ORANGUTAN CULTURES?

TOOL USE, SOCIAL TRANSMISSION AND POPULATION DIFFERENCES

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by

Michelle Yvonne Merrill

Department of Biological Anthropology and Anatomy
Duke University

Date:_________________________

Approved:

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Carel P. van Schaik, Supervisor

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
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This dissertation considers the evidence for orangutan (*Pongo pygmaeus*) cultures. Eight long-term orangutan research sites were compared using the geographic approach. Correlation between rare behavior count and observation intensity showed innovation is fairly consistent across sites. Lack of correlation between observation intensity and number of cultural behaviors indicates that something else explains this variation. Cultural behaviors were classified into subsistence skills, weal skills, reference variants, display variants and those whose function remains unknown. Types of behaviors that vary culturally in orangutans were similar to those reported for chimpanzees (*Pan troglodytes*).

Further evidence for the role of social learning and proximity is based on data from focal animal follows of wild orangutans at Ketambe and Suaq

Balimbing on Sumatra. Suaq Balimbing had more cultural variants requiring close proximity for observational learning, including tool use. Adult female orangutans at Suaq Balimbing (particularly in the sub-group with greater tree-hole tool-use specialization) spent more time with independent conspecifics and had more diverse social partners at close proximity.

Behaviors related to nest building were examined in detail. Data from nests built with or without the nest raspberry (ubiquitous at Suaq Balimbing, absent at Ketambe) were investigated. Duration of nest-building activities is related to nest raspberry production. Nest raspberries were not related to nearest neighbor proximity or nest position; their adaptive function is not apparent. Adult females at both sites tended to be alone (no independent conspecifics within 50m) more often when building a night nest than during the rest of the active day, but this trend was stronger at Ketambe.

Evidence for vertical social transmission of a limited traditional behavior was based on published work, interviews with previous field researchers, and videotape and data collected during fieldwork at Ketambe. The persistence of unusual behaviors within rehabiltant matrilines, and the failure of these behaviors to spread throughout the wild population, may result from

selectivity in social learning.

The presence of complex cultural variation in orangutans and chimpanzees suggests that the capacity for such behavior was present over 12 million years ago, in the last common ancestor of the great apes.

DEDICATION

For Erik, without whose incredible patience, understanding and support I could never have done this, and for the orangutans Abby, Agus, Andai, Ani, Ans, Arno, Ati, Beki, Bestel, Binjei, Brus, Budi, Caca, Chris, David, Diana, Doba, Elisa, Hanes, Herdi, Ida, Karen, Mira, Musa, Ngon, Novi, Olly, Pelet, Pluis, Sela, Tevi, Tomi, William, X, Yet, Yinta, Yenni, Yop, Zuar and especially Payung – hang in there, guys!

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Table 1.1 Mammalian taxa exhibiting potentially socially transmitted adjustable behaviors that vary between wild populations.

TAXON	VARIABLE BEHAVIOR	REFERENCES
Chimpanzee *Pan troglodytes*	Tool use for foraging (e.g. nut-hammer, ant-dip)	Reviewed in Whiten et al., 2001, 2003, also Boesch, 1993; McGrew, 1992; McGrew, 1994b; Sugiyama, 1993; Sugiyama, 1994; Boesch et al., 1994; Fay and Carroll, 1994; Joulian, 1994; Boesch, 1996; McGrew et al., 1997; Sugiyama, 1997
	Tool use for grooming or comfort (e.g. leaf-napkin, seat-vegetation)	Reviewed in Whiten et al., 2001, 2003, also Boesch, 1993; Boesch and Boesch, 1993; Sugiyama, 1993; McGrew, 1994a; McGrew, 1994b; Sugiyama, 1994; Boesch et al., 1994; Fay and Carroll, 1994; Joulian, 1994; Boesch, 1996; McGrew et al., 1997; Sugiyama, 1997
	Allogrooming techniques	Reviewed in Whiten et al., 2001, 2003, also McGrew and Tutin, 1978; McGrew, 1994a; Boesch, 1995; Boesch, 1996; De Waal and Seres, 1997
	Attention-getting object interaction (e.g. buttress-drumming, leaf-clipping)	Reviewed in Whiten et al., 2001, 2003, also Boesch, 1995, Boesch, 1996
	Food choice	Nishida et al., 1983; McGrew, 1983; Boesch and Boesch, 1993; Fay and Carroll, 1994; Sugiyama, 1994; McGrew et al., 1997; Uehara, 1997
	Food processing technique	Nishida et al., 1983
	Vocalization dialect	Mitani et al., 1992; Mitani and Brandt, 1994; Arcadi, 1996
	Self-medication	Huffman, 1997; Huffman and Caton, 2001
Pygmy chimpanzee Pan paniscus	Prey choice	Reviewed in Hohmann, 2003
	Buttress-drumming technique	Reviewed in Hohmann, 2003
	Tool use for grooming or comfort (e.g. leaf-napkin, toothpick)	Reviewed in Hohmann, 2003
Mountain gorilla *Gorilla gorilla beringei*	Food choice	Tutin and Fernandez, 1992
	Food processing technique (leaves)	Byrne and Byrne, 1993
Orangutan *Pongo pygmaeus*	**See Tables 2.2 and 2.3**	van Schaik et al., 2003, Chapter 2

Table 1.1. ***continued***

TAXON	VARIABLE BEHAVIOR	REFERENCES
Japanese macaque *Macaca fuscata*	Grass-roots washing	Nakamichi et al., 1998
	Stone handling	Huffman, 1984; Huffman and Quiatt, 1986
	Acquiring or processing provisioned foods	Reviewed in Nishida and Hiraiwa-Hasegawa, 1987; Thierry, 1994, Tokida et al., 1994
	Allogrooming techniques	Tanaka 1995, 1998
	Response to humans and novel (provisioned) foods	Reviewed in Nishida, 1987
Chacma baboon *Papio ursinus*	Food choice	Cambefort, 1981
Vervet monkey *Cercopithcus aethiops*	Food choice	Cambefort, 1981
	Foraging tool use	Hauser, 1988
Capuchin monkey *Cebus capucinus*	Food choice	Chapman and Fedigan, 1990b
	Food processing techniques	Rose, 1997; Panger et al., 2002
	Social conventions	Perry et al., 2003
Humpback whale *Megaptera novaengliae*	Song dialect	Reviewed in Herman and Tavolga, 1980; reviewed in Rendell and Whitehead, 2001
	Lobtail feeding	Weinrich et al., 1992
Bowhead whale *Balaena* sp.	Songs	Reviewed in Rendell and Whitehead 2001
Sperm whale *Physter macrocephalus*	Coda repertoire (vocalization dialects)	Weilgart and Whitehead, 1997
	Predator defense technique (*postulated, based on scarring differences*)	Reviewed in Rendell and Whitehead 2001
Killer whale *Orcinus orca*	Vocalization repertoire	Ford, 1991; Strager, 1995
	Hunting techniques	Reviewed in Rendell and Whitehead 2001
	Greeting ceremonies	Reviewed in Rendell and Whitehead 2001
	Beach rubbing	Reviewed in Rendell and Whitehead 2001
Bottlenose dolphin *Tursiops* sp.	Sponge carrying	Smolker et al., 1997
	Signature whistle	Smolker and Pepper, 1999
	Feeding techniques (involving humans)	Reviewed in Rendell and Whitehead 2001

Table 1.1. ***continued***

TAXON	VARIABLE BEHAVIOR	REFERENCES
Black rat *Rattus rattus*	Pine nut extractive foraging technique	Aisner and Terkel, 1992; Terkel, 1995
Norway rat *Rattus norvegicus*	Food choice (mollusks)	Reviewed in Nishida and Hiraiwa-Hasegawa, 1987
Greater spear-nosed bats *Phyllostomus hastatus*	Group-specific calls	Boughman, 1998; Boughman and Wilkinson, 1998

Chapter 1

INTRODUCTION TO ORANGUTAN CULTURES

One of the implicit goals in the study of primate behavior (and indeed many studies of animal behavior) is to gain a better understanding of the evolution of behavioral propensities and capacities in human ancestry. The ubiquity of complex, symbolically mediated cultures in modern human populations is clearly a unique feature of our species. No non-human species has demonstrated the rich construction of meaning at the core of all human cultures. This capacity is clearly linked to our species' uniquely complex linguistic capabilities. However, it is likely that there were behavioral and cognitive precursors to advanced human culture in our pre-linguistic ancestors. We might therefore expect to find simple cultures in the behaviors of other living species that exhibit social and cognitive complexity.

This dissertation will explore evidence for culture in orangutans (*Pongo pygmaeus*). I will describe the behavioral variations between eight orangutan populations in detail, and provide some analyses based on the types of behaviors seen to vary culturally in orangutans (van Schaik et al 2003a) and chimpanzees (*Pan troglodytes*, Whiten et al 1999, 2001). I will provide evidence supporting a role for observational learning in those behavioral variations requiring close social proximity by comparing social measures based on focal animal follows in two Sumatran orangutan populations. I will examine the cultural behaviors related to nest building in orangutans, assessing possible functions of one cultural behavior, and showing specific frequency differences between the populations for that and other nest-related behaviors. I will then describe evidence for social transmission of a tradition in one matriline, and selectivity in social learning, by focusing on behaviors of a rehabilitant orangutan and her descendents.

Orangutans are large bodied, sexually dimorphic apes (males can weigh over 70kg, females up to about 40kg). They are found only on the islands of Borneo and Sumatra. They are primarily arboreal; on the island of Sumatra, where there are tigers hunting terrestrially, they almost never come to the ground. Ripe fruit is the mainstay of their diet, though they also eat leaves, pith, cambium, social insects and their products (honey). They are noted for being less social than other great apes (MacKinnon, 1974; Galdikas, 1985, 1988). They are among the closest living relatives to humans; based on genetic information, the orangutan lineage diverged from our own about 13 million years ago (roughly 6 million years before gorillas (*Gorilla gorilla*), 7 million years before chimpanzees (*Pan troglodytes*) and bonobos (*Pan* *paniscus*; Sibley and Alquist, 1987; Ruvolo et al, 1994; Stewart and Disotell, 1998).

Culture: Definitions and Disagreements

In the broader field of anthropology, the term "culture" has been defined in a variety of ways, and has recently faced strong criticism from within cultural anthropology as being excessively essentialist and homogeneous (as opposed to the blurred boundaries and internal variations of the human phenomenon it was intended to describe; reviewed in Brumann, 1999). A heated debate has also long raged over the application of the term "culture" to behavioral variation among those who study non-human species. There are numerous definitions of "culture" used in anthropology, and many (though not all) include aspects of values, beliefs or institutions that are not detectable in other living species (reviewed in Tuttle, 2001; Brumann, 2002; Pagel and Mace, 2004). While there is general agreement that different populations within a given animal species might exhibit different behaviors, and even that some of these differences might be attributable to social learning, there are deep disagreements about what to call such variation, and which kinds of variation might warrant the label "culture" (see review in Fragaszy and Perry, 2003). Some prefer the term "tradition" when referring to this type of behavioral variation in non-humans (e.g. Chapman and Fedigan, 1990a; Fragaszy, 2003; Perry and Manson, 2003). However, "tradition" implies long-term maintenance of the behavior in the population, something that others have suggested as a subset or requirement for culture in a species (McGrew, 1992; McGrew and Tutin, 1978b), but certainly not true of many behaviors in humans that are considered cultural (see also Day et al., 2003).

To investigate the roots of culture in non-human species, it is necessary to use a broad working definition for the phenomenon, one that does not automatically exclude all non-humans, while providing sufficient distinction to exclude superficially similar but non-analogous behavior patterns in other species. Imanishi's 1952 definition of culture as "socially transmitted adjustable behavior" (in Wrangham et al., 1994, pg. 1) is an appropriate starting point for investigation of cultures in non-humans. In this definition, "socially transmitted" can refer to any kind of social learning, including but not limited to social facilitation, stimulus enhancement, goal emulation and imitation (cf. Zentall, 1996). Even with this broad definition, it is still virtually impossible to directly verify social learning in wild populations – only the controlled conditions of laboratory experiments can exclude all other possibilities – but indirect evidence for social learning might be sought.

The term “adjustable” is critical in that it excludes some behaviors that are socially learned early in life but thereafter cease to show plasticity (e.g. some birdsong; Hauser, 1996). Used in this sense, the terms “culture,” “cultural variation” and “cultural learning” are broadly accepted ways of describing such phenomena (see Biro et al., 2003; Boesch, 1996; Cambefort, 1981; de Waal, 1996; Freeberg, 2000; Grant and Grant, 1996; Hohmann and Fruth, 2003; McGrew and Tutin, 1978; Nishida, 1986; Rendell and Whitehead, 2001; Srivastava, 1991; Terkel, 1995; Whiten et al., 1999).

This broad definition of culture focuses on the characteristics of individual behaviors. It may overlook some of the distinctive features of human culture proposed by Boyd and Richerson (1985, 1996), Galef (1992), Heyes (1993), and Tomasello et al. (1993). By overlooking them, a more general definition of culture does not address the need for fidelity in transmission between generations (Heyes, 1993; Tomasello, 1994), or the potential for the evolution of culture through the accumulation of complexity or modifications of behavior (the so-called "ratchet effect," Boyd and Richerson, 1996; Tomasello et al., 1993). Many of these features are related to specific mechanisms of social learning, and are best addressed in controlled laboratory experiments.

While experimental studies of social transmission mechanisms may help to establish to what extent the capacity for culture exists in a given species, they do nothing to illuminate the evolutionary contexts of the origins of culture. Laboratory experiments may not produce results that accurately reflect the extent to which non-human species display cultural features in the natural settings to which they are adapted. They cannot indicate which types of behaviors are most likely to be culturally variable in evolutionary contexts. We can assess this only by observing the diversity of behaviors in wild populations. The benefit of using a broad working definition for what is clearly a multi-facetted phenomenon is that it allows one to study the evolution of human culture as a gradual assembly of components, each with its own immediate function. Such components potentially formed the foundation of culture in the hominid lineage.

Animal “Ethnography”: Using the Geographic Approach

One of the most successful methods for investigating culture in populations of free-ranging non-humans has been a geographic approach focusing on behaviors that vary between locales. The heuristic used to recognize potentially cultural variation involves dismissing behaviors that do not vary between sites, behaviors that vary only where there are major genetic discontinuities and behaviors where the variation clearly coincides with relevant variations in ecological conditions (reviewed in van Schaik, 2003).

Critics of the geographic approach note that it may generate a Type I error, leading to a spurious conclusion that differences between populations are cultural when they are actually a result of undetected ecological differences between sites leading to within-population convergence and between-population divergence through multiple independent innovations and individual learning (Galef 1992, 2003; Tomasello, 1999). The geographic heuristic assumes that ecological differences are more parsimonious than social learning for explaining behavioral variation. An ecological "explanation" for variation actually implies that individuals expressing this behavior have developed it independently, solving the problems in the same way when faced with the appropriate ecological circumstances. Whether multiple independent innovations of certain behaviors, or a universal predisposition to develop the behavior in certain ecological circumstances, provide a more parsimonious explanation for behavioral variation between populations than an explanation that includes a social learning component may be stretching the definition of “parsimony.” As the models proposed by van Schaik and Pradhan (2003) demonstrate, the capacity for socially-mediated learning and gregariousness improves the likelihood of acquisition of complex, adaptive skills more strongly than increases in innovation. However, the geographic approach conservatively excludes behaviors that have clear ecological correlates to reduce doubt about whether a behavior has spread through social learning, given the extreme unlikelihood of verifying innovation followed by social transmission in wild populations.

The presence of ecological correlates of course does not exclude the possibility that the behavior is socially transmitted. Behaviors that do rely on social learning for their maintenance within a population could be overlooked as cultural because they co-vary with ecological conditions (Whiten and Boesch, 2001). Because it is difficult to confirm social learning for wild populations, interpretation of behavioral differences as cultural using the geographic approach must be regarded as provisional unless additional lines of evidence support it (Boesch et al., 1994; McGrew et al., 1997; Humle and Matsuzawa, 2002; van Schaik, 2003).

Genetic discontinuities must also be addressed, to ensure that behavioral variation does not merely reflect differences in subspecies. Variation in chimpanzee tool-use does not correspond to subspecies discontinuities (McGrew, 1992; Sugiyama, 1997). Orangutan variants such as the kiss-squeak with hands and the nest raspberry appear in some populations on both islands, but not in others, and only one likely cultural variant appears in all populations on one island and no populations on the other (slow loris eating on Sumatra but not Borneo, which could also be related to ecological differences; van Schaik, 2003).

Cultural Variation in Other Species

Examples of cultural behavior have been seen in diverse taxa. Table 1.1 lists examples of likely cultural behaviors in mammals. For most of these species, only one type of socially transmitted adjustable behaviors has been reported. Aside from humans, other species where more than three types of behaviors that appear cultural have been seen are chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), Japanese macaques (*Macaca fuscata*) and killer whales (*Orcinus orca*). Most examples from the birds include only call dialect (reviewed in Janik and Slater, 2003), though some skills may also be cultural in some bird species (particularly tool-use in New Caledonian crows, Hunt 2003; others reviewed in Lefebvre and Bouchard, 2003). Local variants in call production are widespread in vertebrates, and often are likely to be the product of social learning (see Janik and Slater, 2003), but their study requires specialized equipment and different methods from other behavioral research on wild populations. This limits the number of sites with readily comparable information in many species (but see Arcadi, 1996; Mitani and Brandt, 1994; Mitani et al., 1992 for chimpanzees).

The most extensive investigation of culture in another species has focused on chimpanzees. Chimpanzees have been studied more intensively than any other great ape species, with modern field research now extending over four decades at Gombe (Goodall, 1965, 1977, 1986; Stanford, 1994; Nishida, 2004). Eight other sites have now had long-term chimpanzee research projects (Whiten et al. 2001). Researchers from these sites compared their observations of chimpanzee behavior, and using the geographic approach presented strong evidence for cultural variation in chimpanzees (Whiten et al. 1999, 2001). Note that the relative paucity of information in most other species may reflect less intensive study, with far fewer long-term field sites available for comparison.

The Study of Orangutan Cultures

The goal of this dissertation is to evaluate evidence for variation in opportunities for social learning, and the role of such opportunities in cultural variation among wild orangutan populations. Orangutan populations are ideal model systems for investigating the origin of culture because they vary widely in their population density and frequency of social interactions (Galdikas, 1985; Mitani et al., 1991; Sugardjito et al., 1987; van Schaik et al. 1999). This range of sociality provides a natural experiment: it can be quantitatively analyzed, making it possible to test hypotheses about the social conditions in which culture can arise. Studies of captive and rehabilitant orangutans illustrate their capacity for behavioral complexity and social learning (Chevalier-Skolnikoff et al., 1982; Chevalier-Skolnikoff, 1983; Miles, 1983; Russon and Galdikas, 1993, 1995; Bard, 1993; Call and Tomasello, 1994, 1995; Visalberghi et al., 1995; Parker, 1996; Chalmeau et al., 1997; Tomasello and Call, 1997). Wild populations of orangutans also show inter-population behavioral variation, including differences in tool manufacture and use, nest building and other behaviors (van Schaik et al., 2003a).

To investigate the relationship between behavioral variants and social learning, I studied two wild Sumatran orangutan populations (Suaq Balimbing and Ketambe) in 1999 and 2000. Researchers who had more experience with orangutans at these and ot.her sites were brought together at the “Orangutans Compared” workshop to develop a geographic comparison of orangutan behavioral variation.

Chapter 2 presents results from collaborative discussions with researchers from eight orangutan study sites, using the geographic approach to investigate culture in orangutans. Carel van Schaik and I organized the “Orangutans Compared” workshop to facilitate the exchange of information about orangutan behaviors that might vary between populations. From a list of over forty candidate behaviors, our conversations (assisted by videotape and pantomime of behaviors) winnowed out about twenty that vary between populations, without clear ecological explanations for the differences. The initial results and analysis of this geographic approach to orangutan cultures were presented in an earlier paper (van Schaik et al., 2003). Chapter 2 includes additional analyses, and some revisions based on new discoveries by researchers looking more closely at the candidate behaviors in their populations. It provides detailed descriptions of the behaviors, and presents a novel approach to categorizing the function of cultural variants. The distribution of cultural behaviors in these categories is compared for chimpanzees and orangutans. Further evidence is provided that the patterns of geographic variation are not merely an artifact of research intensity at the sites and that rates of innovation are fairly consistent across sites, supporting an important role for social learning in explaining the inter-population variation.

Chapter 3 provides a more detailed investigation of variation between and within Suaq Balimbing and Ketambe, looking specifically at differences in opportunities for social learning. The behaviors that vary between and within the two populations are classified according to the proximity probably required for effective observational learning. The time adult female orangutans spend in association at each site was compared at different levels of proximity. I found that the females who were most specialized in tree-hole tool-use (a behavior probably requiring very close proximity for observational learning) had the highest scores in several measures of sociality, and that these differences were always significant for very close distance classes. This provides another level of evidence for the role of social learning in observed orangutan cultural variation.

Chapter 4 again compares these two orangutan populations, looking specifically at cultural variants related to nest building that differed between the two sites, including multi-tree nests and nest raspberries (see Chapter 2). I investigate aspects of nest-building behavior that may provide contextual evidence for the function of the nest raspberry. I also compare opportunities for social learning during night nest building between the sites.

Chapter 5 looks at the perpetuation of unusual behaviors among the descendents of rehabilitant orangutans at Ketambe, and their failure to spread through the wild residents of that site despite opportunities for others to learn. This provides clear evidence for a limited "family tradition" maintained through mother-daughter social learning over three generations, and for selectivity in orangutans about which behaviors to model after observation.

The concluding chapter reviews the results from the previous four chapters, provides some analysis of the functional categories of cultural variants that are reported for other species, and discusses the relevance of these findings to interpreting the evolution of cultural capacities.

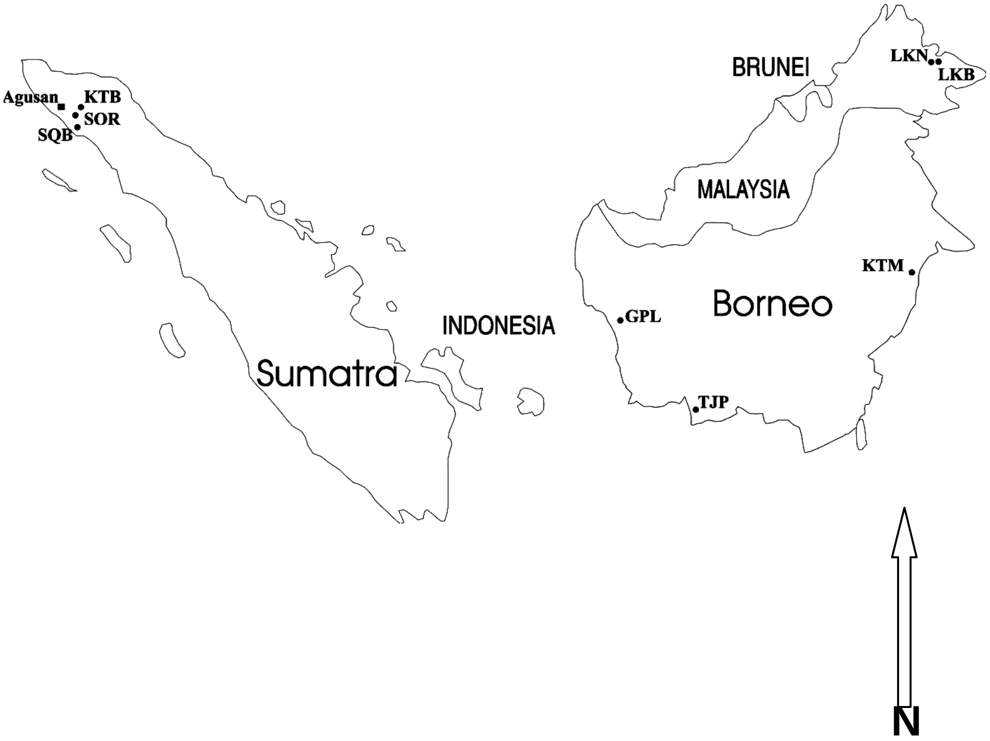

Figure 2.1 Locations of orangutan research sites mentioned in this study. See Table 2.1 for abbreviations of sites included in this study.

