

38. Culture

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38.1 Introduction

Two comprehensive ethograms of Mahale chimpanzees based on data accumulated over 50 years have been published (Nishida *et al.*, 1999, 2010; see Chapter 37). These descriptions of behavioral patterns in the Mahale chimpanzees allowed us to identify novel behaviors not previously included in ethograms, follow the process of their diffusion within the unit-group, and compare behavioral repertoires among the wild chimpanzee unit-groups/populations (see Table 38.1 for the list of putative cultural behaviors in the Mahale K and M groups). Accordingly, studies of wild chimpanzee cultures have focused on variations in behavioral patterns within/among unit-group(s) of chimpanzees that cannot be explained by genetic or ecological factors or on the mechanisms of diffusion and transmission of innovative behaviors within a unit-group (Nishida, 1987; McGrew, 1992, 2004; Wrangham *et al.*, 1994; Whiten *et al.*, 1999, 2001; de Waal, 2001).

Many studies have investigated tool use in wild chimpanzees in terms of culture (for a review, see McGrew, 1992). Such material culture studies have an advantage in that tool/object use can be readily recognized and analysed in unhabituated as well as habituated populations. Furthermore, tool use is associated with higher cognitive ability, which is tacitly regarded as a prerequisite for human culture (Nakamura, 2010a). However, as tool/object use is further discussed in Chapter 42, this chapter focuses on putative cultural behaviors in the social domain of the wild chimpanzees at Mahale. Here, we will

review how studies of the Mahale population have contributed to the current understanding of wild chimpanzee culture.

38.2 Cultural behaviors in Mahale chimpanzees: overview of major findings

38.2.1 In the 1960s and 1970s

Although rarely referred to in the current discussions of chimpanzee culture, the first major findings in Mahale chimpanzees were identification of the “unit-group” as the basic social group and the “fission–fusion” characteristics of the daily ranging pattern (Nishida, 1968; see Chapters 6, 9). Prior to Nishida’s work with the Mahale chimpanzees in the 1960s, Japanese primatologists had conducted empirical and theoretical studies of the ecology, social structure, and culture of Japanese macaques (*Macaca fuscata*) (Itani and Nishimura, 1973; see Chapter 3). Following previous studies in Japanese macaques, Nishida adopted methods such as individual identification and provisioning for habituation to human observers. He also set up a long-term study that allowed him to identify the unit-group as the basic social unit of wild chimpanzees (Nishida, 1968), and identify several cultural behaviors (summarized below). Moreover, under the mentorship of Kinji Imanishi (Imanishi, 1952), the founder of Japanese primatology, Nishida recognized that nonhuman animals with continuous group living had their own culture (Nishida, 1987, 2003). Imanishi’s view of culture, which has been

