

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 matriline 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 descendants 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 matriline.

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 co-

created 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 transmission 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 matriline 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 matriline), 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.