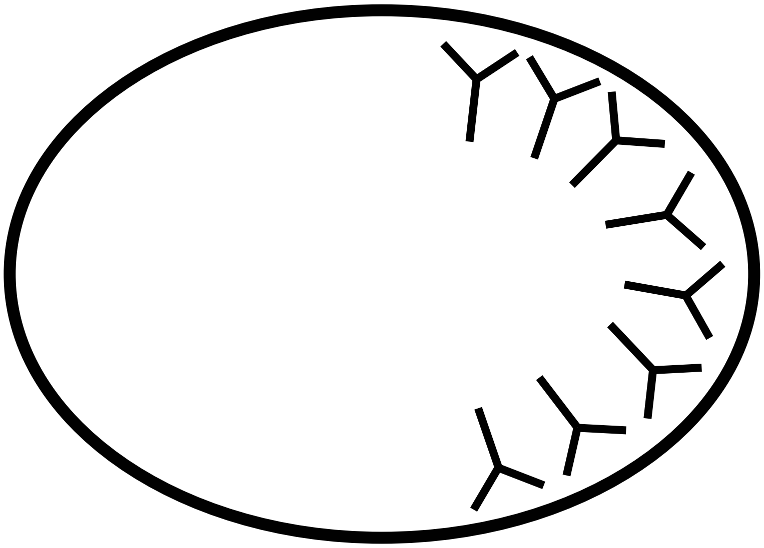

Figure 2.2 A schematic representation of the arrangement of twigs in a nest, seen in the **artistic pillows** made by orangutans at Tanjung Puting (Drawing by Biruté M. F. Galdikas).

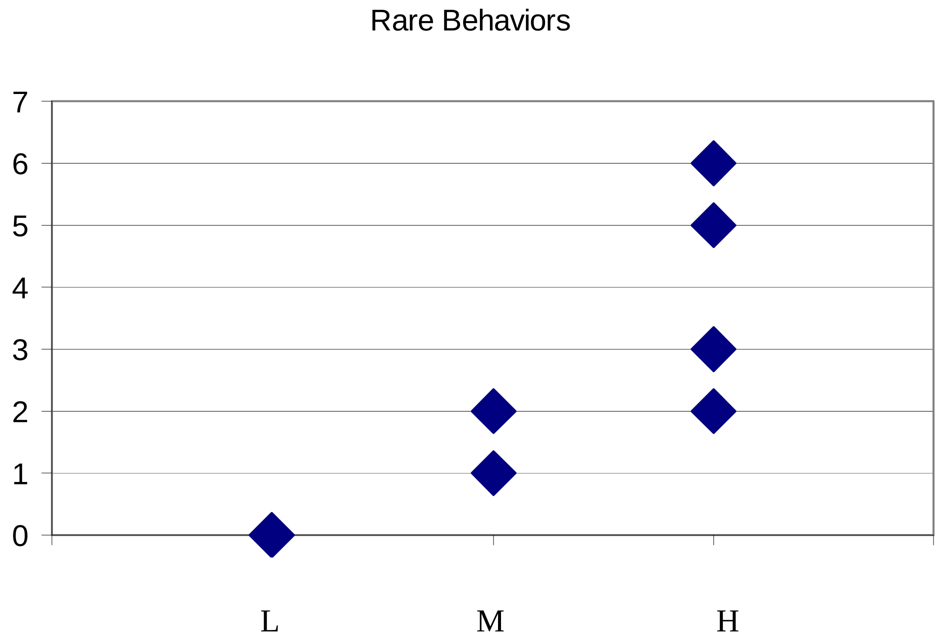

Figure 2.3 Number of rare behaviors observed at each site (by observation intensity at site). Note that both SOR and LKN had no observations of apparently rare behaviors.

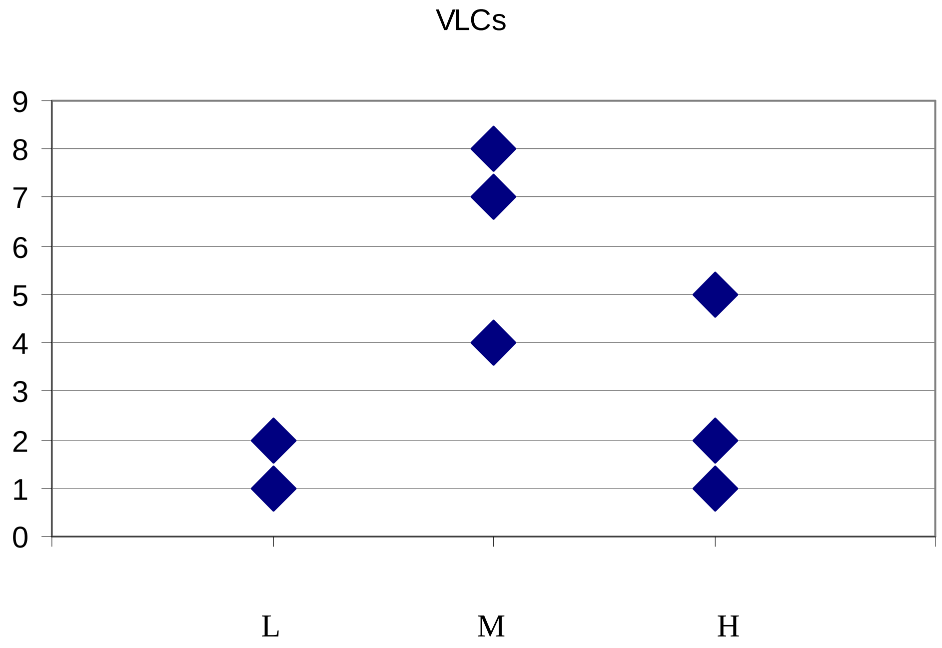

Figure 2.4 Number of VLC behaviors observed at the customary or habitual level at each site (by observation intensity at site).

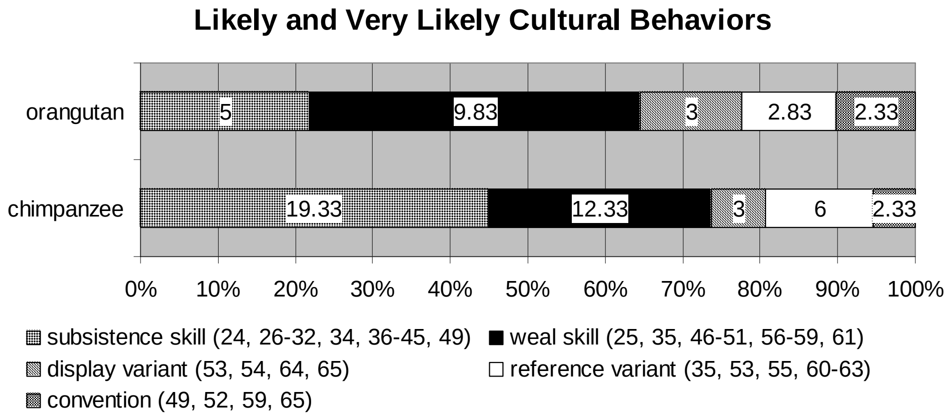

Figure 2.5 Likely and Very Likely Cultural Behaviors of Orangutans and Chimpanzees. Numbers in parentheses in legend indicate corresponding chimpanzee behaviors in Table 1 of Whiten et al. 2001.

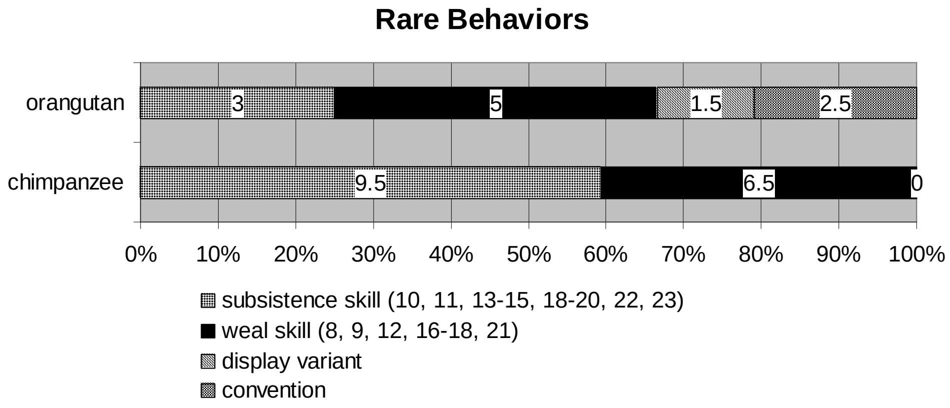

Figure 2.6 Rare Behaviors of Orangutans and Chimpanzees. Numbers in parentheses in legend indicate corresponding chimpanzee behaviors in Table 1 of Whiten et al. 2001.

Table 2.1 Orangutan study sites

	Gunung Leuser, Suaq Balimbing	Gunung Leuser, Soraya	Gunung Leuser, Ketambe	Gunung Palung, Cabang Panti	Tanjung Puting, Camp Leakey	Kutai, Mentoko and Kutai Taman Nasional	Lokan	Lower Kinaba-tangan
abbreviation	**SQB**	**SOR**	**KTB**	**GPL**	**TJP**	**KTM**	**LKN**	**LKB**
observation intensity	M	L	H	H	H	M	L	M
country, island	Indonesia, Sumatra	Indonesia, Sumatra	Indonesia, Sumatra	Indonesia, Borneo	Indonesia, Borneo	Indonesia, Borneo	Malaysia, Borneo	Malaysia, Borneo
location	3°04’N, 97°26’E	2°55’N, 97°55’E	3°40’ N, 97°40’E	1°13’S, 110°7’E	2°46’S, 111°7’E	0°35'N, 177°30'E	5°29’N, 117°41’E	5°30’N, 118°00’E
study area size (ha)	2000	500	450	2000	5000	5000	1600	600
altitude (meters above sea level)	0-50	75-150	300-800	0-350	0-30	20-350	20-150	0-50
forest type	freshwater swamp, peat swamp and some low hill dipterocarp forest	selectively logged lowland hill and riverine forest	primary hill and riverine forest	mixed swamp, alluvial and lowland hill dipterocarp forest	mixed lowland dipterocarp, peat swamp and riverine swamp	mixed lowland dipterocarp	primary lowland dipterocarp and riverine swamp forest	overexploited forest: riverine, swamp, semi-inundated, limestone forests
population density (individuals/km^2)	7	0.43	5	1.85	2	1.0-1.5	1.32	4.5
% time in association	45.5	6.4	46.1	1.6	10	1.6 -10	unknown	14.4

Table 2.2 Very Likely Cultural Behaviors (C=Customary, H=Habitual, P=Present at unknown frequency, R=Rare, E=absent for clear Ecological reasons, A=Absent without clear ecological reasons; darker fills indicate higher frequency)

Behavior	***Category***	**SQB**	**SOR**	**KTB**	**GPL**	**TJP**	**KTM**	**LKN**	**LKB**
Tree-hole tool-use	subsistence skill	C	?	A	A	A	A	A	A
Seed-extraction tool-use	subsistence skill	C	E	E	A	A	E	E	A
Branch scoop	subsistence skill	H	A	A	A	A	A	A	A
Leaf padding	weal skill	E	?	H	A	R	A	A	A
Branch swatter	weal skill	H	?	H	R	R	H	A	H
Leaf napkin	weal skill	A	A	A	A	A	C	A	A
Scratch stick	weal skill	A	P	A	A	R	H	A	A
Autoerotic tool	weal skill	A	?	C	A	A	P	A	A
Bunk nests	weal skill	A	A	A	A	P	A	H	H
Sun cover	weal skill	A	A?	H	A	?	C	R	C
Shelter under nest	weal skill	A	A	R	A	R	C	R	P
Symmetric scratch	weal skill or unknown	C	A	R	A	A	A	A	A
Snag riding	display variant	A	A	A	A	C	A	A	A
Kiss-squeak with hands	display variant	H	C	C	R	R	H	?	A
Kiss-squeak with leaves	display variant	A	A	A	C	A	H	A	A
Leaf wipe	reference variant	A	A	A	A	C	A	A	A
Nest raspberry	reference variant or	C	C?	A	A	A	A	A	H
Twig biting	unknown	C	A	A	A	A	A	A	A

Table 2.3 Likely Cultural Behaviors (C=Customary, H=Habitual, P=Present at unknown frequency, R=Rare, E=absent for clear Ecological reasons, A=Absent without clear ecological reasons; darker fills indicate higher frequency)

Behavior	**Category**	**SQB**	**SOR**	**KTB**	**GPL**	**TJP**	**KTM**	**LKN**	**LKB**
Bouquet feeding	label or subsistence skill	**C**	?	**C**	**C**	**C**	A or E	?	**R**
Dead twig sucking	label or subsistence skill	**C**	?	**C**	A?	**C**	A?	?	A or E
Nest destruction	label or subsistence skill	**H**	?	**H**	**H**	**C**	**P**	?	A or E
Slow loris eating	label or subsistence skill	**H**	?	**H**	A or E	A or E	A or E	?	A or E
Multi-tree nests	weal skill	**C**	**P**	**R**	**C**	**C**	A or E	A	**H**

Table 2.4 Rare Behaviors (**P**=Present at unknown frequency, **R**=Rare, E=absent for clear Ecological reasons, A=Absent without clear ecological reasons, ?=presence or absence uncertain)

Behavior	**Category**	**SQB**	**SOR**	**KTB**	**GPL**	**TJP**	**KTM**	**LKN**	**LKB**
Leaf dipper	subsistence skill	A	?	A	**R**	A	A	A	A
Sponging	subsistence skill	A	?	**R**	A	A	A	?	A
Stick as chisel	subsistence skill	A	?	**R**	A	A	A	?	A
Branch hide	weal skill	A	?	**R**	A	**R**	**P**	A	**R**
Bridge nest	weal skill	A	?	A	A	**R**	A	A	A
Leaf autogroom	weal skill	A	?	A	**R**	A	A	A	A
Severed vine swing	weal skill	**R**	?	A	A	**R**	A	A	A
Genito-genital rub	weal skill or reference variant	**R**	A	A	**R**	**R**	A	A	A
Stealth nest approach	weal skill or unknown	A	?	A	**R**	A	A	**R**	A
Branch-dragging display	reference variant	A	?	A	A	A	?	A	**R**
Artistic pillows	unknown	?	?	?	A	**P**	?	?	A
Leaf "doll"	unknown	A	?	A	**R**	**R**	A	A	**R**

Chapter 2

THE CONTENT OF ORANGUTAN CULTURES

with David Agee, Marc Ancrenaz, Biruté M.F. Galdikas,
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Introduction: The search for non-human culture

One of the implicit goals in the study of primate behavior (and indeed many studies of animal behavior) is to gain a better understanding of the evolution of behavioral propensities and capacities in human ancestry. No serious researcher would claim that any non-human species has demonstrated the rich construction of meaning at the core of all human cultures. However, it is likely that there were behavioral and cognitive precursors to advanced human culture in our pre-linguistic ancestors. By looking for inter-population variation in potentially socially transmitted behaviors, we have found such simple cultures in the behaviors of other living species that also exhibit social and cognitive complexity (Rendell & Whitehead 2001, Whiten & Boesch 2001, Whiten et al 1999, Whiten et al 2001).

Some have noted that field studies cannot establish social transmission as the mechanism creating these differences between populations, and suggest that investigations of the potential for culture in other species are best performed in controlled laboratory situations (e.g. Galef 1992, Heyes 1993, Tomasello et al. 1993). While experimental studies of social transmission mechanisms may help to establish to what extent the capacity for culture exists in a given species, they do nothing to illuminate the evolutionary contexts of the origins of culture. Laboratory experiments may not produce results that accurately reflect the extent to which non-human species display cultural features in the natural settings to which they are adapted, nor indicate which types of behaviors are most likely to be culturally variable. We can assess this only by observing the diversity of behaviors in wild populations.

The context and behavioral content of orangutan cultures were explored through collaborative discussions with researchers from eight orangutan study sites. Twenty-three likely or very likely cultural behaviors for orangutans, discovered using the geographic method applied to chimpanzees by Whiten et al (1999, 2001), are described in detail and classified among two types of skill variants, two types of signal variants, or behavior variants whose function is unclear. A comparison with Whiten et al’s (1999, 2001) findings showed that orangutan and chimpanzee cultural variants are similarly distributed amongst categories of skills, signals and variants whose function is unknown. The distributions of very likely cultural and rare behaviors reported for sites of varying observation intensity supported the conclusion that rates of innovation are fairly consistent across orangutan populations. This suggested that differences in social learning account for differences in numbers of cultural behaviors at different sites.

The geographic approach

A broad working definition of culture allows for investigations of cultural behaviors among wild populations. Ideally, it does not require direct observation of innovation or confirmation of social transmission of a behavior. It also does not require confirmation of the presence of tradition (McGrew & Tutin 1978). Such observations are very difficult to achieve in natural settings amongst long-lived, slow-reproducing species like the great apes.

A productive approach for field researchers is to make hypotheses about expected patterns of geographic distribution of socially learned behaviors. In particular, researchers can look for instances where a certain behavior is widespread in one or more populations, but absent in at least one other population without any clear ecological explanation for the absence (Boesch 1996). This geographic approach assumes that differences between populations that are not explained by ecological differences are the result of an innovation in one or more populations that is spread and maintained by social learning, whereas populations lacking the behavior either never hosted the innovation, or the innovation failed to spread through social learning, or social learning failed to maintain the behavior over time.

The presence of ecological correlates of course does not exclude the possibility that the behavior is socially transmitted (Whiten et al 2001). Conservative dismissal of behavioral differences with ecological correlates is merely a heuristic. It assumes that ecological differences are more parsimonious than social learning for explaining behavioral variation. A cultural explanation refers to ontogeny of the behavior, whereas any ecological "explanation" refers to the likelihood that individuals expressing this behavior have developed it independently when faced with the appropriate ecological circumstances. Because it is difficult to confirm social learning for wild populations, our interpretation of such differences as cultural behaviors must be regarded as provisional unless additional lines of evidence support it (Boesch et al 1994).

Whiten et al. (1999, 2001) use the geographic approach to show that the distribution of chimpanzee (*Pan troglodytes*) behaviors are consistent with a cultural interpretation. In their study, field researchers most familiar with chimpanzee populations at long-term study sites exchanged correspondence to produce a list of candidate behaviors, and then reported on the occurrence of these behaviors in each population (noting where the absence of a behavior could be explained by environmental factors). They found 39 behaviors whose occurrence patterns were consistent with culture in chimpanzees. These behaviors included signals and other social behaviors, foraging skills, tool-use (in signaling, autogrooming, foraging or social contexts) and some behaviors whose function remains mysterious (i.e. rain dances and leaf-groom). Each of the nine sites included in their study had a unique suite of cultural behaviors, and many of the behaviors were present in more than one subspecies, but absent in other populations within that subspecies.

The content of culture

Labels, skills, and signals are broad categories of behavior that may be socially transmitted in non-humans and have been observed to vary in wild chimpanzee and orangutan populations (van Schaik et al 2003, Whiten & Boesch 2001, Whiten et al 1999). Labels (recognizing species as potential food, predators, or other relevant relationship) and skills (manipulating objects or the environment to improve access to resources, reduce potential injury or discomfort, and so on) provide apparent adaptive benefits to the individual. Signals are behaviors that serve some communication role in interactions with conspecifics. Distinctive acoustical signatures in different populations ("dialects" as reported for many species of birds, cetaceans and some primates) could be considered a type of signal variant, though one that generally requires special equipment and analysis to confirm. In addition, the adaptive function or communicative context of some behaviors is unclear, yet the occurrence of these behaviors exhibits patterning consistent with the geographical definition of culture.

The aim of this paper is to develop the evidence for culture in orangutans, using the geographic method to compare wild orangutan populations, as initially outlined by van Schaik et al. (2003). We present more detailed information on the proposed cultural behaviors for orangutans and their geographic distribution patterns, including revisions based on new information, and some data from additional orangutan research sites. We compare the behavioral content of cultural variation in orangutans and chimpanzees. We also discuss and the roles of ecology, innovation, and social transmission in non-human cultures.

Methods

The results presented in this paper are a distillation of the information from the Orangutans Compared workshop, hosted by the L.S.B. Leakey Foundation in San Anselmo, California on February 14-17, 2002. Researchers representing all long-term field studies of orangutans presented and discussed the orangutan behaviors observed at their field sites. The sites to be discussed in this paper are described in Table 2.1 and shown in Figure 2.1.

We grouped the study sites into three levels of observation intensity. “High” observation intensity refers to sites where there has been over 25,000 hours of focal observation of orangutans, involving at least 15 focal animals. “Medium” observation intensity includes sites with 3,000 to 25,000 focal observation hours on at least 10 focal animals. “Low” observation intensity refers to sites with fewer than 3,000 focal observation hours or fewer than 10 focal animals followed.

Note that for most of these sites, the reported observation hours include the work of multiple field researchers. Our assessment of behavioral presence or absence was generally based on workshop participants' discussions of information with the research team at the site. For several of the sites, multiple researchers were present to discuss their findings during the workshop.

With some slight modification, we followed Whiten et al.'s (1999, 2001) codes for reporting the frequency of behavioral patterns as:

Customary (C): seen in all or most members of at least one age-sex class in the given population

Habitual (H): seen repeatedly in multiple individuals in the population, but not as widespread as customary behaviors

Rare (R): seen very few times in one or more individuals

Present (P): seen at least once, but frequency is unknown and probably rare

Absent (A): has never been seen in the population, despite observations of orangutans in appropriate behavioral context, and there is no clear, relevant ecological difference from populations where the behavior is present

Ecological explanation (E): has never been seen, but ecological explanations for absence cannot be ruled out

Unknown (?): behavior has not been seen, but there may be insufficient observations of orangutans in appropriate behavioral context

Even with the depth and breadth of research experience represented by the Orangutans Compared attendees, our assignment of observed behaviors to C’s and H’s is provisional. As this workshop was the first discussion of these behaviors, not all potentially cultural behaviors have been systematically studied at all sites, so the codes are based on the recollections of the site representatives and their discussions with others who have worked at the sites.

For comparative purposes, low observation intensity sites are primarily interesting when a potentially cultural behavior can be described as “customary” or “habitual.” Apparently absent behaviors at low observation intensity sites may be a simple result of too few hours or too few different focal individuals to have observed a habitual behavioral pattern. This is much less likely to be the case in those sites with medium or high levels of observation intensity. A reported absence of a behavior at a low observation intensity site is generally ignored when looking at the distribution of that behavior.

We tested whether behavioral repertoire size was related to observation intensity, for behaviors that were rare (rare or present at unknown frequency at some sites, but nowhere reported as customary or habitual) and for behaviors that could be classified as very likely cultural (customary or habitual for at least one site, but absent from at least one other site with no clear ecological explanation). The rare behavior and very likely cultural behavior repertoire sizes for each site were compared to the level of observation intensity using the Spearman rank correlation coefficient.