Table 38.1 Cultural behaviors observed in the Mahale K and M groups

Behavior	Mahale K	Mahale M	Source
Aimed throw	Present	Customary	K: Nishida and Hiraiwa, 1982 M: Nishida, 1994, 2003
Ant-fish	Customary	Customary	K: Nishida, 1973; Nishida and Hiraiwa, 1982 M: Nishida and Hiraiwa, 1982; Nishie, 2011
Bee probe	Present	–	K: Nishida and Hiraiwa, 1982
Drum metal wall	–	Customary	M: Nishida, 1994, 2003
Expel/stir	Habitual	Habitual	K: Nishida, 1973; Nishida and Hiraiwa, 1982 M: Huffman and Kalunde, 1993; Nakamura and Itoh, 2008
Fluid dip	Habitual	Habitual	K: Nishida and Hiraiwa, 1982 M: Matsusaka and Kutsukake, 2002; Matsusaka <i>et al.</i> , 2006
Ground groom	–	Present	M: Nishida, 1994, 2003
Hand-clasp grooming	Customary	Customary	K: McGrew and Tutin, 1978; McGrew <i>et al.</i> , 2001; Nakamura and Uehara, 2004 M: McGrew <i>et al.</i> , 2001; Nakamura, 2002; Nakamura and Uehara, 2004
Knuckle knock	Customary	Customary	K: Whiten <i>et al.</i> , 1999 M: Nishida, 1997 (<i>thump</i>) ^a ; Nishida <i>et al.</i> , 1999 (<i>rap</i>)
Leaf clip	Customary	Customary	K: Nishida, 1980b M: Nishida, 1980b, 1987, 1997
Leaf groom	Customary	Customary	K: Nishida, 1980b M: Zamma, 2002, 2006
Leaf napkin	Present	Present	K: Nishida and Hiraiwa, 1982 M: Nishida, 2003; Corp <i>et al.</i> , 2009
Leaf strip	–	Present	M: Nishida <i>et al.</i> , 1999 (<i>pull-through</i>)
Nipple press	–	Present	M: Nishida, 1994; Marchant and McGrew, 1999
Rain dance	Customary	Customary	K: Whiten <i>et al.</i> , 1999 M: Nishida <i>et al.</i> , 1999 (<i>display, rain</i>)
Shrub bend	–	Customary	M: Nishida, 1987, 1994, 1997
Social scratch	Customary	Customary	K: Nishida, 1983 (<i>scratch or rub</i>) M: Nakamura <i>et al.</i> , 2000
Stem pull-through	–	Habitual	M: Nishida, 1994, 1997
Termite fish	Customary	Present	K: Nishida and Uehara, 1980; Uehara, 1982 M: Takahata, 1982
The putative cultural behaviors on the list and the status of each behavior are based on Whiten <i>et al.</i> (2001).			
^a The italic names in parentheses are synonyms used in respective references.			

tacitly incorporated in Japanese primatology, was not limited to higher cognitive behaviors such as the sweet potato washing observed in Japanese macaques or tool use in chimpanzees, nor did it have connotations of the noble, intentional, sophisticated, and complex aspects of intellectual activities often regarded as prerequisites for human culture. Imanishi's notion extended to broader social phenomena among group-living animals including social structure, dominance rank, and the characters of individuals in various social contexts (Itani and Nishimura, 1973; Nishida, 1987, 2003; Nakamura and Nishida, 2006; Nakamura, 2010a). Accordingly, Mahale researchers recently proposed the application of broader and more holistic perspectives to chimpanzee cultural studies including social structure, ranging pattern, microscopic formation of social gatherings, and the manner of social interaction (Nakamura, 2003, 2010a; Nakamura and Nishida, 2006; Nishie, 2008, 2012; see below).

In the early to mid-1970s, tool-use behaviors such as *Camponotus* ant fishing, termite fishing, and leaf clipping, and medicinal use of leaves were discovered one after another (see reviews in Chapters 24, 42). Current cultural primatologists point to these early discoveries as examples of variation and plasticity of the chimpanzee behavioral repertoire and the extensive knowledge of their habitat, which appears to be learned and shared socially among members of the unit-group.

The grooming hand-clasp was first documented as a social custom among the K-group chimpanzees at Mahale in the mid-1970s (McGrew and Tutin, 1978). The authors, who had studied chimpanzees at Gombe, Tanzania, witnessed the behavior at Mahale and noted that it had never been observed at Gombe. They concluded that this difference between two chimpanzee unit-groups was derived from social customs or cultural variations of the respective groups. However, several influential cultural anthropologists were highly critical of this interpretation and rejected it, insisting that the concept of culture could not be applied to nonhuman species because they do not have the linguistic ability to teach or learn knowledge as tradition (Lévi-Strauss, 1967; Washburn and Benedict, 1979; Sperber, 1982).

38.2.2 In the 1980s and 1990s

By the 1980s, knowledge accumulated over 15 years enabled comparisons between Mahale and Gombe chimpanzees and the discovery of novel behavioral patterns at Mahale.

Nishida (1980a) compared the reaction of Mahale and Gombe chimpanzees to water and concluded that the Mahale chimpanzees were less hydrophobic than those in Gombe. Mahale, but not Gombe, chimpanzees were observed wading in streams, drinking water from the lake, and becoming wet while gathering aquatic plants from the swamp. (Additional observations have been reported sporadically at Mahale; Hosaka, 1995.) Nishida suggested that these differences were cultural rather than idiosyncratic.

