly supports an important role for very close observational learning for the tool-use behaviors at Suaq Balimbing.

The southern/central females at Suaq Balimbing specialize in tree-hole tool use to a greater extent than the northern females (van Schaik et al., 2003b). Again, in every measure of sociality, the southern/central Suaq Balimbing females scored higher than the northern females or the Ketambe females. These differences were significant in all cases at the $\leq 2\text{m}$ distances, and often at $\leq 50\text{m}$ distances as well. The greater social tolerance in the southern/central Suaq Balimbing females may be a result of the high density of the most important food tree (*Tetramerista glabra*) in the south of the study area (Singleton and van Schaik, 2001). The consequences of their social tolerance include greater opportunities for social learning that may have resulted in their tool-use specialization.

The pattern of difference in mean party size between populations in this study shows that Suaq Balimbing females have higher mean party sizes than

Ketambe females, especially at $\leq 2\text{m}$ distances. There were striking differences in MPS between the southern/central and northern Suaq Balimbing females, with the northern Suaq Balimbing females having a lower average MPS than even the Ketambe females at $\leq 50\text{m}$ and $\leq 10\text{m}$ distances. One difference that seemed apparent between the two sites was the apparently greater tendency of females at Ketambe to spend time with the next oldest (usually sub-adult) offspring, relative to their other social interactions. While this seemed to hold true (decreasing the P-value of differences between sites), it did not have an impact on the pattern of which inter-population differences were statistically significant.

The mean party size measure may confound the size of parties with the time spent in parties. Individuals who are often in larger parties but who do not spend as much total time in parties may not have as much actual opportunity to learn socially from experienced models of a behavior, as it is unlikely that an individual in a group of five can adequately observe the behaviors of all five social partners simultaneously. Percent time in parties may give a better indication of observation opportunities. By this measure, as with MPS, the females at Suaq Balimbing have more time in proximity to possible models (particularly at $\leq 2\text{m}$ distances) than those at Ketambe, especially the

southern/central Suaq Balimbing females.

The southern/central females of Suaq Balimbing encountered different social partners at a higher rate than females in northern Suaq Balimbing or Ketambe. This means that novices are more likely to contact innovators or experienced early adopters. They have more models to observe if social learning plays an ongoing role in improving the performance of complex behaviors, which is probably important given the observations of experienced seed-extraction tool-users pausing in their feeding to approach and closely observe others performing this behavior. The results showed that differences between Suaq Balimbing south/central females and the other populations were increasing with increasing number of observation days for number of unique social partners encountered at $\leq 50\text{m}$ and $\leq 10\text{m}$ distance classes. Longer-term study might reveal even more significant differences between populations at 20 or 30 days of observation for each focal, and might reveal even more striking differences at $\leq 2\text{m}$ distance.

Van Schaik et al. (2003a) found that cultural repertoire size in orangutans was not correlated with either time spent resting (an indicator of free time) or time spent feeding on cambium (an indicator of food scarcity, when compared to repertoire of feeding-related variants), but that repertoire size

was related to time spent in association for orangutan and chimpanzee populations. However, higher numbers of partners or more time spent with nearest neighbors less than 50m away does not necessarily translate into more or better opportunities to learn. Finer distinctions of proximity reveal differences between Ketambe and Suaq Balimbing orangutans, two populations at the higher end of both sociality and cultural repertoire size. How a focal individual's social time is distributed among social partners can vary tremendously. Analysis of the percentage of each focal individual's social time spent with different partners showed that southern/central females at Suaq Balimbing distribute their time more evenly than northern females or the females at Ketambe. This means, especially for behaviors that are performed less frequently, Suaq Balimbing's southern/central females have a better relative opportunity for the behaviors to spread from innovators and experienced learners to novices. This might be especially critical for tree-hole tool-use, where opportunities to perform or learn the behavior are widely distributed in space and time.

So how are northern Suaq Balimbing females learning feeding-tool use and the other behaviors characterized as customary throughout the population if their sociality scores are even lower than those at Ketambe? The two social

clusters at Suaq Balimbing are interconnected, with occasional contacts between females and contacts with the same males by females of both groups. One likely explanation is that behaviors spread rapidly and are maintained in the southern/central cluster, and their ubiquity in that social network ensures their endurance and spread throughout the interconnected population. A more detailed study of the networks of dyadic social interactions of all age/sex classes in the Suaq Balimbing population should provide further insight to this question.