Potentially cultural and rare behaviors were classified into five categories, based on their contexts and observed sequelae:

> **Labels** are identifications of other species as potential food, predators, or other relevant relationship (recognized by observing orangutans' functional interactions with a species, when those interactions are not exhibited by all orangutans encountering said species). For the purposes of this study, we only considered

differences in food species choice as **labels** when the difference was also tied to a potentially learned acquisition or processing skill.

Subsistence skills are those variable behaviors that relate specifically to acquiring consumable resources, generally food and water (similar to "subsistence" in McGrew, 2002). We did not consider differences in feeding techniques for a given food species, unless the difference was related to tool-use.

Weal[1] skills are manipulations of objects, the environment or the orangutan's own body, related to grooming, locomotion or minimizing discomfort (similar to "maintenance" in McGrew, 2002).

Display variants exist where there are small but noticeable differences between populations in otherwise similar signal behaviors that occur in similar contexts across sites (e.g *kiss-squeak with hand* or *kiss-squeak with leaves*, (van Schaik et al 2003). Consistent with Whiten et al. (1991, 2001), we did not consider acoustics (which require specialized recording equipment for adequate analysis).

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[1] "Weal" is a somewhat obscure, English word meaning "well-being, prosperity or happiness" (Random House Webster's College Dictionary 1991)

> **Reference variants** exist where an apparent signal behavior for a given context is seen in some populations but not in others, or where similar display behaviors are used in very different contexts at different sites (e.g. *leaf clip with teeth*, Whiten et al 2001). We also classify behaviors that occur specifically in social contexts as reference variants, on the assumption that the behavior plays some role in communication between conspecifics.
>
> **Unknown** is our preliminary classification of those variable behaviors whose adaptive or communicative function is unclear from what has been observed and reported of the behavior's context.

The percent of orangutan and chimpanzee cultural variants in the different behavior categories were compared using Chi-square analysis. Some behavior patterns may include aspects of more than one of these behavioral categories. Behaviors that were potentially classified into two or three categories (e.g. reference variant or weal skill) were counted as 0.5 or 0.33 in each category for comparative analysis. Comparative data for chimpanzees were classified based on the descriptions in Whiten et al (2001). Whiten et al (2001) chose not to include behavioral variations that might be classified as labels, so these were omitted from the comparative analysis.

Results

Orangutan behaviors

The Orangutans Compared workshop yielded evidence for 23 behaviors that are likely to be cultural. Eighteen of these we classify as *very likely cultural variants*, because they were found at customary or habitual levels in some sites, but were absent in others where no ecological explanation for the difference was evident. The remaining five we classified as *likely cultural variants*, because at sites where the behavior was absent, we could not rule out plausible ecological explanations for that absence, though we suspect there is a large social learning component to its transmission and distribution at different sites. The following sections describe each of these cultural behaviors in more detail, as well as some rare and universal behaviors. The results presented here differ somewhat from the results in van Schaik et al (2003a), based on new information from some of the research sites.

Very Likely Cultural Variants

A summary of the geographic distribution of very likely cultural variants is presented in Table 2.2. This includes 3 subsistence skills, 8 weal skills, a behavior that may be considered either a weal skill or a behavior with unknown function, 3 display variants, one reference variant, one behavioral variant that may be a reference variant has an unknown function, and one behavior whose function is entirely unknown.

Tree-hole tool use: Orangutans at all sites are known to forage for social insects and their products (usually honey from stingless bees) in holes in trees. At most sites, they do this either by inserting a finger or hand in the tree-hole, or by breaking into the tree to widen the opening. Only at Suaq Balimbing have orangutans been observed inserting twig tools into tree holes to obtain social insects or their products. There, tree-hole tool-use is widespread and common.

Seed extraction tool use: Another ubiquitous form of tool use at Suaq Balimbing is seen when orangutans extract seeds from the fruits of *Neesia* sp. These seeds are embedded in irritating hairs, hidden within the very tough outer casing of the fruit, and exposed only through slowly opening fissures in the fruit's valves as the fruit dehisces. When available, the seeds of *Neesia* are a preferred food for all independent orangutans at Suaq Balimbing, and any orangutan observed feeding on *Neesia* (every orangutan observed for over 100 hours) has been observed using a tool. At Gunung

Palung and Lower Kinabatangan, *Neesia* seeds are an orangutan food, but the seeds are only accessed by breaking off valves from the fruit and extracting seeds by hand (van Schaik & Knott 2001). In a survey to assess the geographic distribution of *Neesia* tool use, it was found in several major swamp areas on Sumatra's western coast, but not in similar orangutan habitat across the Alas river where there was evidence of orangutans feeding on *Neesia* seeds (*Neesia* with broken valves, van Schaik & Knott 2001).

Branch scoop: Yet another type of tool use seen with habitual frequencies at Suaq Balimbing, but not known elsewhere, is the use of a leafy branch to extract water from deep tree holes. The orangutans at Suaq Balimbing insert the leafy distal end of a broken branch (usually freshly broken with green leaves) into a tree hole with water at the bottom, then drink the water dripping from the leaves.

Leaf padding: Spiny durians (*Durio* sp.) are a preferred food for orangutans at many study sites. One adult female orangutan at Ketambe was seen using leaves to pad her hands when manipulating durian and other fruits with spines, and 3 adult females and 1 adolescent male were observed using leaves as seat cushions in trees with spines (*Erythrina* sp. and *Bombax* sp.). At Agusan, 35km north of Ketambe in the same valley (Figure 2.1), an orangutan was observed using leaf pads in a similar fashion, to protect his hands from thorns while feeding in *Erythrina* trees (Fox & bin'Muhammad 2002).

Branch swatter: When an orangutan is attacked by a swarm of insects (generally bees or wasps, whose nest the orangutan is raiding), it may use a detached leafy branch to ward them off. Use of a branch swatter is reported as habitual at four sites, but is rare at Gunung Palung and Tanjung Putting (where they do feed from wasp and bee nests). At Lower Kinabatangan, a branch swatter was also used against a monitor lizard in one observation.

Leaf napkin: It is customary for orangutans at Kutai to use a handful of leaves to wipe latex off their chin after eating some fruits. Similar fruits, producing abundant latex, are eaten at other sites, but orangutans elsewhere have not been observed using leaves to wipe away the latex that dribbles down their chins.

Scratch stick: This refers to the use of a tool for auto-grooming. Many orangutans at Kutai use a (detached) stick to scratch out-of-reach parts of their own body.

Autoerotic tool: At Ketambe, several female and male orangutans have been observed using a tool (generally a detached stick) to stimulate their genitals.

Bunk nests: At all field sites, orangutans have been observed to use leaves or leafy branches as umbrellas, and to build additional overhead shelters for their nests during rain. Only at Lower Kinabatangan and Lokan, however, are orangutans reported to habitually build a second nest, a short distance above the nest used for resting, as a rain-shelter.

Sun cover: Another variation on supplemental nest sheltering is the practice of building a cover on a day nest exposed to bright sunshine (rather than rain). This is customary at Kutai and Lower Kinabatangan, and habitual at Ketambe, but has never been seen at Gunung Palung or Suaq Balimbing.

Shelter under nest: In this nest-shelter variation, orangutans at Kutai customarily build a nest, but rather than resting in it they move under it to seek shelter during rain. This behavior may be present or rare at Tanjung Puting, Lower Kinabatangan and Ketambe, but has never been reported at Gunung Palung or Suaq Balimbing.

Symmetric scratch: This behavior, reported as customary at Suaq Balimbing, rare at Ketambe, and absent elsewhere, involves exaggerated, long, slow, symmetric scratching movements. The orangutans use both arms and draw their hands up the sides of their torso simultaneously, then reach up, out and down to repeat the process, in something that resembles calisthenics or t'ai chi. Similar behavior can be seen among captive orangutans (R. Shumaker, pers. com., I. Singleton, pers. obs.).

Snag riding: At many sites, adult male orangutans incorporate **snag crashing** into their display behaviors (see below). However, only the males at Tanjung Puting are observed to push over a dead tree (snag), then hold on to the snag and ride down as it falls, grabbing on to nearby vegetation to stop their own fall before the snag crashes to the ground.

Kiss-squeak with hands: The kiss-squeak vocalization is commonly given by orangutans in contexts suggesting mild alarm or annoyance (such as when an unhabituated orangutan encounters a human, or when an adult male approaches a subadult male, Rijksen 1978) or when an orangutan encounters some other mildly threatening species such as monitor lizards or snakes (M. Ancrenaz, pers. obs.). At some sites, the orangutan accompanies the kiss-squeak with a hand near the mouth, either in a fist in front of the mouth (like a trumpet), or as a flat hand on or near the mouth (Peters 2001). This behavior was seen most often at Ketambe and Soraya, but was also often seen at Suaq Balimbing and Kutai, rarely witnessed at Gunung Palung or

Tanjung Puting, and had never been seen at Lower Kinabatangan. It has also been observed in Sumatran orangutans at Dairi, near Sidikalang 93 °, 16min E, 2°, 41min N (I. Singleton, pers. obs.).

Kiss-squeak with leaves: In this display variant, leaves are held near or in front of the mouth during the kiss-squeak (Peters 2001), then the leaves are allowed to fall. The **kiss-squeak with leaves** is ubiquitous at Gunung Palung, and is seen in some orangutans at Kutai.

Leaf wipe: This display occurs in similar contexts to the kiss-squeak (and often accompanies the kiss-squeak). It is seen regularly at Tanjung Puting, but nowhere else. The orangutan wipes vigorously around its face in a circular motion with a fistful of crumpled leaves, and then drops the leaves or throws them at the observer (Galdikas 1982).

Nest Raspberry: This refers to spluttering sounds (made by expelling air through relaxed, pouted lips) associated with nest building. The sound is very soft, and would not be audible at distances where the orangutan's other nest building activities could not be heard clearly. At Lower Kinabatangan, some (flanged) adult male orangutans make raspberry noises before entering their night nest and sometimes after the nest completion. At Suaq Balimbing, all well-studied orangutans have been observed giving nest raspberries as they are completing their nests (most often with night nests, see Chapter 4). One male and several females at Soraya were seen giving raspberries at the end of nest-building, and it is possible that this behavior is customary there as well. No indication of raspberries has ever been found at nearby Ketambe, despite active comparative investigation for this behavior (see Chapter 4).

Twig biting: Orangutans at Suaq Balimbing are regularly observed systematically passing the broken ends of leafy twigs in front of their mouth before adding the twigs to the lining of their nests. This behavior sometimes includes actually biting the end of the twig. It often co-occurs with the **nest raspberry** at Suaq Balimbing, but it has not been reported at any other sites.

Likely cultural variants

These behaviors had distributions similar to the above behaviors, where they were customary or habitual for at least one site, and were absent for at least one other (Table 2.3). However, the absences may be associated with relevant ecological differences, so using the geographic method we must acknowledge that the current evidence does not support a social learning explanation any more strongly than an ecological explanation (i.e. the scarcity of a food species at a site). Nonetheless, these behaviors may be socially learned, and their inclusion here, based on currently available evidence, does not preclude the possibility that additional evidence from other sites (or a more careful exploration of the ecological circumstances at each site) will lead us to conclude that these are very likely cultural variants. Four of these likely cultural variants may be labels or subsistence skills, and one is a weal skill.

Bouquet feeding: Certain genera of ants make their nests in leaves (Rijksen 1978). Orangutans have often been observed grabbing a fistful of leaves (fresh, dry, or rotting), stripping them from a twig, holding the leaves as one would hold a bouquet, then using their lips to pick ants from the leaves. The orangutans apparently use the leaves to protect their hands from the biting ants, while eating those that crawl out onto the leaf edges. This feeding behavior has not been seen at Kutai, and is rare at Kinabatangan, but is customary at all other sites. We cannot yet dismiss the possibility that the distribution of this behavior may simply reflect the distribution of ants that build nests in leaves that can be handled by bouquet feeding.

Dead twig sucking: In some populations, orangutans customarily eat ants found by breaking hollow (dead) twigs. The orangutan then sucks the broken twig to eat the ants from inside. We do not have conclusive evidence that the appropriate ant and tree genera are present at all sites.

Nest destruction: Orangutans sometimes search for insects by taking apart old nests encountered while foraging. The varied distribution of this behavior may reflect a lack of recognition of the foraging opportunities afforded by old nests, or may be related to differences in insect species that colonize orangutan nests, or different "optimal diets" at different sites.

Slow loris eating: The capture and consumption of slow lorises (*Nycticebus coucang*) is reported as habitual for female orangutans at the two well-documented Sumatran orangutan populations, but has never been reported at the sites on Borneo. Because catching a slow loris can involve lengthy visual inspection, it may require a "search image" for the favorite hiding places of this small, nocturnal prosimian. The acquisition of this search image or the techniques for locating and dispatching a loris are potentially cultural. It is possible that lorises are too rare to make slow loris predation ecologically viable for those populations on Borneo where it is never seen. As slow lorises were often discovered during insect foraging (Utami & van Hooff 1997), the rate of insect foraging at different sites may also be a critical ecological factor.

Multi-tree nests: Orangutans can sometimes weave together the terminal branches of several different individual trees when building a nest. The only long-term study site where this is has not been seen is Kutai, which may have fewer interlinking tree crowns due to fire and other habitat disruption.

Rare behaviors

These behaviors have only been seen one or a few times at each site where they are reported, never frequently enough to warrant being rated as habitual (Table 2.4). They may represent independent innovation by each individual seen performing the behavior. Eight of these rare behaviors are skills, one is a signal, one may be interpreted as a skill or a signal, and two do not appear to serve any adaptive or social function.

Leaf dipper: At Gunung Palung, in two instances orangutans were seen using leaves as a vessel to carry water from a pool or stream to their mouths, and drinking water directly from the leaf vessel.

Sponging: At Ketambe an orangutan was seen using crumpled leaves to absorb water from a tree hole then drink the water from the leaves. Chimpanzees have also been observed using leaves as sponges (Whiten et al

1999, 2001).

Stick as chisel: Another rare form of tool use seen at Ketambe was an orangutan using a stick to break open a termite nest in a log on the ground. This individual, a very old adult male, performed the behavior regularly. Because the behavior was performed only by a thoroughly solitary male while on the ground, it is unlikely that the behavior could have spread through observational learning.

Branch hide: At all long-term study sites except for Gunung Palung and Suaq Balimbing, orangutans have been seen using a detached branch as a screen to hide from predators or humans.

Bridge nest: Orangutans sometimes build nests that join the terminal branches of two trees (see **multi-tree nests**, above). At Tanjung Puting, an orangutan was observed building such a nest between two trees on the opposite banks of river. Rather than resting in this nest, the orangutan used it to cross the river and continued moving on the other side.

Leaf autogroom: This has been seen twice at Gunung Palung. In the first instance an adult male wiped his forearms several times (about 6-7 repetitions) with a *Neesia* leaf (the underside of which has fairly prominent raised venation) following feeding on fruit of the same tree. It appeared that maybe he was trying to remove the fiberglass-like *Neesia* fibers from his hair that got on him while opening up the *Neesia* fruit. The second observation was of an adult female who had a large undeveloped male near her. As the male approached she sat back, reached out and grabbed a leaf of an epiphyte that was growing on the side of the branch and stroked it up and down the side of her belly 3-4 times. The male seemed to be excited by this display, although it was not followed by further contact or mating.

Severed vine swing: It is common for orangutans to use vines and lianas to travel between trees with a pendulum-like swing. Typically, they use a bend of vine or liana that hangs between two trees and is secure at either end. At Tanjung Puting and Suaq Balimbing, orangutans have been witnessed biting through a vine, apparently to increase the arc of their swing as they use the severed vine to cross to another tree.

Genito-genital rub: Pairs of female orangutans at Gunung Palung, Tanjung Puting and Suaq Balimbing were seen rubbing their genitals together (similar to the behavior commonly reported for female bonobos, *Pan paniscus*). This may serve a social function, or may simply be a mutual discovery of a pleasurable activity.

Stealth nest approach: At Gunung Palung, an unflanged male was observed cautiously approaching a flanged male in a durian tree. The smaller, unflanged male built a series of nests as he approached, not using the nests for resting, but instead using them like a blind as he moved closer.

Branch-dragging display: Orangutans at Lower Kinabatangan have been observed dragging a broken branch as they move across the forest floor, in a display similar to the agonistic display of bonobos.

Artistic pillows: When looking at the nests constructed by orangutans, observers at Tanjung Puting noticed that some nests were lined with a row of twigs, all of similar size and all radially-oriented along the nest perimeter with the forked or leafy end pointing outwards (Figure 2.2). Orangutan observers rarely have the opportunity to look into orangutan nests from above, so its frequency and distribution at Tanjung Puting is uncertain, and the presence or absence of this behavior pattern cannot be ascertained at some other long-term orangutan study sites, but it was not seen in nest observations at Gunung Palung or Lower Kinabatangan.

Leaf "doll": At Gunung Palung, Tanjung Puting and Kinabatangan, orangutans have been observed gathering a bundle of leaves and taking them into their nests.

Universals

There are numerous behaviors characteristic of orangutans which we did not include in our discussion of possibly cultural orangutan behaviors, simply because we did not expect them to vary. The behaviors below were discussed at the Orangutans Compared conference because we initially suspected they might largely depend on social learning. We discovered that these behaviors were customary or habitual in all well-studied orangutan populations. All but **play nests** and **snag crashing** were also observed at Lokan and all but **play nests** were observed at Soraya. We cannot consider these behaviors “cultural” using the geographic method. They are included here because it is possible that we may find an orangutan population where one or more of these behaviors are absent, leading us to re-assess their classification. These orangutan universals may also prove interesting in comparisons with other primate species.

Leaf “umbrellas”: This skill involves using large leaves or leafy branches to cover the head during rain.

Nest covers: This skill is the assembling of leaves or leafy branches above a nest in which the orangutan shelters during rain.

Missiles: This skill includes throwing or aimed dropping of branches, large fruits or other objects toward terrestrial predators (or humans), apparently to drive them away.

Leaf stripping: This skill involves obtaining foliage by drawing a segment of vine, liana or branch rapidly through a partially-closed hand, to gather a handful of leaves before consumption. Orangutans also accomplish this by drawing the stem rapidly through their mouth. This behavior is reported as cultural for chimpanzees, when performed in a threat context (Whiten et al. 2001), but it is not clear that it is ever performed by orangutans in a non-feeding context.

Play nests: Orangutans everywhere build nests for sleeping at night, and will occasionally build a nest for resting or sleeping during the day. Infants and juveniles (and sometimes adults) at most sites commonly build a day nest for social play (wherein no resting occurs).

Snag crashing: The aimed pushing of dead standing trees, as a display by flanged adult males, was habitual at Ketambe and customary at most other well-studied sites. It was also recently observed at Kinabatangan. Because Kinabatangan was previously logged and is a recovering forest, it is likely that it has far fewer standing dead trees than at all the other study sites, leading to fewer ecological opportunities to display the behavior.

Relationship of observation intensity and observed behaviors

We expected that the number of behaviors observed would increase with increasing observation intensity, and this is in fact what we found when we compared rare behaviors (r_s= 0.918, P=0.0028 one-tailed, Figure 2.3a). However, this prediction does not hold when we compare very likely cultural behaviors (r_s= 0.207, P=0.356 one-tailed, Figure 2.3b). When only those sites with medium and high observation intensities are considered, the expected correlation is still quite strong for rare behaviors (r_s= 0.792, P=0.0647 one-tailed) but is negative for very likely cultural behaviors (r_s= -0.683, P=0.903 one-tailed).

Behavioral categories: comparison with chimpanzees

The proportions of reference variants, display variants, subsistence skills, weal skills and conventions that vary between orangutan populations were compared to those reported for chimpanzees by Whiten et al. (2001). There were no significant differences in the relative frequencies for different categories of very likely cultural behaviors ($X^2 = 6.393$, P = 0.171), nor were differences significant when the very likely and likely cultural behaviors were combined ($X^2 = 5.140$, P = 0.273, figure 2.4). Chimpanzees did have a noticeably higher percentage of subsistence skills than orangutans (46% vs. 24%), and orangutans a higher percentage of weal skills than chimpanzees (45% vs. 27%). There were more discrepancies in the rare behaviors reported, with chimpanzees again having a much higher percentage of subsistence skills than orangutans (59% vs. 25%, Figure 2.5), but these differences also did not reach significance ($X^2 = 7.832$, P = 0.098).

Discussion

The roles of ecology, innovation and social transmission

The geographic approach to investigating culture in non-humans is plagued by issues regarding ecological influences on the distributions of behaviors. Some critics (e.g. Galef 2003) have expressed concern that ecological similarities might lead to parallel *individual* innovation at sites where a behavior is customary or habitual, while the innovation could never occur at sites where ecological factors are different. This could lead to a pattern of presence and absence that would appear cultural using the geographic approach, but may be produced without any need for social transmission.

We found no relevant ecological components that vary across sites for most of the *very likely cultural behaviors* (VLCs). For instance, all healthy orangutans observed have hands, and all orangutan habitats are replete with leaves, but at only certain sites do orangutans use hands or leaves to embellish their kiss-squeak vocalization. For a few of the VLCs in orangutans, we did find some sites where the behavior was absent because the appropriate ecological context was absent (e.g. the lack of *Neesia* fruit at some sites for **seed-extraction tool-use**), but in these cases there were other sites where the appropriate ecological context was present and yet the behavior was absent (Van Schaik & Knott 2001).

For the five *likely cultural variants*, we were unable to exclude ecological explanations. However, in none of these instances are we certain that the behavior is absent due to the lack of the appropriate ecological context at all the sites where it has not been seen. The **dead twig sucking** behavior is a case in point: where it does occur, orangutans use this technique to feed on the ant mutualists of certain tree genera with hollow branches. Ant-tree mutualisms of this kind are ubiquitous in orangutan habitats (Whitmore 1984), so it is likely that similar genera are found at the sites where the behavior is absent, but we do not yet have details about what ant or tree genera are present and in what frequencies for all sites. Similarly, orangutans on Borneo may not view slow lorises as prey items because the density of slow lorises may be lower, reducing encounter rates and the opportunity for orangutan individuals to either discover the edibility of slow lorises (that is, insufficient opportunities for innovation of this behavior) or to learn how other orangutans locate, capture and eat them (insufficient opportunities for social transmission of the behavior). There is also the possibility that orangutan encounters with slow loris are so rare on Borneo that no scientific observer has witnessed one. If a researcher were to witness an orangutan encountering a slow loris up-close, but failing to eat it, this would bolster the idea that slow-loris eating represents a cultural variation in label (recognizing a slow loris as edible) or skill (knowing how to capture and consume a loris).

Signal behaviors that vary between populations (including **display variants** and **reference variants**) and other behaviors that occur exclusively in social contexts (e.g. **play nests**) can be considered social conventions. These behaviors may serve as a way to establish or confirm social bonds within a group (Perry et al 2003). Social conventions take place in a social context, and their usefulness may be constrained by the comprehension of conspecifics witnessing or participating in the behavior, so virtually by definition they are likely to be socially-learned. If they are widespread in certain populations and absent in others, they clearly meet our definition of "cultural behaviors."

The geographic approach necessarily dismisses universal behaviors, but these may in fact be culturally learned. The six universal behaviors described herein are unlikely to be "instinctive," in the sense that they are genetically determined. Instead, they are probably good examples of behaviors that orangutans are likely to discover given the similarities of their habitats, anatomy, and intelligence (Huffman & Hirata 2003). These are regular, predictable orangutan innovations. For instance, the species-wide distribution of rain covers for nests or leaf "umbrellas" may reflect the fact that orangutans live in habitats with high rainfall where large leaves and leafy branches are abundant. It is possible that the use of leaf "umbrellas" is merely a product of an innate orangutan propensity for putting things on their head (rehabilitant and captive orangutans are known to do this, even when they are not in the rain, A. Russon, pers. comm., M. Merrill, pers. obs., I. Singleton, pers. obs.). The universality of leaf "umbrellas" in orangutan populations is particularly noteworthy in light of the fact that, while similar behavior has been observed in bonobos (Kano 1982) chimpanzees are not known to do this (Whiten et al 2001). Of course, this ease of innovation for universal behaviors makes it nigh impossible to determine in the course of regular field studies whether the behavior was independently discovered by each individual, or was learned socially after a single individual in a population made the innovation.