Nishida *et al.* (1983) identified differences in the plant-food repertoires of the Mahale and Gombe chimpanzees. They argued that because the differences in plant-food species and feeding techniques could not be fully explained by ecological factors in the respective habitats, and the plant-feeding habit in each group was likely to be transmitted across generations through social learning, they represented cultural differences between two unit-groups.

Between 1981 and 1982, Mahale chimpanzees were observed to incorporate fruit species such as guava, mango, and lemon into their food repertoire (Takasaki, 1983; Takahata *et al.*, 1986). Mangos did not become an important dietary item for the M group because most were eaten by baboons before ripening, although chimpanzees have been observed to eat them sporadically. On the other hand, lemons and guavas are currently important foods for the M group (Nishida, 2003).

In 1987, the M-group chimpanzees were observed to consume leaves and juice from the pith of shoots for medicinal use on two occasions (see Chapter 24).

In 1997, the first case of predation on a yellow baboon by the M-group chimpanzees was observed, and several additional cases followed (see Chapter 20). Newly observed cases of tool use for probing tree holes to hunt mammalian prey were reported in the 1990s, and similar cases were reported in the following decade (see Chapter 42).

In the late 1990s, the “social scratch” (see below for behavioral description) behavior observed in the M group was reported as another example of a locale-specific social custom, as the behavior had not been observed at any of the other long-term study sites (Nakamura *et al.*, 2000). However, the social scratch was later observed at Gombe (Shimada, 2002) and Ngogo, Uganda (Nishida *et al.*, 2004), although the type of scratching differed among sites (see below).

In the late 1990s, the function of leaf grooming, in which chimpanzees seize and manipulate a leaf in a grooming context as if they “groom” the leaf, was found to be squashing ectoparasites (lice) (Zamma, 2002). Subsequent studies revealed local variations in the pattern of squashing ectoparasites among the Mahale (leaf grooming; Zamma, 2002, 2006), Gombe (leaf grooming; Boesch, 1995), Taï, Côte d’Ivoire (index hit; Boesch, 1995), and Bossou, Guinea (index to palm; Nakamura and Nishida, 2006) chimpanzees (see also Chapters 34, 42).

The first exhaustive ethogram of Mahale chimpanzees was published in 1999 (Nishida *et al.*, 1999). In the same year, a seminal article on chimpanzee culture was published, summarizing local variations in the behavioral repertoires of wild chimpanzees in the seven long-term study sites across Africa (Whiten *et al.*, 1999).

38.2.3 After the 2000s

The flourishing studies of chimpanzee culture in the 1990s (McGrew, 1992; Wrangham *et al.*, 1994; Nishida *et al.*, 1999; de Waal, 1999; Whiten *et al.*, 1999) have been followed by several recent investigations of local variation in the behavioral repertoires of wild chimpanzee unit-groups/populations.

Detailed comparisons of the behavioral patterns involved in the grooming hand-clasp were conducted between the K and M groups at Mahale (McGrew *et al.*, 2001; Nakamura and Uehara, 2004). Nakamura (2002) investigated local variations in the grooming hand clasp across wild chimpanzee populations that could not be explained by genetic or ecological conditions in the respective populations.

The use of tools for drinking water was rare among Mahale chimpanzees in the 1990s, but became

prevalent among immature chimpanzees in the M group in the early 2000s (see Chapter 42). Moreover, leaf-pile pulling, a playful behavior, has been observed frequently among immature chimpanzees of the M group (see Chapter 42 for details). Leaf-pile pulling has never been documented in other chimpanzee populations, with the exception of a few cases at Gombe, and thus is regarded as an example of chimpanzee cultural variation (Nishida and Wallauer, 2003). Corp *et al.* (2009) described muzzle/hand rubbing, a tool/object use behavior that increased from 1998, reached a peak around 2000, and declined after 2002 (Nishida, 2003; see Chapter 42 for details).

