

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 Frigaszy 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-faceted 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 other 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.