This predictability of orangutan innovation can also plays a role in behavioral variants that appear to have had multiple origins. For example, the **nest raspberry** has appeared at two neighboring sites on Sumatra and at one site on Borneo. This coincidence probably resulted from the extreme flexibility and dexterity of orangutan lips, and the universality of nest building in the species. The fact that it occurs toward the end of nest building may point toward an original function (using the mouth to assist in handling the smaller twigs and plant matter used to line the nest) that became ritualized. Such convergent innovation confounds the relationship between culture and independent innovation in a way that can be hard to resolve in the field. The absence of such behaviors at most sites, including Ketambe (where observers familiar with the behavior at Suaq Balimbing were specifically looking for nest raspberries or other vocalizations, see Chapter 4), seems a clear indication that this innovation is only maintained in a population under certain conditions, which likely includes reinforcement through social learning.

The interaction between the propensity toward certain types of innovation and the geographic distribution of those behaviors can help explain apparently cultural variations between different species. (Hohmann & Fruth 2003) found that bonobos (*Pan paniscus*) at Lomako shared many behavioral patterns reported as cultural variants in chimpanzees (*P. troglodytes*) by (Whiten et al 1999, Whiten et al 2001), . The similarity of chimpanzees and bonobos in their anatomy, physiology and apparent cognitive capacities may have led to parallel innovation in some chimpanzee and bonobo populations. Likewise, several of the behaviors reported for orangutans (e.g. **tree-hole tool use**, **leaf "napkin**,**" branch swatter**) bear strong resemblances to those reported in chimpanzees and bonobos (bee-probe, leaf-napkin and fly-whisk, respectively, (Whiten et al 1999, Whiten et al 2001), again reflecting the broad similarities in morphology and cognitive capacity among the great apes.

We found that the number of observed rare behaviors increased in sites with higher observation intensity, as predicted when the rate of innovation in orangutans is fairly consistent across sites. The finding that the number of observed VLCs did not increase with increased observation intensity supports our conclusion that something other than innovation is responsible for the distribution and maintenance of these cultural behaviors in a population.

The notion that many of these innovations are maintained through social learning is supported by our earlier work showing a significant relationship between geographic distance and cultural repertoire similarity in orangutans (van Schaik et al. 2003). This suggests that cultural diffusion occurs between sites. Findings from the low observation intensity sites bolster this conclusion. For example, Soraya (which lies roughly between Suaq Balimbing and Ketambe— Figure 2.1) has **nest raspberries** in common with Suaq Balimbing and **kiss-squeak with hands** in common with Ketambe. Several orangutans at Lokan, like in nearby Lower Kinabatangan, were seen building **bunk nests**.

The likely role of social learning is further supported by our earlier finding that the number of VLCs seen in a population increases with increasing sociality (as measured by average party size), but there was no correlation between the number of VLCs and population density (van Schaik et al. 2003a). This suggests that the number of potential models is less important than the encounter rate with them and how much time is spent in close proximity. A more detailed assessment of differences in sociality between sites will clarify the effects of social learning opportunities on VLC repertoires. This should consider not only how much time is spent in close proximity to at least one other independent individual, but also the size and density of orangutans' social networks at each site and the levels of proximity tolerated. With culture now firmly established in chimpanzees and orangutans, we can concentrate on the question of the balance of independent innovation versus socially biased acquisition of behaviors in natural populations.

Behavioral categories – cultural content

While most behaviors can be easily recognized as labels, subsistence skills, weal skills, display variants, reference variants, or conventions, some behaviors have aspects of more than one of these categories. For instance, self-medication in chimpanzees often appears to require both a label (recognizing consumption of a specific plant as an appropriate response to illness or discomfort) and a skill (rolling leaves and swallowing them whole, or other special techniques for processing and ingesting the medicinal plant, Huffman & Caton 2001). As another example, stone handling in Japanese macaques might be a reference variant (perhaps communicating a disinterest in social interaction, as macaques engaged in this behavior tend not to respond to solicitations for mating or play), a weal skill (Huffman 1996), or it may be a convention (engaging in stone handling may be a way to demonstrate group membership, serving to reassure other members of the group).

Labels and skills provide apparent adaptive benefits to the individual. Individual innovation and learning could be sufficient to maintain labels or skills if the innovation were sufficiently common. Signals and conventions are behaviors that would be adaptive only in a social context, and only if they elicit appropriate responses from others (even if they are not adopted by others); therefore, social interactions almost certainly play some role in the maintenance of a signal or convention innovation. The very existence of such behavioral conventions as the symmetric scratch in orangutans, stone handling in macaques (Huffman & Quiatt 1986) or sponging in dolphins (Rendell & Whitehead 2001) may reflect the power of social learning to maintain behavioral patterns that have little or no adaptive value. Behavioral patterns based on learned labels or skills that bring immediate and tangible rewards, such as improved food intake, would likely remain intact over a longer time than variant signals or conventions. Reports of chimpanzees in Sierra Leone using stone hammers to crack nuts nearly 400 years ago are consistent with this prediction (Sept & Brooks 1994).

Different types of behavior would have different requirements for social learning. Labels probably require the simplest possible social learning (social enhancement or facilitation), and in many cases this learning could be accomplished without very close (within 10m) proximity. For instance, an orangutan who spots another orangutan feeding by taking apart an old nest need not approach very closely to observe the details of the **nest destruction** foraging technique; she might simply pay more attention to the next old nest she encounters, and could independently discover that old nests contain plentiful insects that are easy to locate and consume. In these circumstances, it is hard to assess whether the skill component was acquired through socially-mediated learning or was learned independently. Labels are generally not identified using the geographic method because the presence or absence of a food species or its inclusion in the diet might also be explained ecologically (Boesch et al 2002). We suspect that complex skills such as tool use involve both intensive social and independent learning, as chimpanzees are known to improve their technique over years of practice (Boesch 1991, Boesch & Boesch 1984).

As Whiten and colleagues note (2001), choices made in splitting or lumping behavioral variations mean that the numbers of cultural variants identified is somewhat arbitrary. However, the process used by the chimpanzee researchers and that used by the orangutan researchers were sufficiently similar to warrant some comparison.

We found overall similarity in the proportions of reference variants, display variants, subsistence skills, weal skills and conventions in the cultural behaviors of orangutans and chimpanzees. This suggests that culture is functioning in similar ways in these great ape species. The largest apparent difference was in the proportions of subsistence skills and weal skills in the two species. Much of this may be attributed to the variability of tool-use skills that may be culturally learned, including some notable variations-on-a-theme. Chimpanzees show widespread feeding tool-use in almost all of the populations under long-term observation, and many chimpanzee cultural behaviors are variations in tool-use techniques (e.g. using different materials for hammers and anvils for cracking nuts). Feeding tool-use is customary in only one well-studied orangutan population, but various forms of protective or grooming tool-use are widespread and customary among orangutans (e.g. the universal use of leaf "umbrellas" for rain, and the various uses of leaves for sun and nest shelters against rain in different populations).

The different distributions of rare behaviors reported, with chimpanzees again having a much higher percentage of subsistence skills than orangutans, may seem unsurprising given the above. However, the percentage of weal skills in the rare behaviors of the two species is almost equal. There were two rare behaviors among orangutans (**artistic pillows** and **leaf dolls**) that had no discernable function, and three others (**stealth nest approach**, **branch drag display** and **genito-genital rub**) that by definition took place in social contexts, whereas all of the reported rare chimpanzee behaviors are either subsistence or weal skills with clear adaptive functions. This difference may simply reflect the different perceptions of what is noteworthy among researchers studying each species. Alternatively, it may reflect some key differences between the species. As orangutans are more arboreal and in some ways more "alien" to us than are chimpanzees, we may naturally find some of their behaviors more inscrutable. Social interactions are generally less frequent among the adult orangutans usually followed as focals than among adult chimpanzees, so perhaps orangutans have more motivation to innovate in social situations.

Perhaps it is this very difference in sociality that has lead to the remarkable propensity of captive and rehabilitant orangutans to mimic (Tomasello 1996). Rendel and Whitehead (2001, based on Richerson & Boyd 1998) discuss a synergistic relationship between the evolution of imitation and conformism. This could explain the extensive mimicry amongst rehabilitant orangutans (both of their human rehabilitators and of their rehab peers), particularly of such apparently maladaptive behaviors as stealing and washing clothes, using paint, etc. (Russon 1996, Russon & Galdikas 1993, Russon & Galdikas 1995). Such behaviors may even be socially transmitted to successive generations, as the observation of one rehabilitant female orangutan's daughter and granddaughter continuing her tradition of taking clothes from clotheslines at a research camp (Chapter 5). This behavior often looks more like mimicry than like program-level imitation or emulation (Tomasello 1996, Tomasello et al 1993) – the orangutans may not "get the point" of these behaviors, and they may not be rewarded for them, so perhaps they are simply attempting to reproduce the behaviors to which they are exposed primarily for conformity's sake (though one could argue that the orangutans find behaviors like clothes theft intrinsically rewarding for either their amusement value or the taste of the soap and salts when chewed). Orangutans may be more motivated to copy such behaviors, testing what is learned socially, simply because their opportunities for social learning are generally fewer. If the behavior itself is reproduced, perhaps the mimicking orangutan can discover what, if any, adaptive benefits it yields.

Future study suggestions

As this was the first discussion among orangutan researchers of these behavioral variants, not all potentially cultural behaviors have been systematically studied at all sites. Already since our conversations in February 2002 and subsequent publication (van Schaik et al 2003), increased alertness to potentially cultural behaviors has led to new observations which change some of our previous results. To improve our understanding of orangutan cultures, researchers could begin to record rates of these behaviors observed in different individuals. Right now, our assignment of behaviors as customary, habitual or rare was based largely on impressions and recollections of the workshop participants, rather than on systematic recording of the behavior's occurrences in different individuals in each population. Such careful investigations may lead to further revisions. Better species lists and more information about how often orangutans could find or utilize different species will improve our ability to assess ecological opportunities for the expression of different behavior patterns. More cross-site collaboration and the use of some standardized observational methods and definitions can aid in our investigation of orangutan behavioral diversity. Videotaping can improve our ability to compare behavior patterns between sites.

Another important question to answer in the study of non-human cultures is whether putative cultural behaviors vary more between sites than they do within them. While the comparative approach we have used makes clear distinctions between gross behavioral categories that are either present or absent, much more subtle distinctions are possible in detailed comparative studies of individuals within and between sites. Such studies are difficult to manage given the logistical vagaries of fieldwork, but they are not impossible, and they should be encouraged as the next logical step in non-human cultural investigations.

For much of this work, videotape will be a useful (perhaps necessary) compliment to field notes for discerning variations at the individual level. In our usual approach to recording orangutan behavioral observations, we use functional definitions of behaviors (e.g. “**nest covers**”) to simplify data gathering. In so doing, we may be overlooking systematic differences in the actual morphology of the behavior that would be even clearer evidence of culture. For example, "tying shoes" may seem a straightforward description of a human behavior, but in fact there are different approaches to shoe tying that are more prevalent in different parts of the world, and even local variations within communities based on who taught whom to tie their shoes. Video analysis is ideal for detecting these fine-grained differences in how behaviors are performed, further illuminating differences between sites and allowing us to look for patterns that may be indicative of social learning within sites. Such a study of chimpanzee hand-clasp grooming, using photographs and video stills, led to the discovery of interesting patterns of inter- and intra-population differences (Nakamura & Uehara 2004).

The establishment of additional orangutan research sites will further enhance our understanding of orangutan cultural variation and the range of orangutan innovation. Every orangutan population studied so far has a unique cultural repertoire. Every well-established site yields unique rare behaviors. Sometimes new behaviors are seen soon after the site is opened, such as the observation of leaf pad and branch hook use for locomotion at Agusan within the first 15 hours of unhabituated orangutan follows (Fox & bin'Muhammad

2002). The rapid loss of intact orangutan habitat makes the need for more widespread field research all the more urgent.

The exchange of observers between sites will improve our ability to detect cultural differences. Human ethnographers frequently have the benefit of extensive first-hand experience with at least two different cultures in their study species: the one they chose to study, and the one in which they were raised. This is often not the case for those studying non-human primates, yet individual familiarity with multiple populations is an essential step for producing a more accurate and nuanced description of culture in another species.

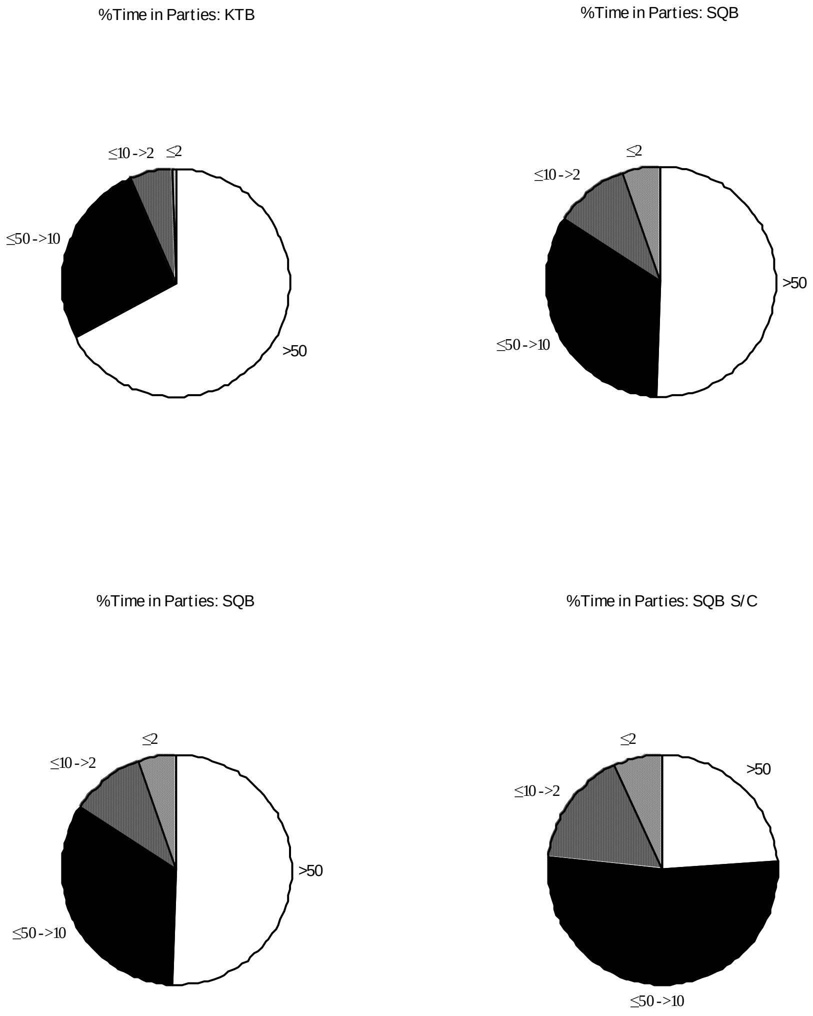
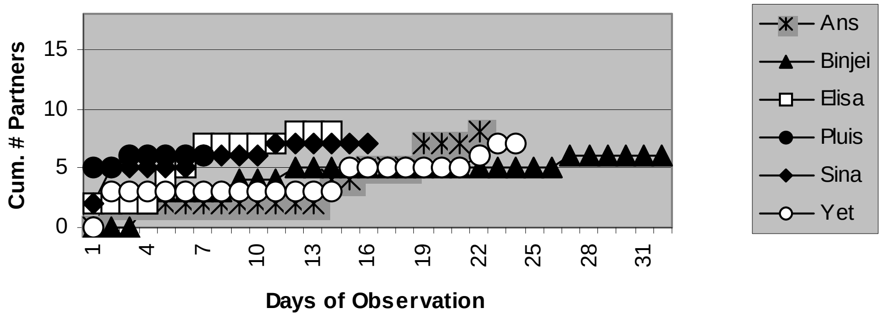
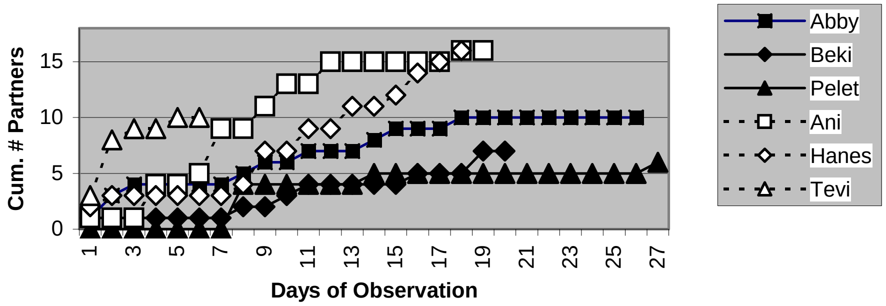


Figure 3.1 Percent Time in Parties (by Nearest Neighbor Distance)

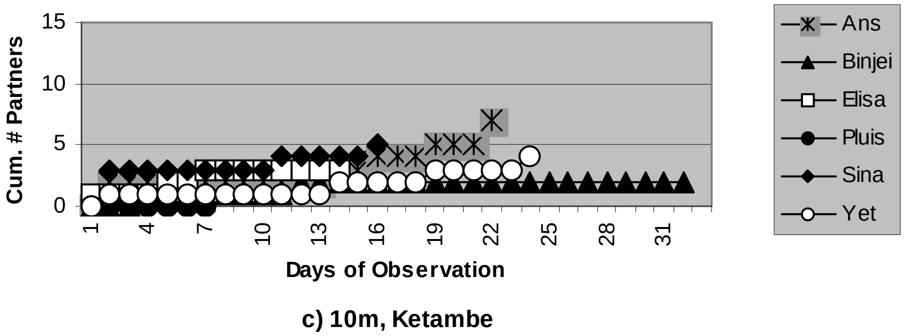


a) 50m, Ketambe

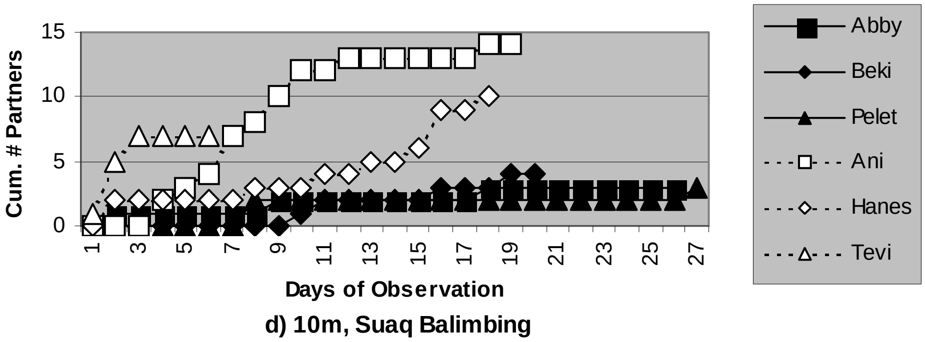


b) 50m, Suaq Balimbing

Figures 3.2a-b Cumulative number of partners by observation day for each focal at Ketambe and Suaq Balimbing (northern females designated with squares, southern/central females with triangle), for ≤50m distances.

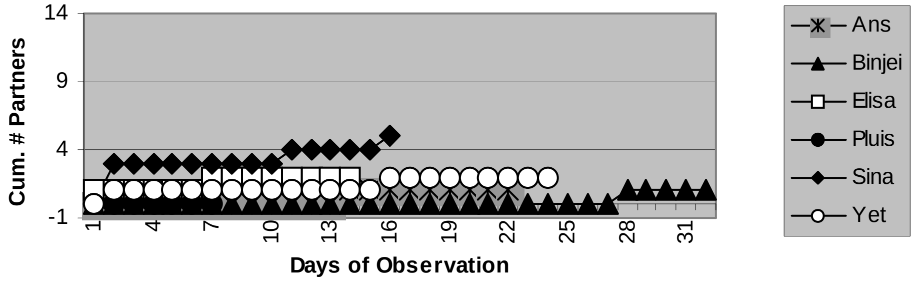


c) 10m, Ketambe

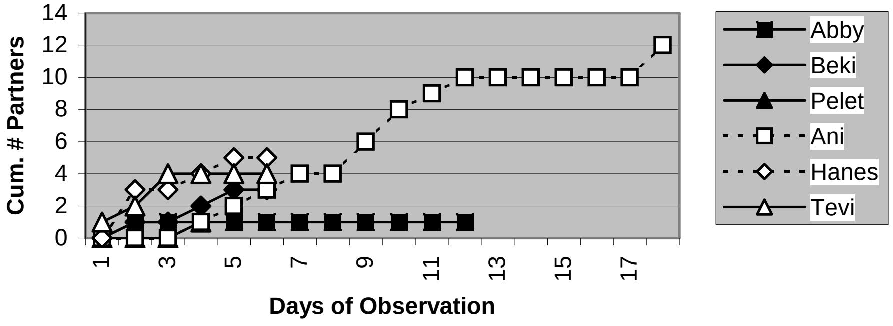


d) 10m, Suaq Balimbing

Figures 3.2c-d Cumulative number of partners by observation day for each focal at Ketambe and Suaq Balimbing (northern females designated with squares, southern/central females with triangle), for ≤10m distances.