The Y group, an unhabituated chimpanzee group at Mahale, has been observed and heard occasionally in the former range of the K group since the late 1990s (Chapter 11). A preliminary survey of the Y group revealed novel feeding habits that differed from those of the M group, including frequently feeding on *Camponotus brutus* ants and young stems of the *Cissus oliveri*, both of which were rarely, if ever, eaten by the K and M groups (Nishida and Uehara, 1983; Sakamaki *et al.*, 2007; Nishie, 2012). Although the Y-group chimpanzees are not habituated to human observers, we expect to document more behavioral diversity between the neighboring unit-groups in Mahale.

In the 2000s, Mahale researchers visited other long-term study sites as a “culture hunting” (Nishida, 2012) mission to compare behavioral patterns and repertoires among the long-term wild chimpanzee study sites. Nishida (2003, 2012; Nishida *et al.*, 2004) visited Ngogo in August 2001 and observed several behavioral differences between Ngogo and Mahale chimpanzees, such as the type of social scratch (see above and below), the sounds uttered during social grooming (“lip smacking” and “teeth clacking” at Mahale versus “sputtering” at Ngogo; Nishida *et al.*, 2004), and the frequency of pant-grunt among adult males (frequently observed from adult males to the alpha male at Mahale, but rarely observed among adult males at Ngogo; Nishida, 2012). Shimada (2002) visited Gombe and observed social scratch by three chimpanzees, which had not been previously observed in Gombe chimpanzees. In 2003, Nakamura visited Bossou and reported subtle behavioral

variations *compared* with the Mahale chimpanzees, such as “mutual genital touch,” “heel tap,” “index to palm,” and “sputter” (Nakamura and Nishida, 2006).

In 2010, a comprehensive ethogram of Mahale chimpanzees was published as an audio-visual encyclopedia based on video images recorded since 1999 (Nishida *et al.*, 2010). The ethogram will enable chimpanzee researchers who have never visited Mahale to view the behavioral patterns performed by Mahale chimpanzees on the video footage and to compare them with those of chimpanzees in other study sites. Thus, the audio-visual encyclopedia is expected to facilitate identification of local variations in the behavioral patterns/repertoires of wild chimpanzees, which is a possible starting point in characterizing specific chimpanzee cultures (Whiten *et al.*, 1999; McGrew, 2004).

38.3 Cultural behaviors in the social domain

In this section, we review in detail the social behaviors thought to signify culture and discuss the social aspects of culture in wild chimpanzees.

38.3.1 Grooming behaviors

Grooming hand-clasp

The grooming hand-clasp (McGrew and Tutin 1978; Nakamura, 2002) is a classic example of cultural variation outside tool use. For this behavior, two chimpanzees sit face to face, clasp their corresponding hands or wrists (either right or left) overhead to form an “A-frame” and groom each other’s underarm with their free hands (Figure 38.1). This behavioral pattern



Figure 38.1 (a) Grooming hand clasp between an adult male and an adult female of the Mahale K group. ©Shigeo Uehara. (b) Grooming hand clasp between two adult males of the Mahale M group. ©M. Nakamura.

is customarily performed by chimpanzees at Mahale (M and K groups), Kibale (Kanyawara and Ngogo groups: Uganda), Kalinzu (Uganda), and Lopé (Gabon), whereas it has been observed in only a few chimpanzees at Taï and has never been reported at Gombe, Budongo (Uganda), or Bossou (Nakamura, 2002). The pattern has also been observed in captive chimpanzees at the Yerkes Primate Center in the United States (de Waal and Seres, 1997; Bonnie and de Waal, 2006).

McGrew and Tutin (1978) first documented this behavior describing it as a candidate for a social custom, or even “culture,” if the definition of culture were sufficiently broad to include nonhuman species. However, apart from one negative response (Washburn and Benedict, 1979), their discovery was largely forgotten by anthropologists and primatologists because the time for “cultural primatology” had not yet arrived, at least in the West (McGrew, 2004). Cultural primatology came of age in the 1990s, following McGrew’s review (1992) of tool use among wild chimpanzees (de Waal, 1999). The landmark *Nature* paper by Whiten *et al.* (1999) included social behaviors such as the grooming hand-clasp; however, most of the behavioral patterns they described were related to feeding or material objects.

