

Chapter 2

THE CONTENT OF ORANGUTAN CULTURES

*with David Agee, Marc Ancrenaz, Biruté M.F. Galdikas,
Cheryl D. Knott, Dolly Priatna, Ian Singleton, Akira Suzuki, Sri
Suci Utami, and Carel P. van Schaik*

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.

Weal¹ 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).

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 play 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 led 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) complement 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.