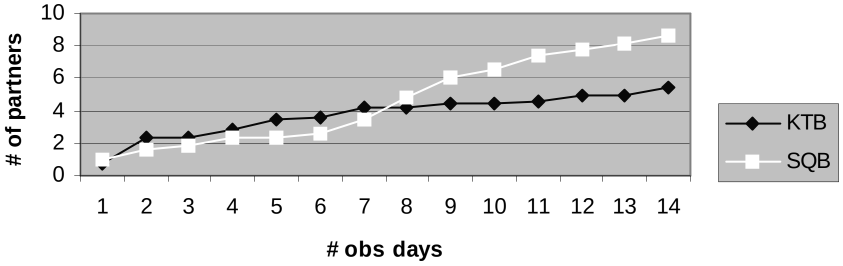


e) 2m, Ketambe

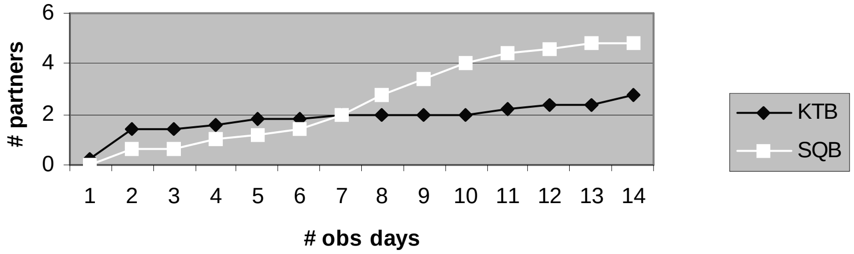


f) 2m, Suaq Balimbing

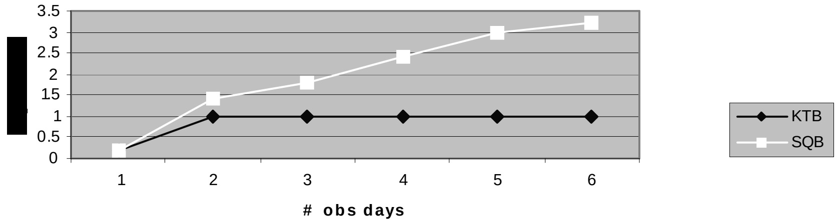
Figures 3.2e-f Cumulative number of partners by observation day for each focal at Ketambe and Suaq Balimbing (northern females designated with squares, southern/central females with triangle), for ≤10m distances.



a) 50m Mean Cumulative # of Partners

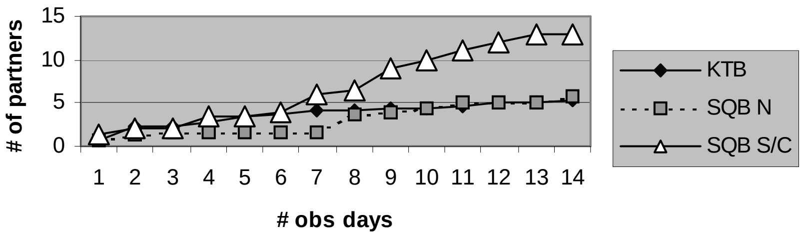


b) 10m Mean Cumulative # of Partners

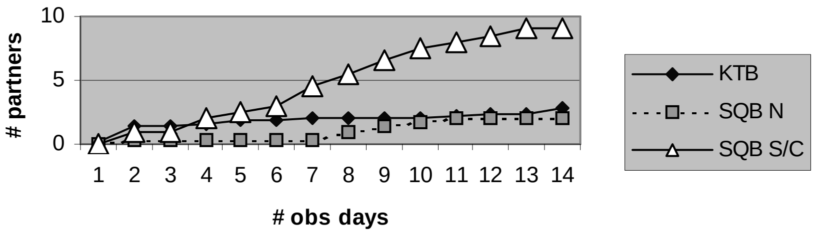


c) 2m Mean Cumulative # of Partners

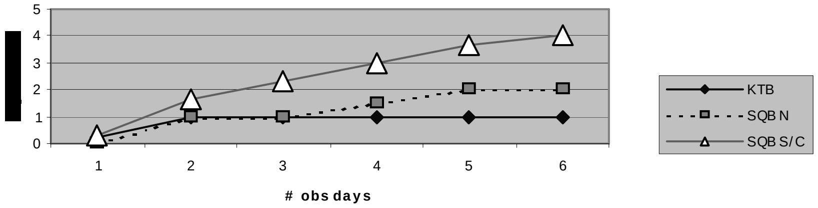
Figures 3.3a-c Means of the cumulative number of partners for each observation day with the focal.



a) 50m Mean Cumulative # of Partners



b) 10m Mean Cumulative # of Partners



c) 2m Mean Cumulative # of Partners

Figures 3.4a-c Means of the cumulative number of partners for each observation day with the focal.

Table 3.1 Very likely cultural behaviors at Suaq Balimbing and Ketambe (C=Customary, H=Habitual, R=Rare, P=Present at unknown frequency, E=absent for clear Ecological reasons, A=Absent without clear ecological reasons; darker fills indicate higher frequency)

Behavior	Category	SQB	KTB	Minimum Learning Distance (meters)
Symmetric scratch	weal skill or convention	C	R	50
Sun cover	weal skill	A	H	50
Twig biting	convention	C	A	10
Nest raspberry	reference variant or convention	C	A	10
Branch scoop	subsistence skill	H	A	10
Autoerotic tool	weal skill	A	C	10
Leaf padding	weal skill	E	H	10
Tree-hole tool-use	subsistence skill	C	A	2
Seed-extraction tool-use	subsistence skill	C	E	2

Table 3.2 Research Sites

site (abbreviation)	**Suaq Balimbing (SQB)**	**Ketambe (KTB)**
year orangutan research began	1992 [4]	1971[1]
location	3°04'N, 97°26'E [4]	3°40' N, 97°40'E [1]
study area size	2000 ha[4]	450 ha[1]
altitude	0-50 m above sea level[4]	300-800 m above sea level[1]
forest type	freshwater swamp, peat swamp and some low hill dipterocarp forest	primary hill and riverine forest, with some secondary forest[1]
annual rainfall	3400mm [2]	3000mm [1]
population density	7 individuals/km^2 [2]	5.5 individuals/km^2 [2]
# habituated orangutans	55 [2]	40 [3]
references	*1. Rijksen 1978* *2. van Schaik et al 1995* *3. te Boekhorst et al 1990* *4. C. van Schaik, unpub.*	

Table 3.3 Information on Focal Individuals

		Observations				Most Recent Offspring		
name	**site**	**first day**	**last day**	**hours**	**days**	**born**	**age (yrs)** †	**sex**
Ans	KTB	5/30/99	4/24/00	227	22	3/96	4	f
Binjei	KTB	7/4/99	4/3/00	322	32	4/98	1	m
Elisa	KTB	6/9/99	4/23/00	137	14	4/98	1	m
Pluis	KTB	9/21/99	10/15/99	63	7	6/93	6	f
Sina	KTB	5/17/99	5/25/00	166	16	1/93	7	m
Yet	KTB	5/10/99	4/6/00	255	24	8/92	7	m
Abby	SQB N	4/17/99	8/16/99	260 (114)*	26 (12)*	6/90	9	f
Beki	SQB N	8/27/97	6/14/99	162 (53)*	20 (6)*	10/97	1	m
Pelet	SQB N	2/2/98	7/30/99	189 (20)*	27 (4)*	1/92	7	m
Ani	SQB S/C	5/19/99	8/15/99	191	19	6/96	3	f
Hanes	SQB S/C	3/21/98	8/7/99	155 (46)*	18 (6)*	1/99	0	?
Tevi	SQB S/C	6/22/99	7/13/99	37	6	1/96	4	m

* Numbers in parentheses are used for any analysis regarding parties at ≤2m distances and for percent time in parties; this information was not available in the database provided by Carel van Schaik. All other information in this table includes the entries from that database.

† Age of current offspring is given based on the midpoint of observations recorded for that individual. In the case of the Suaq Balimbing females, the age of the offspring given is at the midpoint of observations that include the extra data added from Carel van Schaik's database.

Table 3.4 Mean Party Size, Ketambe vs. Suaq Balimbing

	Means		Mann-Whitney (Wilcoxon)	
	KTB	SQB	Test Statistic	P-value
50m	1.445	1.976	21	0.6889
10m	1.065	1.170	25	0.2980
2m	1.005	1.058	**33**	**0.0202**

Table 3.5 Mean Party Size, Ketambe, Suaq Balimbing North and Suaq Balimbing South/Central

	Means			Kruskal-Wallis	
	KTB	SQB N	SQB S/C	Test Statistic	P-value
50m	1.445	1.127	2.824	**7.6154**	**0.0222**
10m	1.065	1.031	1.310	5.4103	0.0669
2m	1.005	1.039	1.076	**6.5897**	**0.0371**

Table 3.6 Mean Party Size (without next youngest offspring), Ketambe vs. Suaq Balimbing

	Means		Mann-Whitney (Wilcoxon)	
	KTB	SQB	Test Statistic	P-value
50m	1.300	1.792	24	0.3785
10m	1.039	1.130	29	0.0927
2m	1.005	1.057	**34**	**0.0131**

Table 3.7 Mean Party Size (without next youngest offspring), Ketambe, Suaq Balimbing North and Suaq Balimbing South/Central

	Means			Kruskal-Wallis	
	KTB	SQB N	SQB S/C	Test Statistic	P-value
50m	1.300	1.127	2.456	**6.5769**	**0.0373**
10m	1.039	1.031	1.229	5.6154	0.0603
2m	1.005	1.039	1.074	**7.1923**	**0.0274**

Table 3.8 Percent time in parties, Ketambe and Suaq Balimbing

	Means		**Mann-Whitney (Wilcoxon)**	
	KTB	SQB	Test Statistic	P-value
≤50m	0.32987	0.49503	25	0.297952
≤10m	0.06369	0.15764	25	0.297952
≤2m	0.00503	0.05428	**33**	**0.020241**

Table 3.9 Percent time in parties, Ketambe, Suaq Balimbing North and Suaq Balimbing South/Central

	Means			**Kruskal-Wallis**	
	KTB	SQB N	SQB S/C	Test Statistic	P-value
≤50m	0.32987	0.22761	0.76245	**6.38462**	**0.04108**
≤10m	0.06369	0.08254	0.23274	2.53846	0.28105
≤2m	0.00503	0.0392	0.06936	**6.58974**	**0.03707**

Table 3.10 Cumulative Number of Partners (by day)

		Mean				Mann-Whitney (Wilcoxon)		Kruskal-Wallis	
distance	day	KTB	SQB	SQB N	SQB S/C	Test statistic	P-value	Test statistic	P-value
≤50m	10	4.4	6.6	4.33	10	17	0.398	3.933	0.140
	15	5.25	9	6	13.5	14.5	0.317	4.403	0.111
≤10m	10	2	4	1.67	7.5	15	0.664	3.824	0.148
	15	2.75	5	2	9.5	11	0.893	**5.880**	**$0.02<P<0.05$**
≤2m	6	0.83	2.83	1.67	4	**31**	**0.039**	**6.595**	**0.037**

Table 3.11 Comparisons of differences between mean cumulative number of partners by observation day for KTB and SQB (signed rank test)

	KTB-SQB	
	Test Statistic	P-value
≤50m	1.2562	0.2091
≤10m	1.3821	0.1669
≤2m	**1.8869**	**0.0592**

Table 3.12 Comparisons of differences between mean cumulative number of partners by observation day for KTB, SQB N and SQB S/C (signed rank test)

	KTB-SQB N		SQB N - SQB S/C		KTB - SQB S/C	
	Test Statistic	P-value	Test Statistic	P-value	Test Statistic	P-value
≤50m	**2.3553**	**0.0185**	**3.2652**	**0.0011**	**2.8906**	**0.0038**
≤10m	**3.2668**	**0.0011**	**3.2032**	**0.0014**	**2.8277**	**0.0047**
≤2m	0.8433	0.3991	**2.0966**	**0.0360**	**2.0966**	**0.0360**

Table 3.13 Indices of Partner Diversity, Ketambe and Suaq Balimbing

	Means		Mann-Whitney (Wilcoxon) Results	
	KTB	SQB	Test Statistic	P-Value
≥50m H'	0.544	0.728	27	0.173
≥50m J'	0.433	0.457	20	0.810
≥10m H'	0.241	0.538	27	**0.036**
≥10m J'	0.189	0.354	26	0.055
≥2m H'	0.178	0.304	19	0.513
≥2m J'	0.155	0.230	19	0.513

Table 3.14 Indices of Partner Diversity, Ketambe, Suaq Balimbing North and Suaq Balimbing South/Central

	Means			Kruskal-Wallis Results	
	KTB	SQB N	SQB S/C	Test Statistic	P-Value
≥50m H'	0.544	0.560	0.896	6.231	**0.044**
≥50m J'	0.433	0.352	0.563	5.756	0.056
≥10m H'	0.241	0.350	0.726	6.982	**0.030**
≥10m J'	0.189	0.231	0.478	6.594	**0.037**
≥2m H'	0.178	0.061	0.547	**6.908**	**0.032**
≥2m J'	0.155	0.046	0.414	**6.908**	**0.032**

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 ≤50m 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

$$\mathbf{MPS} = \frac{\Sigma\, \mathbf{n}_{p}}{\mathbf{a}} + 1$$

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 (≤50m, ≤10m and ≤2m), 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 matrilines 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 ≤50m and ≤10m distance classes, day 6 for the ≤2m 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 ≤2m 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 ≤50m distances. The KTB females had significantly lower MPS at ≤2m 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 ≤2m distances than Ketambe females, and southern/central Suaq Balimbing females spent significantly more time with partners at ≤10m and ≤2m 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 ≤50m, ≤10m and ≤2m distances) are shown in Figures 3.2a-f. The cumulative minimum number of partners for each focal on days 10 and 15 (for the ≤50m and ≤10m distances) and day 6 (for the ≤2m 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 ≤10m distances (for KTB, SQB N, and SQB S/C) and on day 6 for the ≤2m 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 ≤50m and ≤10m 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 ≤2m 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 ≤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 ≤2m 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 ≤2m distances, and often at ≤50m 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 ≤2m 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 ≤50m and ≤10m 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 ≤2m 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 ≤50m and ≤10m 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 ≤2m 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.

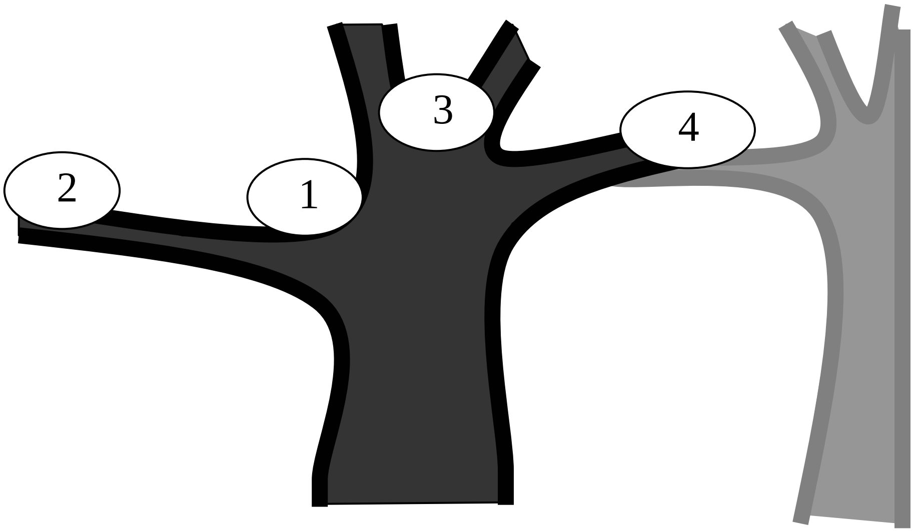


Figure 4.1 Nest positions in tree: 1) on horizontal branch near trunk (often where two horizontal branches emerge); 2) on horizontal branch(es) away from trunk; 3) in acute angle of large branches/trunk split; 4) branches from two trees woven together.

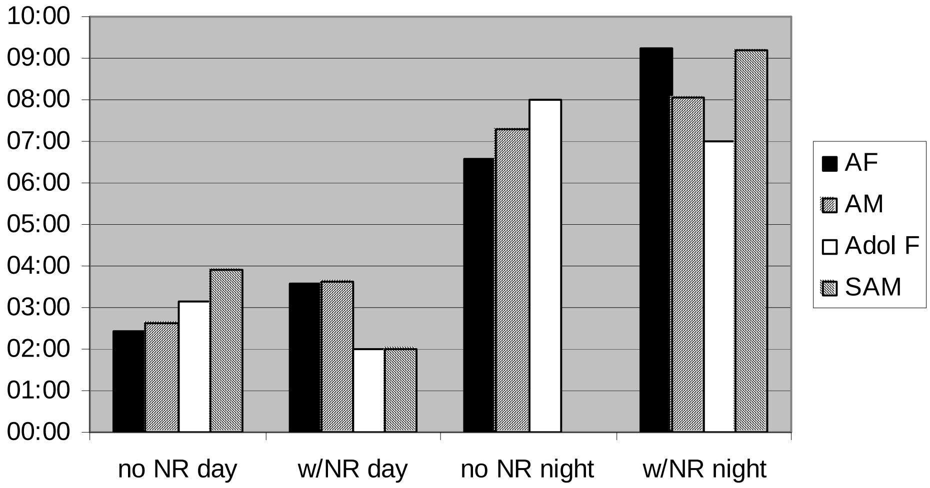


Figure 4.2 Average nest building duration by age/sex class and presence/absence of nest raspberries (NR). *Age/Sex Classes*: AF=Adult (parous) Female; AM=Adult (flanged) Male; Adol. F = Adolescent Female (recently independent, not sexually mature); SAM=Sub-Adult (unflanged, sexually mature) Male.

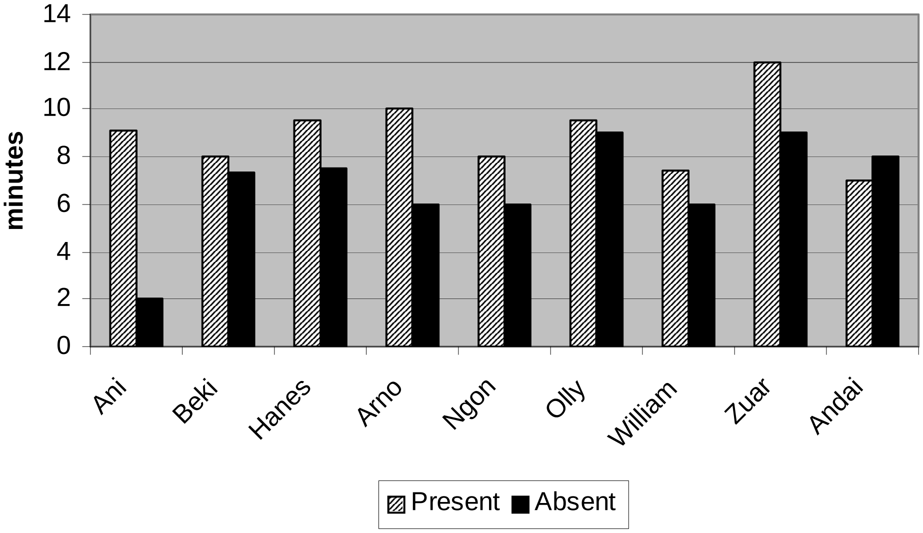


Figure 4.3 Mean night nest building duration for individuals, for nests where the nest raspberry was recorded as present or absent.

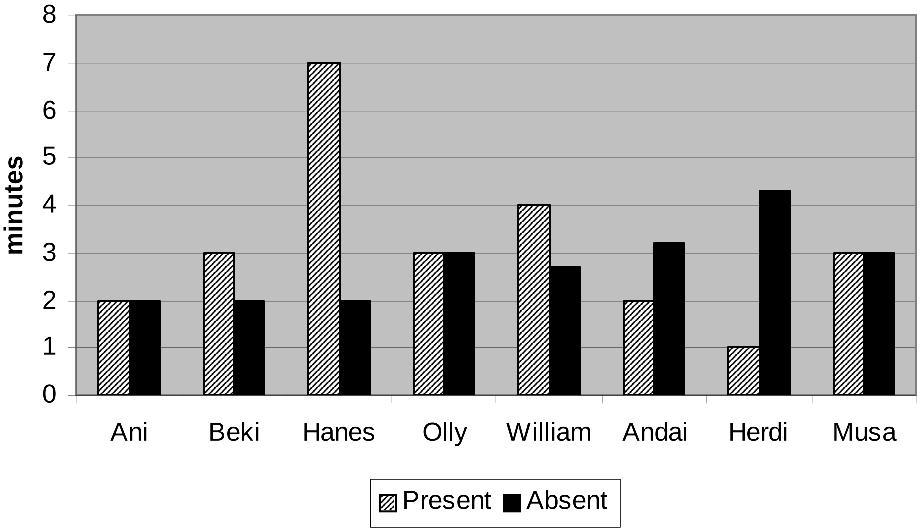


Figure 4.4 Mean day nest building duration for individuals, for nests where the nest raspberry was recorded as present or absent.

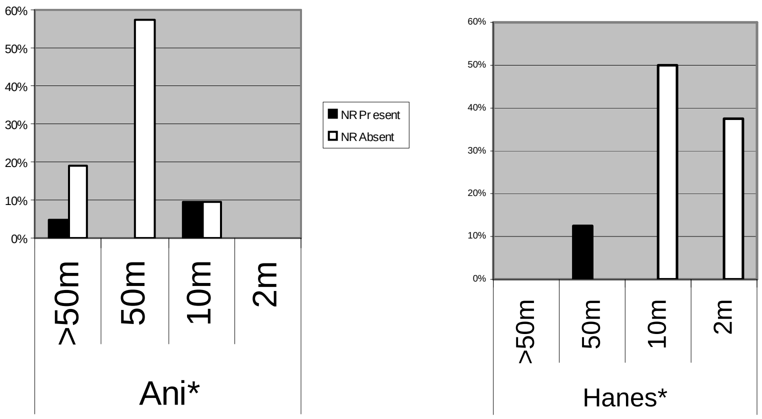


Figure 4.5 Percent of day nests with or without nest raspberries (NR Present or NR Absent) with nearest neighbors at each distance class: >50m (no independent conspecific present), ≤50m, ≤10m or ≤2m, for focals with significant $\boldsymbol{X}^2$ relationships.

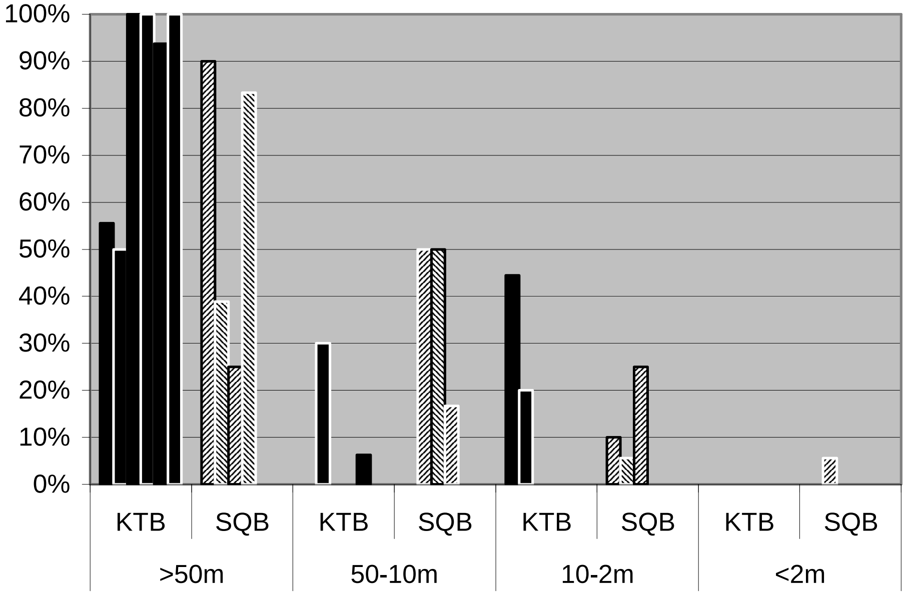


Figure 4.6 Percent of nests built with nearest neighbor at various distance classes for Ketambe (solid) and Suaq Balimbing (striped) females.

Table 4.1 Nest-related behaviors that vary between Suaq Balimbing and Ketambe. (C=Customary, H=Habitual, R=Rare, P=Present at unknown frequency, E=absent for clear Ecological reasons, A=Absent without clear ecological reasons; darker fills indicate higher frequency)

Behavior	Category	SQB	KTB
Sun cover	weal skill	A	**H**
Shelter under nest	weal skill	A	**R**
Nest raspberry	reference variant or unknown	**C**	A
Twig biting	unknown	**C**	A
Multi-tree nests	weal skill	**C**	**P**

Table 4.2 Number of identified focal individuals by age/sex class at each site included in this study, with age/sex class abbreviations defined.

Class	Definition	# at Ketambe	# at Suaq Balimbing
AF	Adult (parous) Female	6	13
AM	Adult (flanged) Male	2	10
SAM	Sub-Adult (unflanged, sexually mature) Male	2	4
Adol. F	Adolescent Female (recently independent, not sexually mature)	1	1
Adol. M	Adolescent Male (recently independent, not sexually mature, no larger than adult females)	0	0

Table 4.3 Presence or absence of nest raspberry during nest building observations at Suaq Balimbing (P: present; A: absent; ?: unknown; **bold** names indicate individuals used for nest raspberry comparisons).