McGrew *et al.* (2001) described two different patterns of the grooming hand-clasp: palm-to-palm and non-palm-to-palm hand-clasp. In the former pattern, groomers clasp each other’s palm, whereas in the latter, their wrists are often flexed and one hand rests on the other. The authors noted that the palm-to-palm pattern dominated in the Mahale K group, but was not observed in the M group. However, re-examination of a larger dataset revealed that the palm-to-palm pattern was performed in the M group, albeit infrequently; however, all of the observed cases involved an immigrant female from the K group, Gwekulo (Nakamura and Uehara, 2004). Thus, the authors concluded that the palm-to-palm pattern was not transmitted successfully to the M group, but was performed only during interactions with Gwekulo, who continued to perform the customary pattern of the K group.

Nakamura (2002) reviewed the distributions of hand-clasp and branch-clasp grooming among the

long-term study sites; the behaviors differ only in that chimpanzees grasp an overhead branch instead of clasping their hands in branch-clasp grooming. He found that in contrast to the hand-clasp, branch-clasp grooming has been observed in all the long-term wild chimpanzee study sites, and it therefore may be considered universal. Nakamura noted that hand-clasp grooming is a rare example of culture as a “pure” social behavior that does not use material objects. He argued that inter-population variations in the behavior could not be attributed to ecological or genetic differences and that the use of hand-clasp grooming was completely arbitrary because the same function, cleaning the underarm region, could be attained using the ubiquitous form of branch-clasp grooming.

Social scratch

The social scratch, in which an individual scratches the body, usually the back, of another individual during social grooming, is customarily performed at Mahale (Nishida *et al.*, 1999; Nakamura *et al.*, 2000). This behavior has been observed at Gombe (Shimada, 2002) and Ngogo (Nishida *et al.*, 2004), but not at Kanyawara, Bossou, or Taï (Nakamura *et al.*, 2000). This interaction is so straightforward – simply scratching another’s body – that Nishida (2012) was amazed to find that chimpanzees at other sites did not engage in the behavior. Furthermore, Nishida *et al.* (2004) noted a difference in social scratch behavioral patterns between Mahale and Ngogo chimpanzees such that Ngogo chimpanzees scratched using their fingers to *poke* the body of their grooming partner while keeping their fingers straight, whereas most Mahale chimpanzees used flexed fingers to *stroke* the body of their partner, although an adult female in the Mahale M group, Ako, and her daughter, Acadia, displayed the poke-type behavior (Nishida *et al.*, 2004; Nakamura, 2010b).

Grooming “density” and development of a grooming network

Most studies of chimpanzee culture have focused on distinctive patterns of complex behaviors (implying complex cognitive abilities and intelligence) such as

tool/object use; however, Nakamura (2010a) argued that there are more quantitative than qualitative local differences in social behavior among sites that can be described as cultural variations. Using published datasets, Nakamura compared the densities of male–male and female–female grooming networks, determined by plotting the number of grooming partners against the number of individuals of each sex, among the long-term wild chimpanzee study sites. He found that male grooming networks were very dense in general, although the density of Ngogo male networks appeared to be lower than that of the other sites, presumably owing to the large number of males at Ngogo. The female grooming networks were relatively sparse in Gombe, Kanyawara (Kibale), and Sonso (Budongo), whereas the grooming densities of Bossou and Mahale females were as high as those of the males. At Mahale, mothers had up to 40 grooming partners and averaged about 20.3 partners each, similar to the pattern of adult males (average: 19.3 partners each), whereas juvenile and older female infants had 10–20 grooming partners (average: 14.3 partners each).

Nakamura (2010a) argued that the differences among female grooming densities across sites could not be explained simply by differences in group size, subspecies, degree of habituation to human observers, observation methods, or local cultural variations, but was likely a result of a confluence of these factors. Nevertheless, it may be that female sociality and other social behaviors have cultural significance in their respective societies because culture and other factors are not mutually exclusive, but rather are interactive. Moreover, Nakamura suggested that grooming networks among mothers could affect those of their offspring; thus, it may be that the social breadth (sociality) of female chimpanzees is socially inherited as culture in respective societies of wild chimpanzees.

38.3.2 Feeding habits

Nishida *et al.* (1983) compared the types of food and food species consumed by chimpanzees at Mahale and Gombe. Among the 143 potential plant-food species, 85 (59.4%) were eaten at both sites. Of the 286

potential food types, 104 (36.4%) were eaten at both sites, whereas the remaining 182 (63.6%) types were ignored by either of the populations. Furthermore, the authors observed differences in feeding techniques; for example, Gombe chimpanzees banged the hard-shelled fruits of *Strychnos* spp. against a tree trunk or a rock to open them, whereas Mahale chimpanzees always bit them open.

Local differences in diet have been largely ignored in studies of wild chimpanzee culture because feeding habits, with the exception of tool/object use feeding behaviors, have been regarded as subsistence activities that are largely determined by ecological, not cultural, factors. Thus, feeding habits or local differences in diet have been studied in terms of ecology, not culture, because subsistence activities do not meet the classic criteria for culture in nonhuman animals (cf. McGrew and Tutin, 1978). However, as early as the 1980s, Nishida *et al.* (1983) maintained that if local differences in diet were transmitted from generation to generation through social learning, they may be reasonably referred to as cultural differences, despite their being influenced by or originating from various environmental factors, including ecological ones. This point resonated with recent animal culture debates, some of which criticized the dichotomy between culture and nature (ecology/genetics).

At Mahale, chimpanzees incorporated new food items into their diet between the 1980s and 1990s. Conversely, the consumption of other food species or items decreased. For example, Sally, a newly immigrated adolescent female, was observed eating algae in a stream three times in 1997 (Sakamaki, 1998; Chapter 11); however, the behavior has not been observed since (Nishida *et al.*, 2009). The impact of ecological and cultural factors on chronological changes in feeding habits requires further study.

38.3.3 Play behaviors

With the exception of leaf-pile pulling (see above and Chapters 36, 40, 42), play behavior among chimpanzees has not been studied in terms of culture;

thus, little is known about local variation in play. Perhaps play has been ignored because it is often viewed as “functionless”; however, play behaviors may provide examples of local variation, innovation, and behavioral diffusion (Chapter 40), and they should thus be considered in studies of chimpanzee culture, much like children’s culture has recently received growing attention in studies of human behavior.

38.3.4 Grouping patterns

Although grouping patterns have not been considered in current studies of wild chimpanzee culture, here we review differences in grouping patterns or cohesiveness among study sites that may have been shaped by culture.

Itoh and Nishida (2007) investigated the correlation between party size (cohesiveness) and food (fruit) availability in the M-group chimpanzees at Mahale. They found that the size of the “nomadic party” was correlated with fruiting plant density and mean potential patch size, whereas the size of the “face-to-face party” was weakly or not correlated with density and potential patch size (see Chapter 9 for definitions of the two types of parties). Furthermore, the authors compared nomadic and face-to-face party sizes among unit-groups. The cohesiveness of the Mahale and Bossou unit-groups, estimated by relative nomadic party size, was greater than that of the Kanyawara unit-group. The maximum face-to-face party size relative to unit-group size was higher among the Mahale K and M, Bossou, and Budongo groups than among groups in other sites in some years. Thus, the Mahale K and M and the Bossou unit-groups were likely to be capable of higher cohesiveness when ranging, whereas cohesiveness when ranging tended to be lower at the unit-group level in other sites. Nakamura (Chapter 8) also noted similarities in the grouping pattern of Mahale and Bossou chimpanzees based on his observations at both sites.

Grouping pattern, or cohesiveness of the unit-group, has been studied primarily in relation to