Focal	Age/Sex	Day Nests			*Day Nest Totals*	Night Nests			*Night Nest Totals*	Grand Total
		P	A	?		P	A	?		
Abby	AF		12		*12*	9		1	*10*	**22**
Agus	AM		1		*1*					**1**
Andai	Adol. F	1	6		*7*	1	1		*2*	**9**
Ani	AF	3	18	1	*22*	15	1	2	*18*	**40**
Arno	AM		5		*5*	1	3		*4*	**9**
Beki	AF	3	6		*9*	2	4		*6*	**15**
Bestel	SAM					1			*1*	**1**
Brus	AM		1		*1*	1			*1*	**2**
Budy	AM		3		*3*					**3**
Caca	AM	1			*1*	1			*1*	**2**
David	AM					1			*1*	**1**
Diana	AF					2			*2*	**2**
Hanes	AF	1	7		*8*	2	2		*4*	**12**
Herdi	SAM	1	7		*8*	1			*1*	**9**
Karen	AF					1			*1*	**1**
Mira	AF		2		*2*	1			*1*	**3**
Musa	SAM	1	1		*2*	1			*1*	**3**
Ngon	AM		3		*3*	1	1		*2*	**5**
Novi	AF		2		*2*					**2**
Olly	AM	1	11		*12*	2	2		*4*	**16**
Payung	SAM					1			*1*	**1**
Pelet	AF					2			*2*	**2**
Sela	AF		1		*1*					**1**
Tevi	AF		6		*6*	2			*2*	**8**
William	AM	1	12		*13*	5	1		*6*	**19**
Yinta	AF		2		*2*			1	*1*	**3**
Zuar	AM		4		*4*	1	1		*2*	**6**
Grand Total		**13**	**110**	**1**	***124***	**54**	**16**	**4**	***74***	**198**

Table 4.4 Mean day and night nest building duration for each age/sex class at Suaq Balimbing, with comparisons of day and night nest building duration within each class.

	Day Nests		Night Nests		Wilcoxen Signed Rank	
	Mean building duration	N	Mean building duration	N	Test Statistic	P-value
AF	1.8	12	8.2	13	2.85	0.00443
AM	2.4	11	7.5	10	2.63	0.00867
Adol F	3	1	7	1	--	--
SAM	2.7	3	9.2	5	1.34	0.181

Table 4.5 Day and Night Nests With or Without Nest Raspberries

Focal	**Ani**	**Becky**	**Hanes**
# day nests	21	9	8
# with nest raspberry	3	3	1
Average duration with raspberry (minutes)	2.7	3.3	7
Range of duration with raspberry (minutes)	2-4	2-5	7
Average duration without raspberry (minutes)	2.7	2.2	2.4
Range of duration without raspberry (minutes)	1-7	2-3	1-4
Test Statistic	25.5	4	n/a
P-Value	0.915	0.165	n/a
# night nests	16	6	4
# without nest raspberry	1	4	2
Average duration with raspberry (minutes)	9.1	8	9.5
Range of duration with raspberry (minutes)	4-13	5-11	8-11
Average duration without raspberry (minutes)	2	7.3	7.5
Range of duration without raspberry (minutes)	2	5-11	6-9
Test Statistic	n/a	4.0	1.0
P-Value	n/a	0.812	0.699

Table 4.6 Individual comparisons for nest position and presence or absence of the nest raspberry (italicized values are with Yates' correction).

	Day Nests		Night Nests	
	X^2	P-value	X^2	P-value
Ani	1.13	0.770	--	--
Beki	1.50	0.682	3.00	0.223
Hanes	8.00	**0.046**	2.00	0.379
Arno	1.33	0.513	--	--
Olly	5.45	0.141	2.00	0.368
William	*0.00*	*1.000*	*0.00*	*1.000*
Andai	0.88	0.646	0.00	1.000
Herdi	3.43	0.180	--	--
Musa	*0.00*	*1.000*	--	--

Table 4.7 Comparisons for pooled Adult Females (AF) and Adult Males (AM) of nest position and presence or absence of the nest raspberry.

	Day Nests		Night Nests	
	X^2	P-value	X^2	P-value
AF	5.74	0.125	1.60	0.449
AM	5.01	0.171	1.28	0.735

Table 4.8 Paired-sample signed rank tests for distance between nest and top of tree for nests with and without nest raspberries.

	Day Nests		Night Nests	
	Test statistic	P-value	Test statistic	P-value
AF	0.00	0.999	0.80	0.423
AM	0.89	0.371	1.08	0.279
SAM	0.89	0.371	--	--

Table 4.9 Results of X^2 analysis of nearest neighbor distance effects on whether a nest raspberry was given for either day nests or night nests (**bold** are significant values, italicized are with Yates' correction)

	Day Nests		Night Nests	
	X^2	P-value	X^2	P-value
Ani	6.30	**0.043**	1.07	0.59
Beki	*0.08*	*0.777*	*0.00*	*1.000*
Hanes	8.00	**0.018**	2.00	0.368
Arno	--	--	*0.00*	*1.000*
Olly	2.18	0.336	4.00	0.135
William	2.44	0.296	*0.00*	*1.000*
Andai	2.92	0.405	--	--
Herdi	1.14	0.565	--	--
Musa	*0.00*	*1.000*	--	--

Table 4.10 Results of X^2 analysis (*with Yates' correction*) and Fisher's Exact Test (FE2P = P-value for two-tailed test) of nearest neighbor's line-of-sight relationship with whether a nest raspberry was given when day nests or night nests were built.

	Day			Night		
	X^2	P-value	FE2P	X^2	P-value	FE2P
Ani	*0.33*	*0.568*	0.48	*0.00*	*1.00*	1.00
Hanes	*1.47*	*0.225*	0.13	*0.19*	*0.665*	0.33
Ngon	--	--	--	*0.00*	*1.00*	1.00
Andai	*0.00*	*1.000*	1.0	--	--	--
Herdi	*0.00*	*1.000*	1.0	--	--	--

Table 4.11 Results of X^2 analysis (*with Yates' correction*) of focal female's infant distance effects on whether a nest raspberry was given.

	X^2	P-Value
Ani Day Nests	*0.7*	*0.402*
Beki Day Nests	*0.0*	*1.00*
Beki Night Nests	*0.0*	*1.00*

Table 4.12 Comparisons of percent of multi-tree nests (AM=Adult Male, AF=Adult Female), Mann-Whitney/Wilcoxon.

	W (test statistic)	P-value
AM v. AF Day Nests	14.0	0.383
AM v. AF Night Nests	11.0	0.096
Day v. Night Nests AF	8.0	0.687
Day v. Night Nests AM	10.0	0.212

Table 4.13 Dispersion tendency for females (percent of night nests without independent conspecific <50m distant - percent time without independent conspecific <50m distant) at Ketambe and Suaq Balimbing (Signed Rank Test).

	KTB	SQB
Mean	0.16	0.07
Test statistic	1.47	1.28
P-value	0.142	0.201

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 Galiginae 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 ≤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 (>50m, ≤50m, ≤10m or ≤2m) 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 >50m) 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 >50m, ≤50m, ≤10m or ≤2m) 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 aerially 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.

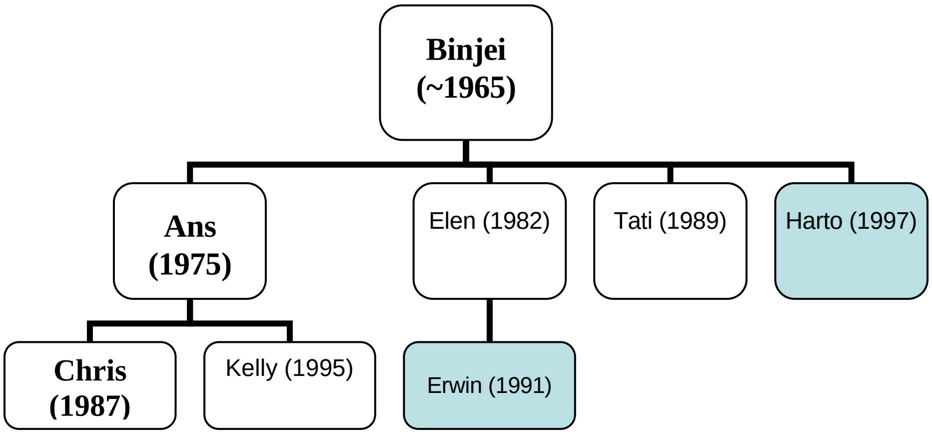
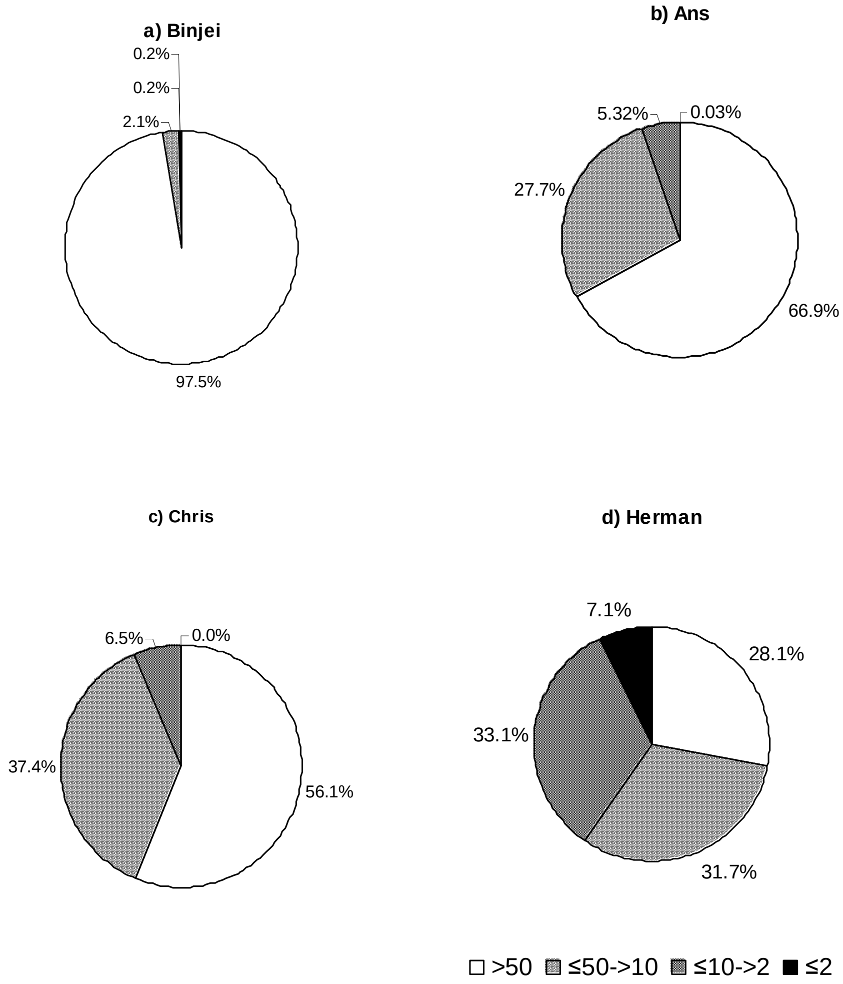


Figure 5.1 Binjei's family, with year of birth noted (males shaded, females open, key focal animals in **bold**).



Figures 5.2a-d Percent of focal observation time that each focal had nearest neighbors at ≤50m, ≤10m, and ≤2m.

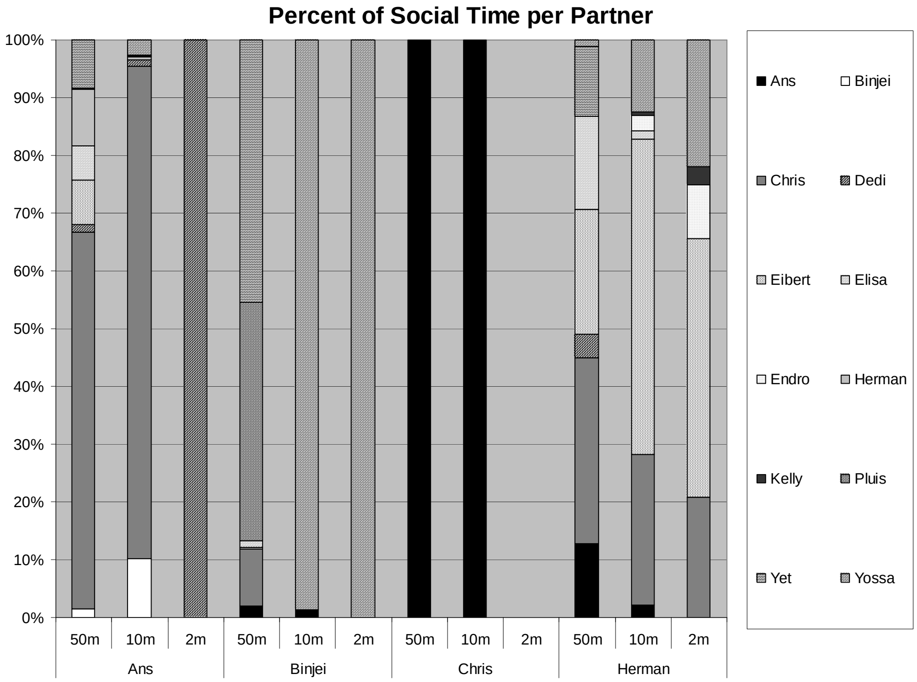


Figure 5.3 Percent of each focal's time spent in parties that was spent with each social partner for ≤50m, ≤10m, and ≤2m distance classes.

Table 5.1 Focal Observaion Times for Rehabilitants and Their Descendents

	Binjei	Ans	Chris	Herman
Focal Observation Hours (Hours:Minutes)	322:09	227:11	40:52	98:21
Focal Observation Days	32	22	5	10

Table 5.2 Observed and Reported Unusual Behaviors (N=Noted in this study (videotape or focal follow notes); R=Reported by other Ketambe researchers; **bold** indicates rehabilitant or descendant of rehabilitant).

Focal	**Observation Hours**	**enter camp**	**taking/ handling clothes**	**taking/ chewing cardboard**	**get water near pump**	**travel on ground**
Ans	227:11	N	R	R	N	N
Binjei	322:09	R	R	R	R	R
Bobi	44:05					
Chris	40:52	N	N			
Dedi	127:28	R				
Doba	30:54	R				
Eibert	25:05					
Elisa	136:41					
Herman	98:21	N,R	R	R	N	N
Pluis	62:39	R				
Sina	165:46					
X	38:16					
Yet	255:12	R				
Yop	49:52					
Yossa	0	N				

Table 5.3 Orangutans entering camp, August – September 1999.

Date	**Name**	**Time Arrived Camp**	**Time Left Camp**	**Major Activities**
8/3/1999	Chris	11:32	13:38	eat *Ficus racemosa,* watch a person pump water
8/3/1999	Yossa (adolescent male, son of Yet)	11:32	13:38	eat *Ficus racemosa*
8/14/1999	Chris	14:00	Nest beside camp (time unknown)	eat *Ficus racemosa*
8/14/1999	Herman	14:00	Nest beside camp (time unknown)	eat *Ficus racemosa*
8/14/1999	Ans and Kelly	14:00	Nest beside camp (time unknown)	eat *Ficus racemosa*
9/24/1999	Ans and Kelly	8:27	Nest beside camp (time unknown)	eat *Ficus racemosa*, drink water from behind pump
9/25/1999	Ans and Kelly	6:20	8:40	eat *Ficus racemosa*
9/26/1999	Ans and Kelly	7:32	Nest beside camp (time unknown)	eat *Ficus racemosa*
9/27/1999	Ans and Kelly	6:40	11:58	eat *Ficus racemosa*

Table 5.4 Other focal orangutans with whom rehabilitants or their descendents were observed at ≤50m, ≤10m, and ≤2m distance classes, with percent of total time spent with partners at that distance class.

Age/Sex Classes: AF=Adult (parous) Female; AM=Adult (flanged) Male; Adol = Adolescent (recently independent, not sexually mature); I/J=dependent Infant/Juvenile; SAM=Sub-Adult (unflanged, sexually mature) Male.

Scores: P=Partner during focal follow of rehabilitant/descendant; O=rehabilitant/descendant was partner during focal follow of Other.

Partners		Ans			Binjei			Chris			Herman		
	Age/Sex	50 m	10 m	2 m	50 m	10 m	2 m	50 m	10 m	2 m	50 m	10 m	2 m
Ans	AF	---	---	---	P	P		P, O	P, O		P, O	P, O	
Binjei	AF	P, O	P, O		---	---	---	O					
Bobi	AM	O	O										
Christ	Adol F	P, O	P, O		P			---	---	---	P	P	P
Dedi	SAM	P, O	P, O	P	O			O	O	O	P, O	O	
Doba	AM				O						O		
Eibert	Adol M	P			P						P	P	P
Elisa	AF	P			P			O			P, O	P	
Endro	I/J M											P	P
Herman	Adol M	P, O	P, O					O			---	---	---
Kelly	I/J F	---	---	---								P	P
Pluis	AF	P	P		P, O								
X	SAM										O		
Yet	AF	P	P		P, O						P	P	
Yossa	I/J M		P			P	P				P	P	P

Chapter 5

REHABILITANT ORANGUTANS AND THEIR DESCENDANTS AT KETAMBE: THE ROLE OF SOCIAL LEARNING IN INTRA-POPULATION DIFFERENCES

Introduction

Ex-captive orangutans introduced into natural populations provide a unique opportunity to explore issues related to social learning of variable behaviors. In this chapter, I will examine the unusual behaviors exhibited by a rehabilitant orangutan and descendants of rehabilitants at Ketambe, and evidence for opportunities for social learning by other resident orangutans.

To address the possibility of culture in non-human species, Imanishi (1952; reviewed in Nishida, 1987; and Wrangham et al., 1994) defined culture as “socially transmitted adjustable behavior.” To investigate the distribution of cultural behaviors in chimpanzees and orangutans, researchers have looked for evidence of behaviors that vary between populations without any clear, relevant ecological differences (van Schaik et al., 2003a; Whiten et al., 1999, Chapter 2; Whiten et al., 2001).

However, “socially transmitted adjustable behavior” can also vary within populations. Sometimes, it is simply a matter of degree: tree-hole tool use by orangutans (*Pongo pygmaeus abelii*) at Suaq Balimbing is far more commonly performed by females in the southern/central social cluster than the northern social cluster (van Schaik et al., 2003b). At other times, behaviors can be absent in certain age or sex classes: in chimpanzees (*Pan troglodytes*) at Mahale, grooming-hand-clasp is performed only by adults, although younger individuals appear to know how to perform it (Nakamura, 2002). Similarly, the leaf-clip display is used by certain age/sex classes in chimpanzees in different contexts at different sites. In Mahale, it is performed by young adult males and estrus adult females (Nishida, 1980), but in Taï, adult males leaf-clip as part of their drumming display sequence (Boesch, 1995).

In some cases, variation in behavior can more clearly be attributed to different opportunities for social learning. Among Japanese macaques (*Macaca fuscata*), novel behaviors spread most rapidly to the innovators' most frequent social partners, such that more than four years after the innovation of sweet-potato washing, those outside the innovator's social circle still did not display the behavior (Kawamura, 1959; reviewed in Nishida, 1987). Other innovations in this species involving special louse-egg-handling techniques during grooming spread first through one matriline (Tanaka, 1998). It also appears that the unusual behaviors exhibited by rehabilitant orangutans can be attributed to observational learning differences, in that the orangutans performing these behaviors are more often in close proximity to humans who (usually inadvertently) model behaviors that rehabilitant orangutans later reproduce (e.g. Russon and Galdikas, 1993).

In this chapter, I will provide evidence for the perpetuation of unusual behaviors in rehabilitant orangutans and their descendants, and highlight what it reveals about social learning. One rehabilitant female, her wild-born daughter and her grand-daughter continued to perform unusual and possibly maladaptive behaviors, 27 years after her initial introduction to the site. Wild residents and their descendents at Ketambe do not perform these behaviors, despite evidence for opportunities to learn the behaviors from the rehabilitants and their descendants. The persistence of these behaviors in the rehabilitant descendants is a clear example of vertical social transmission of a limited, matrilineal tradition among orangutans. The absence of such behaviors in wild orangutans, despite evidence of opportunities for social learning, indicates selectivity in either the types of behaviors or the models chosen for observational learning in orangutans.

Selectivity in social learning

Social transmission of adjustable behaviors refers to some form of learning that is influenced by social interaction. Generally, we assume that observation of a model performing a behavior has influenced the learner to understand something new about the environment and its affordances, or to observe and replicate specific aspects of the model's behavior (cf. social learning or imitation, Heyes, 1993). While debate has raged over the exact definitions and processes involved in such learning, there is little doubt that the ability to learn socially is widespread in anthropoid primates and many other vertebrate taxa (see Chapter 1 for review). Observational learning between conspecifics can lead to "vertical" social transmission (offspring learning from a parent), "horizontal" social transmission (individuals of the same generation learning from one another) or "oblique" social transmission (unrelated individuals of different generations learning from one another, Cavalli-Sforza and Feldman, 1981).

Socially learned behaviors can include different types of skills and signals (see Chapter 2). While mockingbirds may replicate sounds somewhat indiscriminately (e.g. car alarms in cities), most primates studied appear more selective about which behaviors they will reproduce. A laboratory study of chimpanzees found that they were most likely to imitate behaviors that were clearly useful in solving a problem; the chimpanzees follow strategies they see working to achieve a goal, and ignore other unsuccessful strategies that are demonstrated (Myowa-Yamakoshi and Matsuzawa, 2000). Another such study revealed that chimpanzees are more likely to reproduce behaviors that are just beyond their current level of competence than behaviors that are too simple or too advanced (Myowa-Yamakoshi and Matsuzawa, 1999).

Primate social learning may also depend on the learner's relationship with the model or the perceived value of the model. Field experiments with chimpanzees showed that they were much more likely to attend to the behavior of models who were older or in the same age-group as themselves, and unlikely to attend to models younger than themselves (Biro et al., 2003). A similar process may explain the spread of sweet-potato washing in Japanese macaques (described above). This preference for attending to the actions of older demonstrators implies that learners seek models likely to know something useful. This interpretation is bolstered by another laboratory tool-use experiment with chimpanzees showing that they observe experienced tool-users only if they have not successfully completed the task themselves (Hirata and Morimura, 2000).

Finally, research has revealed the importance of affinitive social bonds in observational learning. Laboratory studies with capuchin monkeys (*Cebus apella*) show that innovation and learning are inhibited when social vigilance is required (Fragaszy and Visalberghi, 1990). Differences in the expression of tool-use between and within primate species are related to social tolerance (van Schaik et al., 1999). Rehabilitant orangutans are more likely to copy behavior of either humans or other orangutans with whom they share an affinitive bond (Russon and Galdikas, 1995).

Rehabilitant orangutans

There are several past and present projects focused on reintroducing captive orangutans into wild orangutan habitat. Early projects attempted to do this at locations where wild orangutans were found, with researchers simultaneously studying the wild population and their ex-captive charges (Rijksen, 1978). Researchers have noted the propensity of these young rehabilitant orangutans to copy the behaviors they observe while in the care of humans, even if such behaviors are not rewarded, occasionally dangerous, and frequently discouraged by human caretakers (Russon and Galdikas, 1993).

At Ketambe, an orangutan rehabilitation project was started in 1971(Rijksen, 1978). Thirty-one ex-captive orangutans were brought to the Ketambe field station between July 1971 and August 1974. Little or nothing was known about the capture and experience of the (generally juvenile) orangutans prior to their confiscation and delivery to the field station. The typical track for a healthy rehabilitant upon arrival was (1) to be kept in a cage at the site for a few weeks or months under quarantine, (2) to be released around camp, receiving daily provisions of food but allowed to roam freely, then (3) have provisioning withdrawn (and often be transported to the far end of the site from camp) as they became competent at surviving in the wild. The young rehabilitants generally formed a cohort that socialized frequently during the period of provisioning. After release at Ketambe, several rehabilitant orangutans died through predation (clouded leopard attacks) or disease, and several others disappeared (Rijksen, 1978) or were transferred to other areas for release (C. van Schaik, pers. com.).

Based on Rijksen's recommendations, the rehabilitation project at Ketambe was halted in 1978, and all of the remaining orangutans not successfully reintroduced to the wild were sent to Bukit Lawang, in the town of Bohorok at the eastern edge of Gunung Leuser National Park, approximately 100km east of Ketambe (C. van Schaik, pers. com.). A rehabilitant male, Usman, left the Ketambe area in 1972, and was seen by a reliable witness about 15km away in association with two wild orangutans in 1974 (Rijksen, 1978). Two ex-captive orangutans remained in the wild at Ketambe, successfully bred with wild orangutans, and were regularly seen in the following years: the females Binjei and Getty. Getty was found dead near the Ketambe River on 16 December 1997. The young infant she was nursing at that time died shortly after Getty's body was found (S. Utami Atmoko, pers. com.). Getty is survived by her adolescent son, Herman, who was often seen in the company of other young orangutans in the Ketambe population in 1999-2000.

History of the Binjei matriline

A female orangutan was brought to Ketambe in 1972, after being confiscated in the town of Binjei near the regional capital, Medan (Rijksen, 1978). She was estimated to be about 7 years old at that time. This orangutan, named Binjei, has since had four offspring and three grand-offspring (Figure 5.1). Elen and Erwin were not seen often in the mid-to-late 1990's, and they may have died (S. Utami Atmoko, pers. com., S. Wich, pers. com.). Tati was occasionally seen at the edge of the study area near the Alas River in 1999 (this study, S. Utami Atmoko, pers. com.) Harto was still nursing and dependent on Binjei at the time of this study. Ans was nursing Kelly, and Chris was an independent (nulliparous) adolescent female at the time of this study.

As a sub-adult, Binjei became the dominant female among the rehabilitant orangutans. When the dominant male among the rehabilitants was removed from the population, Binjei performed behaviors similar to those the male had performed when new rehabilitants were introduced. Where the male had inspected the genitals of newly introduced ex-captive females, and on at least two occasions mounted them (though failing to achieve intromission), Binjei would restrain new females and insert a finger or thumb into their vagina (while stimulating her own genitals with her hallux). Such behavior has not been reported for other female orangutans (Rijksen, 1978).

Rijksen (1978) further reports that Binjei formed close social bonds with several rehabilitant females. As an adolescent, Binjei also formed a close, long-term bond with the adolescent female Yet, a wild resident orangutan. After reaching sexual maturity, Binjei (like most maturing female orangutans) became less socially tolerant with her peers. Rijksen reports that

Binjei became “aggressively intolerant towards other females…, including her former bond partner [Yet]” (1978, pg. 292).

Unusual behaviors seen in rehabilitant orangutans

Rehabilitant orangutans, even once fully reintroduced to the rainforest habitat, frequently exhibit behaviors not seen in wild orangutans, which are likely to be a result of their captivity and subsequent close contact with humans (Rijksen, 1978; Russon and Galdikas, 1993; Russon and Galdikas, 1995). For instance, recent rehabilitants were far more likely to travel on the ground and approach humans than wild orangutans at Ketambe (Rijksen, 1978; see Russon and Galdikas, 1993 for similar behaviors in Bornean orangutans).

Rehabilitants seem to engage in more affinitive behaviors than wild orangutans, often in ways similar to interactions most often seen between mothers and their young in wild orangutans. One behavior reported for Binjei and the other rehabilitant orangutans at Ketambe was the tendency to “bridge” for one another (reach from one tree to the next while traveling, then hold branches from both trees while the other crosses on or next to the bridging orangutan). Rijksen (1978) reports that he observed Binjei helping a new juvenile rehabilitant, who was trapped in a tree, across a gap, noting that this was the first social interaction observed between the two orangutans. Bridging is most often performed by mothers for their juvenile offspring (though females have sometimes been seen to assist their heavier male consorts in this way). Binjei also “fostered” some of the younger rehabilitants, even suckling the ex-captive male Bumi concurrently with her own daughter Ans. Allo-grooming was more common among rehabilitants than wild resident orangutans (though still rare), most often occurring between orangutans who were in frequent close association (what Rijksen describes as “bond-partners”, 1978). Of the few allo-grooming incidents seen with wild orangutans, two were between an adolescent wild orangutan female (Yet) and a rehabilitant juvenile female (Barby). Most other allo-grooming observations were of wild mothers grooming their offspring.

Rijksen (1978) further reports that rehabilitant orangutans were commonly seen chewing cloth or cardboard taken from the field station. He notes that wild orangutans sometimes chewed cloth or cardboard they took from the rehabilitant orangutans, but he does not report wild orangutans coming into camp to take these materials themselves.

Unusual behaviors in rehabilitant orangutans represent clear evidence of behavioral variability within populations. The perpetuation of these behaviors, their distributions within the population at Ketambe, and the social relationships of rehabilitants and their descendants over time illuminate aspects of the role of social learning in behavioral variation within a population. I will present evidence of the persistence of unusual behaviors in the descendents of rehabilitant females over decades and generations. I will show that other, wild resident orangutans probably had opportunities to learn these behaviors, but do not exhibit the behaviors, and I will discuss some possible interpretations for this evidence.

Methods

Both wild-born and rehabilitant orangutans were observed at the Ketambe research site in Gunung Leuser National Park (see Table 3.2 and Figure 2.1).

Only independent adult and adolescent orangutans (both wild resident and rehabilitant matrilines) were chosen for focal follows for this study. Daily activities of focal animals, including social encounters and nest building bouts, were recorded from May 1999 to May 2000 by M. Isa, Nuzuar S. Hut and me. Table 5.1 shows focal observation time for Binjei, Ans, Chris (see figure 5.1) and Herman (adolescent son of the rehabilitant female Getty). Including these four, 14 identified orangutans were followed for a total of

1625 hours.

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. Social contacts with juveniles and adolescents were noted only when their mothers were not within the same distance class (e.g. if the mother was less than 50m but more than 10m away, and her dependent juvenile offspring were within 10m, it would be recorded as 50m for the mother, but the juvenile would only be entered as a unique social partner in the 10m or less distance class). 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.

Videotapes of orangutan behaviors were captured by Nuzuar S. Hut and me on an *ad libitum* basis, using a Canon ES4000 Hi-8 analog camcorder. For each incident videotaped, we noted the identity of the orangutan(s) being videotaped, the identity of any food species (or tree species used for nest-building), and the time (for comparison to the time-code recorded by the camera). In all, about 34 hours of orangutan behavior were videotaped at Ketambe. Some of the videotapes were of animals being followed for focal data, while some was not.

During the months of August and September 1999, M. Isa kept records of which orangutans entered camp, noting the identity of the orangutan, the time they entered and left camp, and the major behaviors performed in camp.

I discussed the unusual behaviors of rehabilitant orangutans and their descendants with several researchers and field assistants while I was at Ketambe in 1999 and 2000. For further clarification and confirmation, I corresponded with Chris Schürmann, who studied orangutans at Ketambe from 1975-1979, Carel van Schaik, who observed orangutans at Ketambe from 1977-1992, Sri Suci Utami Atmoko, who has studied orangutans at Ketambe from 1993 to the present, and Serge Wich, who observed orangutans at Ketambe from 1997 to the present.

Results

Table 5.2 provides a summary of which orangutans were observed or reported in camp, taking cloth or cardboard, drinking near the camp water pump (this study only) or coming to the ground (this study only). In all cases, it is only rehabilitant orangutans or their descendants who perform these behaviors at Ketambe, though wild residents have been reported entering camp.

Other’s reports of unusual behaviors in rehabilitants and their descendants, and wild residents’ opportunities to observe them

Chris Schürmann confirmed that rehabilitant orangutans took cloth and cardboard from camp from 1975-1979. He is certain that wild orangutans never took clothes or cardboard in that time. He noted that the wild adult male Jon, the wild female Yet, and several wild subadult males were frequent social partners of Binjei.

Carel van Schaik reported Binjei and other rehabilitants chewing cardboard taken from camp and taking clothes. He had seen rehabilitants playing with the water pump in camp. He recalled the wild resident males Doba and Jon, and the wild resident females Yet and Pluis coming into camp, but never saw wild resident orangutans taking clothes or cardboard.

Sri Suci Utami Atmoko reported that Getty and Herman, as well as Binjei, Ans and Chris, were known to take clothes and other items from camp. She had never observed or heard of the wild (non-rehabilitant-descended) orangutans taking artifacts or materials from camp, though the wild orangutans Yet, Nur, Boris and Dedi did sometimes enter camp.

Serge Wich confirmed that Binjei, Ans and Chris were the only orangutans coming into camp and taking things in recent years. He noted that few other wild orangutans have entered camp recently, but that Yet probably got the closest to camp the most often.

Several researchers and assistants at Ketambe in 1999 and 2000 indicated that Binjei, Chris and Ans sometimes came into camp and took things, and they advised caution with leaving blankets, shoes and clothes out and unattended where orangutans might take them. They were also very careful to immediately burn cardboard and other refuse to prevent the local wildlife (primarily the orangutans and some long-tailed macaques, *Macaca fasicularis*) from taking things. While I was there in 1999, one researcher lost a shoe that was later found torn and with gnaw-marks, and another discovered a blanket lodged up in a tree at the edge of the clearing around camp (there were no human witnesses to what transpired, but the consensus was that orangutans were to blame).

Video records of rehabilitant descendants in camp

On 31 May 1999, Nuzuar and I followed Chris (I took notes while Nuzuar videotaped). We met her in the forest not far from camp at 08:00. At 11:28 she began moving directly toward camp. By 11:45 she had reached camp and was carrying some dark blue cloth, apparently the tattered remnants of a T-shirt. We did not see her enter camp to take it, so we suspected she had cached it in a tree at the edge of camp (she had probably stolen it off a clothesline at camp at least several days earlier -- I never discovered who had lost a dark blue T-shirt, or when it might have been taken). She kept the cloth with her, focusing her activities on it (sucking, tugging, or twisting it) for stretches of up to 46 minutes, or merely carrying it in a hand (in her mouth or draped over a shoulder), until 16:22. Chris remained in camp, foraging on unripe *Aglaia* sp. fruits, *Ficus racemosa* fruits and the leaves of *Erythina subumbrans*, some epiphyte stems and the cambium of a liana (all items included in wild resident orangutan diets). Ans and Kelly came into camp at 17:18, and remained there with Chris until 19:02 when they built their night nests (see Appendix II for details).

Chris was also videotaped chewing and playing with cloth on 28 April 2000 (by Nuzuar). She spent at least 1 hour and 45 minutes handling cloth on that day.

Herman was videotaped in camp on 29 April 2000 (by Nuzuar). He came to the ground behind the water pump to drink water from a puddle.

Recorded camp visits

Orangutans entered camp on six days while notes were kept (Table 5.3). Herman, Chris, Ans (and her dependent daughter Kelly), and Yossa (the adolescent son of the wild resident female Yet) came into camp during these observations. They primarily entered camp to eat the fruits (figs) of *Ficus racemosa*, though Ans also drank from a puddle of water behind the pump one day. They stayed as few as 2 hours and 20 minutes, but more often remained and built night nests adjacent to camp.

Social partners of rehabilitants and their descendants

Figures 6.2a-d show the percent of observation time that each focal had nearest neighbors at ≤50m, ≤10m, and ≤2m. Binjei, who was nursing a small infant, spent very little time in parties during this study. Herman, an adolescent male, spent over half of his time in parties. The percent of each focal's time spent in parties that was spent with each social partner for ≤50m, ≤10m, and ≤2m distance classes are shown in Figure 5.3. While Chris and Ans spent the majority of their social time in parties with other members of their matriline, this was not the case for Binjei. Herman spent more time with wild orangutans than with rehabilitants or their descendants.

Table 5.4 indicates other focal orangutans that were recorded with rehabilitants or their descendants as social partners in these distance classes, and which social partners the rehabilitants were seen with during their focal follows. Seven wild orangutans were seen with members of the Binjei matriline during their focal observations, including three not seen during focal follows of members of the Binjei matriline. Four wild orangutans were seen with Herman, including two not seen during Herman's focal follows. Records of where these social interactions occurred were not kept, so it is unclear how much of this time was in camp where clothes or other items could be taken and where cloth handling usually occurred

Discussion

Rehabilitant orangutans introduced in habitats with resident wild orangutan populations constitute a sort of unintentional field experiment on the acquisition and persistence of unusual or novel behaviors within a given habitat. The fact that Ketambe's successful rehabilitants and their descendants continue to perform behaviors not seen in wild orangutans is relevant to the issue of social learning in two important ways. First, the fact that these unusual behaviors have been passed down to at least two descendant generations from Binjei, an ex-captive, is clear evidence for vertical social transmission of learned behaviors. Second, the fact that this behavior has not spread from the innovators to other members of the population, despite evidence of opportunities for social learning, indicates that orangutans are selective about what behaviors they adopt after observing them in others.

During the 1970s, when several rehabilitant orangutans were at Ketambe, many of them showed handling of clothes, and Binjei (and perhaps others) were known to eat cardboard taken from the garbage pit. In our terminology (Chapter 2), the handling of clothing would be a weal skill or unknown, whereas the cardboard chewing could be a subsistence skill (since the contents are actually ingested). However, the practice of taking clothes or other items from camp and chewing or handling them has not spread to the rest of the Ketambe population. It is limited to two surviving matrilines: Binjei and her descendants; and Herman (son of the rehabilitant female Getty).

During this study, Chris was the orangutan most often seen going into camp, taking clothes and other items, carrying them and chewing them for extended periods of time. Chris probably learned this behavior from Ans, who had learned it from her mother, Binjei. Binjei may have been the first to adopt this behavior at Ketambe, or she may have learned it from the other rehabilitant orangutans that were there in the 1970's. This fits the definition for "tradition" (a behavior pattern persisting from the innovator's generation to future generations), a proposed condition for attributing culture to a species (McGrew, 1992; McGrew and Tutin, 1978). As this behavior does not appear to serve any adaptive purpose (and in fact may be maladaptive, as it is actively discouraged by the researchers and assistants in camp), it may also fit the "non-subsistence" condition for culture (McGrew, 1992; McGrew and Tutin, 1978).

In just one year of focal observations, four orangutans from rehabilitant lineages came into contact with eight independent wild orangutans. Though records do not indicate whether these contacts took place at camp, where cloth and cardboard might be acquired and there would be opportunities to learn the associated behaviors, it is likely that such opportunities occur. The wild orangutans at Ketambe are very well habituated to human activities after three decades of regular contact with human observers, so human presence and activities should not inhibit wild orangutans from approaching camp. In the past, Binjei had regular, affinitive social contact with Yet (when the two were adolescents), and many wild orangutans (especially males, including Jon, Doba and Boris) followed them and visited camp. Moreover, the wild residents Yet, Nur, Boris and Dedi came into camp during the 1990's, with Yet probably visiting camp most frequently. It is likely that Yet and other wild resident orangutans had many opportunities over the years to observe Binjei, Ans, Chris, Getty or Herman acquire, chew and handle cloth, but the wild residents did not add these behaviors to their repertoires.

Ex-captive orangutans are known to use social learning cues about what items are edible in their new environment. They appear to proceed cautiously, sampling a small quantity of a food item used by a human or another orangutan, then later eating more and adopting the item as part of their dietary repertoire (Rijksen, 1978; Russon, 2002). Rijksen (1978) reported that wild orangutans sometimes chewed cloth or cardboard they took from the rehabilitant orangutans, but he does not report wild orangutans coming into camp to get these materials themselves. Perhaps the wild orangutans were using a similar strategy, but found cloth and cardboard unpalatable upon testing.

The fact that no wild orangutans (original Ketambe residents or descendants of these original residents) engage in cloth-handling or cardboard-chewing behaviors supports the proposal that orangutans are choosy about which behaviors to emulate and/or which models to observe for social learning. To the wild residents, the behavior of the introduced individuals and their descendants is apparently not worth copying, despite ample opportunities to observe these behaviors.

However, the descendants of introduced individuals persist in these unusual behaviors. The persistence of traditions through vertical social transmission within these lineages attests to either the importance of early experience in setting behavioral preferences in orangutans, or the high regard the mother holds as a model in orangutan social learning. This indicates that, while rehabilitants' peculiar behaviors are unlikely to spread throughout the population, caution must be exercised in orangutan reintroduction if such "unnatural" behaviors are to be minimized in the rehabilitant's descendants.

How can the universality of the apparently functionless nest raspberry at Suaq Balimbing (Chapter 4) be reconciled with the failure of the apparently functionless "cloth handling" tradition to spread to others at Ketambe? It could merely be an issue of time-depth in the behavior: the nest raspberry innovation could have arisen centuries ago at Suaq Balimbing, but we know with some certainty that cloth handling did not appear at Ketambe until after 1971 (when the first rehabilitant orangutans were brought there, Rijksen 1978). Perhaps the adoption threshold for nest raspberries is lower than for cloth handling – that is, cloth handling may be more demanding for new adopters (more complex in terms of choosing and acquiring cloth, or with a greater fear barrier to overcome because of proximity to the ground and to humans), or nest raspberries may more intrinsically rewarding to new adopters. Perhaps there is a function for the nest raspberries that was not revealed by comparative analysis of the data available. Or perhaps the nest raspberry was innovated or adopted by a very social Suaq Balimbing orangutan who was considered a "good model" by others, whereas Binjei and Getty were clearly "outsiders" at Ketambe with limited connections and low status ("poor models"). The latter scenario is most likely, given the selectivity shown in model choice by primates (Myowa-Yamakoshi & Matsuzawa 1999, 2000, Biro et al, 2003) and the theoretical work supporting choosiness in cultural learning (Henrich & Gil-White, 2001).

Table 6.1 Mammalian taxa exhibiting potentially socially transmitted adjustable behaviors that vary between wild populations, and the cultural category for those behaviors.

TAXON	VARIABLE BEHAVIOR	CULTURAL CATEGORY	REFERENCES
Chimpanzee *Pan troglodytes*	Tool use for foraging (e.g. nut-hammer, ant-dip)	Subsistence skill	Reviewed in Whiten et al., 2001, 2003, also Boesch, 1993; McGrew, 1992; McGrew, 1994b; Sugiyama, 1993; Sugiyama, 1994; Boesch et al., 1994; Fay and Carroll, 1994; Joulian, 1994; Boesch, 1996; McGrew et al., 1997; Sugiyama, 1997
	Tool use for grooming or comfort (e.g. leaf-napkin, seat-vegetation)	Weal skill	Reviewed in Whiten et al., 2001, 2003, also Boesch, 1993; Boesch and Boesch, 1993; Sugiyama, 1993; McGrew, 1994a; McGrew, 1994b; Sugiyama, 1994; Boesch et al., 1994; Fay and Carroll, 1994; Joulian, 1994; Boesch, 1996; McGrew et al., 1997; Sugiyama, 1997
	Allogrooming techniques	Weal skill or Reference variant	Reviewed in Whiten et al., 2001, 2003, also McGrew and Tutin, 1978; McGrew, 1994a; Boesch, 1995; Boesch, 1996; De Waal and Seres, 1997
	Attention-getting object interaction (e.g. buttress-drumming, leaf-clipping)	Reference variant or Display variant	Reviewed in Whiten et al., 2001, 2003, also Boesch, 1995, Boesch, 1996
	Food choice	Label	Nishida et al., 1983; McGrew, 1983; Boesch and Boesch, 1993; Fay and Carroll, 1994; Sugiyama, 1994; McGrew et al., 1997; Uehara, 1997
	Food processing technique	Subsistence skill	Nishida et al., 1983
	Vocalization dialect	Display variant	Mitani et al., 1992; Mitani and Brandt, 1994; Arcadi, 1996
	Self-medication	Label or Weal skill	Huffman, 1997; Huffman and Caton, 2001
Pygmy chimpanzee *Pan paniscus*	Prey choice	Label or Subsistence skill	Reviewed in Hohmann, 2003
	Buttress-drumming technique	Display variant	Reviewed in Hohmann, 2003
	Tool use for grooming or comfort (e.g. leaf-napkin, toothpick)	Weal skill	Reviewed in Hohmann, 2003
Mountain gorilla *Gorilla gorilla beringei*	Food choice	Label	Tutin and Fernandez, 1992
	Food processing technique (leaves)	Subsistence skill	Byrne and Byrne, 1993

Table 6.1 continued

TAXON	VARIABLE BEHAVIOR	CULTURAL CATEGORY	REFERENCES
Orangutan ***Pongo pygmaeus***	**See Tables 2.2 and 2.3**	Subsistence skill, Weal skill, Display variant, Reference variant and Unknown	van Schaik et al., 2003, Chapter 2
Japanese macaque ***Macaca fuscata***	Grass-roots washing	Subsistence skill	Nakamichi et al., 1998
	Stone handling	Weal skill or unknown	Huffman, 1984; Huffman and Quiatt, 1986
	Acquiring or processing provisioned foods	Subsistence skill	Reviewed in Nishida and Hiraiwa-Hasegawa, 1987; Thierry, 1994, Tokida et al., 1994
	Allogrooming techniques	Weal skill	Tanaka 1995, 1998
	Response to humans and novel (provisioned) foods	Label or Subsistence skill	Reviewed in Nishida, 1987
Chacma baboon ***Papio ursinus***	Food choice	Label	Cambefort, 1981
Vervet monkey ***Cercopithcus aethiops***	Food choice	Label	Cambefort, 1981
	Foraging tool use	Subsistence skill	Hauser, 1988
Capuchin monkey ***Cebus capucinus***	Food choice	Label	Chapman and Fedigan, 1990b
	Food processing techniques	Subsistence skill	Rose, 1997; Panger et al., 2002
	Social conventions	Reference variant or Unknown	Perry et al., 2003

Table 6.1 continued

TAXON	VARIABLE BEHAVIOR	CULTURAL CATEGORY	REFERENCES
Humpback whale ***Megaptera novaengliae***	Song dialect	Display variant	Reviewed in Herman and Tavolga, 1980; reviewed in Rendell and Whitehead, 2001
	Lobtail feeding	Subsistance skill	Weinrich et al., 1992
Bowhead whale ***Balaena*** **sp.**	Songs	Display variant	Reviewed in Rendell and Whitehead 2001
Sperm whale ***Physter macrocephalus***	Coda repertoire (vocalization dialects)	Display variant	Weilgart and Whitehead, 1997
	Predator defense technique (*postulated, based on scarring differences*)	Weal skill	Reviewed in Rendell and Whitehead 2001
Killer whale ***Orcinus orca***	Vocalization repertoire	Display variant	Ford, 1991; Strager, 1995
	Hunting techniques	Subsistence kill	Reviewed in Rendell and Whitehead 2001
	Greeting ceremonies	Reference variant and Display variant	Reviewed in Rendell and Whitehead 2001
	Beach rubbing	Subsistence skill, Reference variant or Unknown	Reviewed in Rendell and Whitehead 2001
Bottlenose dolphin ***Tursiops*** sp.	Sponge carrying	Subsistence skill or Unknown	Smolker et al., 1997
	Signature whistle	Display variant	Smolker and Pepper, 1999
	Feeding techniques (involving humans)	Subsistence skill	Reviewed in Rendell and Whitehead 2001
Black rat ***Rattus rattus***	Pine nut extractive foraging technique	Label and Subsistence skill	Aisner and Terkel, 1992; Terkel, 1995
Norway rat ***Rattus norvegicus***	Food choice (mollusks)	Label	Reviewed in Nishida and Hiraiwa-Hasegawa, 1987
Greater spear-nosed bats ***Phyllostomus hastatus***	Group-specific calls	Display variant	Boughman, 1998; Boughman and Wilkinson, 1998

Chapter 6

DISCUSSION AND CONCLUSIONS ABOUT ORANGUTAN CULTURES

Overview

This dissertation has explored the evidence for orangutan cultures from several angles, between and within populations, focusing on behavior variants and on the opportunities for social learning. The scope of known orangutan behavioral variation, and the types of behaviors that vary between populations were described. Evidence supporting a role for observational learning was presented through a two-site comparison of social proximity. The possible function of one cultural behavior was explored, and the frequency of some cultural variants associated with nest building in orangutans was compared for those two sites. Evidence for vertical social transmission of a traditional behavior within matrilines was presented.

Chapter 2 presented an investigation of the context and behavioral content of orangutan cultures using the geographic approach. Across eight study sites, eighteen behaviors varied between sites without any clear ecological explanation for their absence at certain sites, including 3 subsistence skills, 8 weal skills, 3 display variants, a reference variant, and 3 behaviors whose function was less certain. A further five behaviors (four either labels or subsistence skills and one weal skill) were likely to be cultural, but ecological explanations for their absence could not be ruled out without further in-depth analysis of local habitat differences. Comparison with Whiten et al's (1999; 2001) findings for chimpanzees revealed that orangutan and chimpanzee cultural variants are similarly distributed amongst subsistence skills, weal skills, display variants, reference variants and behavior variants whose function is unclear. A higher number of rare behaviors were reported at sites with higher observation intensity, indicating fairly uniform rates of innovation in orangutan populations. As the number of cultural variants did not correlate with observation intensity at a site, their distribution must be attributable to another factor, presumably social learning differences.

The hypothesis that differences in opportunities for social learning can explain differences in the quantity of cultural variants was supported by the results presented in Chapter 3. Suaq Balimbing, the site with the greatest number of cultural variations, was found to exceed Ketambe in a number of social measures, with significant differences at very close distances (2m or less). Differences in opportunities for social learning were indeed related to cultural differences, including the number of subsistence tools used in the population and a difference in degree of specialization in tree-hole tool use in the two social clusters at Suaq Balimbing.

Chapter 4 examined further differences between Suaq Balimbing and Ketambe involving nest-building behaviors. It confirmed that multi-tree nests were present but rare at Ketambe and customary at Suaq Balimbing. The nest raspberry was also customary at Suaq Balimbing, but unequivocally absent at Ketambe. I assessed several possible contextual factors that could explain the function of the nest raspberry (a cultural variant addressed in Chapter 2 whose function was unknown), but found that only nest-building duration was associated with nest-raspberry production. Orangutan females at both sites were less likely to have conspecifics within 50m when building their night nests than at other times throughout the day. This tendency toward dispersal for night-nests was not as strong at Suaq Balimbing as at Ketambe, but the difference between sites did not reach significance.

The fifth chapter presented evidence for vertical social transmission of some unusual behaviors, particularly cloth handling, in the descendents of rehabilitant orangutans at Ketambe. Several lines of evidence indicated that there were opportunities for others to observe these behaviors, but none of them were assimilated into the behavioral repertoires of wild residents at Ketambe. Other studies had demonstrated selectivity in models and behaviors for observational learning, which is a plausible explanation for the failure of the unusual behaviors to spread beyond the rehabilitant matrilines.

In this concluding chapter, I will place this work in a broader context. I will discuss how the functional classification system I offered can be applied to evidence for cultural variation in other non-humans. I will propose future research options that may be profitable in the study of non-human cultural variation.

Types of Cultural Behaviors

Chapter 2 proposed a scheme for classifying cultural behaviors according to their putative function. Chimpanzees and orangutans both showed variation in subsistence skills, weal skills, display variants, reference variants and labels; some behaviors defied easy functional explanations, such as the nest raspberry investigated in Chapter 3. Chimpanzees had more cultural variants overall (Whiten et al. 1999, 2001). The distribution of cultural behaviors in these functional categories did not differ significantly between chimpanzees and orangutans, though chimpanzees showed a larger proportion of subsistence skills and orangutans had relatively more weal skills and variants without clear functions.

Table 6.1 shows the same set of apparently culturally varying behaviors as seen in Table 1.1, classified as described for orangutan and chimpanzee behaviors in Chapter 2. One important caveat with comparing species in this way is that inter-population variation is only really detectable with multiple, long-term studies of well-habituated animals at different sites. Many species where cultural variation is likely have only been studied sufficiently at one or two sites (e.g. gorillas, bonobos, elephants, most odontocetes).

Only chimpanzees and orangutans are known to have behaviors that show cultural variation in all behavioral categories (including unknown behaviors for both species). Most of the proposed cultural behaviors in other species are labels or subsistence skills; this could be a reflection of observer bias toward foraging activities, but if not, it makes sense from an adaptive standpoint according to the models analyzed by van Schaik and Pradhan (2003), wherein natural selection can favor the capacity for socially-mediated learning of behaviors that directly impact fitness. The next most commonly reported behavioral category was display variants, which again may be more indicative of researcher interest than actual variation pattern, but might also be related to the importance of display variants as a way to clearly communicate group membership in social mammals. Possible cultural variation in weal skills is only reported for five of the sixteen species (orangutans, chimpanzees, bonobos, Japanese macaques and sperm whales); while some of these may be even more adaptively imperative than subsistence skills (particularly predator defense strategies in the whales and self-medication in the chimpanzees), the opportunities to exercise and therefore socially learn such critical weal skills would be low in most species. There were only four species wherein cultural variation in reference variants was reported (chimpanzees, orangutans, white-faced capuchins and killer whales).

While subsistence and weal skills are very important in the study of culture, not least because of their fairly clear and direct adaptive benefits for the performer, they are open to modification and variation in different environments without social learning. I suspect that social learning plays an important role in many of these behaviors, and close observational learning opportunities appear to be critical for the spread and maintenance of tool-use. But the cultural variation in signals, with display variants and particularly with reference variants, is by its very nature a product of social interactions within populations. In many ways, these are the more remarkable cultural behaviors, all the more so given their extreme importance in modern human populations. Reference variants, signals that are given in specific contexts in some populations, but are absent or given in different contexts in other populations, are likely to be the evolutionary precursors of the symbolic communication so refined in modern human languages. In one sense, cultural variation in skills is really about sharing space in one another's brains – storing backups of adaptively useful information in multiple places within a population. In contrast, variation in signals involves consensus-building between population members, such that signals given a certain way in a certain context actually do convey a *meaning* shared between signaler and receiver (King and Shanker, 2003).

One very interesting avenue to explore in the study of non-human cultures is that proposed by King (2002; King and Shanker, 2003) for signals. Socially adjustable communicative behavior can be considered "an intrinsically creative process that unfolds as communicating partners continuously adjust their behaviors to one another" (King and Shanker, 2003 p. 5). The more plastic the behavior is in later life, the more opportunities there are for cocreated innovations to arise; the broader the social network in the population, the more opportunities for the innovated signals to spread to habitual or customary levels within a population. A probable example of this co-creation is the social conventions seen in white-faced capuchins (*Cebus capucinus*, Perry et al., 2003). However, the novel conventions only spread to a few individuals (were only rare or habitual in the populations), and most were not maintained in the population (innovation followed by extinction of the behavior in a few years). In a sense, cultural variation in labels and skills is really about borrowing one another's brains – holographically storing backups of adaptively useful information in multiple places within a population. In contrast, variation in signals involves consensus-building between population members, such that signals given a certain way in a certain context actually do convey a meaning shared between signaler and receiver (King and Shanker, 2003).

One could describe the patterns of intraspecific behavioral variation and social learning as a continuum of cultural complexity. Species showing lower complexity would be those that show variation only in one type of behavior, particularly those where the possibility of modification through social learning is limited to a very brief developmental window. Many, if not most animal taxa have some examples of this level of learning specialization (primarily labels and non-tool-use subsistence skills, e.g. food choice in rats, Terkel, 1996; Galef, 2003). Often these behaviors are learned by such processes as social facilitation or stimulus enhancement (cf. Zentall, 1996), primarily through vertical transmission of information (Cavalli-Sforza and Feldman, 1981) that tend to stay fairly uniform across populations and across time provided environmental factors remain fairly constant. Less plastic behavior variants (usually display variants) such as the vocal repertoires acquired by young songbirds through vertical and oblique social transmission are perhaps an example of a more specialized type of social learning (Irwin, 1988).

At a higher level of complexity, there are species that exhibit two or more cultural variants in different populations, and show evidence for more flexible social learning; even more so if the behaviors are in multiple skill and signal classes. This level may apply to Japanese macaques, capuchins, and many cetaceans (see Table 6.1).

Toward the upper end of this continuum come species with flexible repertoires of several cultural behaviors per population, with strong evidence for horizontal social transmission throughout a population, and the possibility of “fashions” spreading and fading within a single generation. Killer whales and bottlenose dolphins are approaching this level of culture and learning specialization, whereas orangutans and chimpanzees probably exceed them. The most complex cultures known (modern human cultures) include cumulative technologies (via the “ratchet effect,” Tomasello, 1999), learned symbolic languages, abstract rituals and institutions.

Culture in the Context of Human Evolution

Orangutans are one of our closest living relatives (Ruvolo et al., 1994). Recent comparative assessments of both fossil and genetic evidence suggest that the ancestor of all extant apes dispersed out of Africa into Eurasia about 20 million years ago, subsequently fissioning into the lesser apes (now represented by the gibbons and siamangs, family Hylobatidae) and the great apes. By 13 million years ago, the great apes divided into a lineage leading to orangutans and another lineage ancestral to the African apes (gorillas, humans, chimpanzees and bonobos) that later returned to Africa (Stewart and Disotell, 1998). A new exhibit at the Buffalo Museum of Science by J. Grehan has re-ignited some discussion of the possibility that orangutans are more closely related to humans than are the African apes (based on

Schwartz, 1984), but this idea is not broadly accepted.

The earliest evidence of hominin culture comes from artifacts in the African archeological record: Oldowan Industry stone tools found in Gona, Ethiopia dated to 2.6-2.5 million years old (Semaw, 2000). These early artifacts are dated to about the same time as some animal bones showing evidence of butchery practices (cut-marks and hammerstone fractures, in nearby Bouri). There are more artifacts from slightly younger sites in eastern and later southern Africa that also belong to the Oldowan Industry (reviewed in Semaw 2000). Ambrose (Ambrose, 2001) notes that stone tools and the genus *Homo* appear nearly simultaneously in the fossil record around 2.5 Mya.

With the possible exception of stone tools used for nut-cracking by chimpanzees (see Mercader et al., 2002), the cultural variation seen in extant orangutans and chimpanzees would leave little archaeological record. Given the evidence for complex cultural variation discussed above for chimpanzees and orangutans, with some indication of this capacity in bonobos and gorillas (in spite of a dearth of information on wild bonobo and gorilla populations), it is likely that the capacity for complex cultural variation is a general characteristic of great apes. Therefore, quite plausibly this level of cultural complexity was present in our last common ancestor over 13 million years ago.

Conservation of Diversity in Multiple Ethnospheres

What is required for behaviors to become customary in a population prior to their extinction? Models suggest that gregarious animals with a high capacity for socially-mediated learning are the most likely to have tool-use or other adaptive skills reach customary levels in the population, and that social-learning is a more important factor than innovative capacity in the spread and maintenance of cultural behaviors (van Schaik and Pradhan, 2003).

Studies on the spread of novel technologies in human communities show that the structure of the innovator or early adopter's social network is an important determinant of widespread adoption (see Barbási, 2002; Watts, 2003). As previous studies with chimpanzees and orangutans have shown, organisms can be selective in the models they choose for social learning (Myowa-Yamakoshi and Matsuzawa, 1999, 2000; Biro et al., 2003; Russon and Galdikas, 1995). Evidence on the lack of social transmisson of unusual rehabilitant behaviors (reported in Chapter 5) is congruent with these findings.

The spread of technology in human populations has also been linked to larger-scale networks, with weak ties (*sensu* Granovetter, 1973) between societies playing a critical role in the advancement of technological complexity (Diamond, 1999). If there is a similar role for inter-population dispersion in other species (as shown for chimpanzees and orangutans; Whiten et al., 2001; van Schaik et al., 2003a), it could have important implications for conservation in species where habitat is fragmented by human activity. If levels of dispersal between populations, and therefore diffusion of cultural behaviors, are reduced to zero, the risk of cultural diversity loss parallels the risk of losing genetic diversity (see also van Schaik, 2002). Similar losses of ethno-diversity in humans is a growing concern (Davis, 1998, 2002), and a clear idea of the risk and extent of loss in other species might help us to honestly appraise the costs of habitat loss. Pagel and Mace (2004) propose that cultural diversity in humans is a response to ecological richness and locally defensible resources. As these rich habitats disappear, both human and non-human cultural diversity may be diminished.

Future Research Suggestions

Each chapter of this dissertation looked at behavioral variation in orangutans at different levels (between or within populations) to advance an understanding of the cultural continuum in animals. Each provides support for the importance of social learning in cultural variation, and suggests avenues for further profitable investigation.

The geographic method used to determine the distribution of cultural behaviors in orangutans (Chapter 2, van Schaik et al., 2003a) was modeled on the approach used for chimpanzees (Whiten et al., 1999; Whiten et al., 2001). I believe that the face-to-face gathering of fieldworkers (as used to discuss orangutan cultures) has the potential to be much more productive and accurate in providing comparable information than repeated correspondence, particularly when it can be supplemented with videotape of the behaviors of interest. The geographic approach should certainly work for exploring culture in other taxa, provided there are intensively-studied, long-term field sites with comparable information.

The social comparison between Suaq Balimbing and Ketambe orangutans just scratched the surface of what can be done in this area. Further analysis will look more closely at interactions at the dyadic level, in each of these populations yielding a more complete picture of the structure of the social networks. Analysis of the behavior of the focal individuals when in close proximity to others could illuminate the opportunities for social learning of specific types of behaviors.

Clearly, there is much still to be learned about great ape nests. These may prove to be a greater source of cultural variation in species that nest socially. One of the main restrictions to nest research is the limits to visibility for a ground-based observer. It is very hard to see much of what goes on in nest construction. Climbing into the canopy in time to watch the action is impractical at best, and climbing to inspect the artifact after it has been completed leaves out important details of the ape's behavior while building. However, the improvements in lightweight, remote-operated cameras might make observations more practical. A remote-operated video camera, mounted on either a remote-controlled miniature helicopter or a quick-to-assemble telescoping crane, could make a detailed study of nest-building behaviors more feasible in the near future.

Closer investigation of differences between matrilines within populations, including comparison of offspring based on association scores for their mothers, could yield more information about how innovations spread (or fail to spread) through a population.

Whether one looks broadly (between populations) or more narrowly (within populations and within matrilines), there is clear evidence that certain behavioral variations depend on opportunities for social learning. The investigation of cultural variation in other species helps us to understand the extent of diversity, both genetic and behavioral, that is at risk when habitat is destroyed or fragmented. It provides us with clues about how we became such remarkable culture specialists, and a greater appreciation for the subtleties of difference between us and other species. And culture is a concept that is just controversial enough to support lively and productive debate far into future.

APPENDICES

APPENDIX I. SOCIAL PROXIMITY DATA ENTRY AND ANALYSIS PROCEDURES

Priority of closest distance: I decided that the times at 2m were more likely to be recorded and recorded accurately than 10m, so if a social partner was listed at 2m during a time not covered by the 10m listing, I added that time to the 10m listing (adding a 10m entry if there was no overlap, or extending the beginning or end of a 10m entry if there was some overlap). The same judgment call was used for 10m versus 50m discrepancies. The only exceptions to this were when it appeared that an error had been made in one digit of writing a start or end time for one of the listings, in which case I chose a correction that would minimize the total time (erring on the side of less time at close proximity).

Independent individuals: In most cases, only independent adults, sub-adults and adolescents were included in social measures. Of course, there are some gray areas when it comes to distinguishing an independent adolescent from a dependent juvenile (defined as the youngest offspring of a female, who very rarely is more than 50m away from the mother). Adolescents are often seen in proximity to their mother and new sibling.

Juveniles were sometimes seen apart from their mother, and while not followed as focals for this study, they are sometimes recorded as independent social partners of focals if their mother is not in similar proximity to the focal. With younger juveniles, this can sometimes be the case for 10m and 2m measures (even though the mother is within 50m of the focal and the juvenile). These juveniles were not counted in party measures if their mother was also within the same distance radius as the juvenile. For number of partner counts, juveniles and their mothers were not counted separately (for cumulative counts, the mother/juvenile pair was counted as a new individual on the date the first of that pair came into that radius).

Copulations: I added in 2m (and 10m or 50m when necessary) if copulation was recorded on the daily instantaneous data sheet notes, but had not been recorded on the social data sheet, under the assumption that copulating orangutans are by definition closer than 2m apart.

APPENDIX II. CHEWING CLOTHES: A DAY WITH CHRIS

This appendix provides details on the cloth-handling behavior of Chris, the grand-daughter of the rehabilitant orangutan Binjei, from one observation day. Much of this behavior was captured on videotape. These details were supplemented with field notes on Chris' behavior (I took notes while Nuzuar videotaped).

We met Chris in the forest not far from camp at 08:00 on 31 May 1999. She fed on *Mastixia trichotoma* fruits, fruits from a liana, unripe fruits of *Aglaia* sp., young leaves from a liana, and some ants (possibly two different types, one in the root mass of an epiphyte, and the other from inside a treehole), and moved through the forest. At 11:28 she began moving directly toward camp.

By 11:45 she had reached camp and was carrying some dark blue cloth, apparently the tattered remnants of a T-shirt. We did not see her enter camp to take it, so we suspected she had cached it in a tree at the edge of camp (she had probably stolen it off a clothesline at camp at least several days earlier). She began building a day nest a minute later, with the cloth draped over her right shoulder. She rested in the nest quietly for the next hour and a half, save for a minute in the middle of this time when she reached out of the nest, broke off a nearby small, leafy branch and added it to the nest.

At 13:21, Chris began moving in the nest, putting the cloth in her mouth and audibly sucking on it for about nine minutes. She then rested quietly for another hour in the nest. At 14:30 she left the nest with a different piece of T-shirt, moved up into the tree and chewed it until 14:35, when she draped it over her left shoulder and moved back into the day nest she'd just vacated.

For the next forty-six minutes Chris remained in the nest, but actively played with and chewed the cloth. She had it in her mouth and tugged on it with her right hand, then she draped it over her right foot and tugged on it with her left hand. Next she held it in her left hand over her head. Then she held it with her left foot and plucked at it with her left hand. She rested quietly for a minute, then lifted the cloth toward her head with her right foot. She held it high over her head with her right foot and both hands, then shifted most of it to her right hand, then took it up with her right foot. She relaxed and draped the cloth over her right leg. At 15:08 some long-tailed macaques (*Macaca fasicularis*) moved into a nearby tree. Chris continued to play with the cloth, twisting and tugging it for another fourteen minutes, then resting quietly for 5 minutes.

Chris moved out of the nest at 15:27, with some cloth in her mouth and draped over her right shoulder. The cloth hung over her shoulder as she began feeding on some flowers (possibly *Flueggia* sp.) at 15:30. Three minutes later Chris moved again, holding the cloth in her mouth. She paused for a minute, holding the shirt with her right hand and drawing it through her mouth, biting and holding one mouthful at a time. She moved away again with the cloth over her right shoulder, and then carried it in her mouth and right hand. After three minutes traveling, she paused to chew on the cloth again for four minutes, then resumed moving until 15:46, when she ate more flowers for four minutes.

After another four minutes of travel, Chris again focused her behavior on the cloth. At 15:54, she draped it over a branch and sat on part of it, then grabbed the rest with her left hand and pulled it to her mouth for a couple minutes. For about two minutes she sat while holding the cloth with both feet. Then she held it in her mouth and plucked at it with her right hand. She returned it to her feet for a bit, then at 16:03 she once again used her right hand to draw the cloth through her mouth, bite by bite. She held it in her right hand for a few minutes, and then sucked on the cloth, holding it only in her mouth. She pulled the cloth away with her right hand, then held it in her left hand and mouth, then held it with both hands. At 16:14 Chris sucked on the cloth for two minutes, and then she transferred it to her feet and right hand. She draped the cloth over a branch, holding some in her mouth and her right hand. At 16:18 she tore a strip of cloth off with her left foot, while continuing to hold it in her mouth. She moved away with the strip of cloth hanging from her mouth at 16:19, leaving the remainder draped over the branch.

Chris kept the strip of cloth with her until 16:22, when she dropped it and went back to feeding on unripe *Aglaia* sp. fruits at the edge of camp. Twenty-eight minutes later she ate some *Ficus racemosa* figs. At 16:54 she moved on, stopping after two minutes to feed on the leaves of *Erythina subumbrans*. After eight minutes she moved, ate some more *F. racemosa* fruits, moved again, and then chewed something unidentified that caused her to spit out something greenish. She moved again, then rested near the edge of camp at 17:18 as her mother, Ans approached carrying her young sister, Kelly.

By 17:22, Ans had approached to within about 10m of Chris. Chris moved about 2m closer to Ans, and both sat quietly. At 17:30, Chris began looking at Ans and Kelly. Ans was looking away, suckling Kelly. Thirteen minutes later Ans moved a few meters away, then Chris followed, approaching within 6m of Ans and Kelly. Ans looked away from Chris. Chris yawned widely at 17:50, and again two minutes later. About two minutes after that, one of the camp cooks approached (Ans was resting in a tree and Chris was hanging in some lianas just behind the kitchen). The cook stood several meters away and made kissing noises at the orangutans, who watched her. At 18:00, Ans turned toward Chris, and two minutes later Ans and Chris approached one another to within 4m. Chris began feeding on the cambium of a liana at 18:06, then swung to within about 3m of Ans and rested.

At 18:12, Ans moved away from Chris, but Chris followed to maintain about 3m distance. After two minutes, Chris began feeding on the stems of an epiphyte (either *Sindapsus hederaceus* or *Photos oxyphyllus*) while Ans faced away from her. Chris fed for ten minutes, then rested for five before moving away, with Ans now following to maintain about a 3m separation. At 18:31 Ans moved away, increasing her distance from Chris by about 5m, then Chris followed Ans to close the gap back to 3m. Ans moved away again, and Chris again followed, then hesitated and allowed Ans to increase their separation to more than 10m by 18:35. By 18:38 they were 15m apart, and both were feeding on figs in one *F. racemosa* tree. At 18:55, Ans moved out of the fig tree, to about 30m away from where Chris continued to feed. Chris moved out of the tree at 18:58, heading away from camp and into the now dark forest where we could hear her build her nest. Ans built a night nest in a nearby *Parashorea lucida* tree at 19:02.

On this day, Chris spent about four-and-a-half hours (nearly 42% of the observation time) carrying her cloth. For one-and-a-half hours of that time, she was actively manipulating, sucking or chewing on the cloth. Only seven minutes of this time were spent feeding, plus another 3 hours and 44 minutes feeding without the cloth during the course of the observation day.

I never discovered who had lost a dark blue T-shirt, or when it might have been taken.

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Biography

Michelle Yvonne Merrill was born in San Jose, California on February 14, 1970. She married Erik S. Peterson in 1991. She received a Bachelor of Arts in Anthropology, with College Honors and Honors in the Major, from the University of California, Santa Cruz in 1994, and was awarded membership in Phi Beta Kappa. She had earlier completed an Associate of Arts degree at Diablo Valley College in Pleasant Hill, California in 1990, and was awarded permanent membership in the Alpha Gamma Sigma Honor Society.

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