ecological factors such as food availability and seasonal fluctuation or patch size and distribution; however, few studies have considered grouping pattern as a cultural entity. The concept of culture is generally applied narrowly to locale-specific behavioral variation that cannot be explained by ecological or genetic factors (e.g. Nishida, 1987; Whiten *et al.*, 1999; de Waal, 2001). However, several researchers (Fragaszy, 2003; Laland and Janik, 2006, 2007) have criticized this “ethnographic” method (Wrangham, *et al.*, 1994) or “method of exclusion” (Krützen *et al.*, 2007) for seeking to isolate cultural variation by ruling out alternative explanations for behavioral differences among populations. These critics argued that culture is not a stand-alone phenomenon, but rather one that is influenced by several variables including ecological and genetic factors; thus, all factors are expected to be mutually interactive rather than mutually exclusive (Fragaszy, 2003; Laland and Janik, 2006, 2007). If we accept this argument, it follows that grouping pattern or cohesiveness, which has been traditionally considered a response to ecological conditions, is a cultural phenomenon in which animals learn and reproduce conventional or customary responses to specific environmental conditions. For instance, Itoh and Nishida (2007) reported that the Mahale M group showed high cohesiveness and maintained large nomadic parties because the liana species *Saba comorensis* was hyper-dispersed during the high fruiting season. Itoh (2013) subsequently questioned this conclusion: chimpanzees are *merely able to aggregate* when many fruits are available, but they *need not aggregate* because *Saba* fruits are widespread in their home range. She argued that Mahale chimpanzees detected the signs of *Saba* fruiting and used the information to aggregate in conventional ways, which could be described as their doing “*how all others usually do* in such a situation” (Itoh, 2013). In this respect, grouping patterns may be discussed in terms of culture if chimpanzees behave according to “others’ ways of doing”; thus, this meets one of the basic definitions of culture proposed by McGrew (2004): “*the way we do things.*”

38.4 Implications and future directions for chimpanzee culture studies: taking “social” seriously

Culture is a difficult term to define, even in anthropology; however, most would agree that culture is “social” rather than “individual,” whether referring to human or nonhuman animal culture. Here, we review the importance and implications of focusing on the social domain in studies of chimpanzee culture.

Culture is, by definition, social. Nonetheless, most studies of nonhuman animal culture have focused on the “behavior of the individual” as a unit of analysis, downplaying the social aspect as merely “the addition of individuals” or “the process of transmitting information between individuals.” For example, Whiten *et al.* (1999, 2001) referred to local variations in behavioral repertoires as wild chimpanzee cultures and classified the behavioral patterns in relation to their local frequencies of occurrence, i.e. customary, habitual, present, and absent, based on *the number of individuals* who exhibited each behavioral pattern in the respective groups. Thus, their focus was firmly on the behavior of the individual, and “social” merely indicated “the addition of individuals.” Similarly, cognitive psychologists have typically viewed culture as representative knowledge and information installed into an individual’s mind (or brain) to generate certain behavioral patterns or skills and as the process of social learning through which representative knowledge and information is transmitted between individuals. Here, the social domain is trivialized as “the process of transmitting information or knowledge between individuals.” These mainstream contemporary studies of nonhuman animal culture tacitly imply that “atomistic individuals” are the basic agents of culture and “the additions of individuals” and “the transmission of information or knowledge between individuals” is the basis for the social aspect of culture. This view of culture and society (social) has been criticized as a “metaphor of transmission” or “Xerox model” (Ingold, 1998), “individual agent-based information transfer model of culture”

(Nakamura, 2010a), and “cognition-transmission model” (Nishie, 2008, 2012) in which animal culture is viewed in terms of an individual’s cognitive ability to transmit and receive information and knowledge, and to exhibit certain skills based on that knowledge.

These critics argue that we should deal with culture not as assemblies of representative knowledge in individuals minds or as behavioral patterns exhibited by individuals, but as the process of ongoing social practice through which knowledge, not *detachable* from one’s body but *embodied* or *embedded* in it, far from being transmitted or “jumping” from one individual to another, undergoes continuous generation and regeneration in the course of one’s life history within the respective environments (Ingold, 1998).

If we take this argument seriously, it is reasonable to broaden the concept of “social” to include other environmental factors such as “genetic” or “ecological.” We typically use the concept of “social” not only as the opposite of “individual” but also as the opposite of “material” or “biological” which is the root of the culture/nature dichotomy. However, from the more developmental and genuinely ecological (Ingold, 1996) perspective on culture, it makes no sense to describe activities with conspecifics and inanimate components as “social” (or “culture”) and “material” (or “nature”: “ecological” and “genetic”), respectively, because conspecifics, as well as inanimate objects, are part of the total environmental situation in which one dwells, and material objects are as incorporated in the course of one’s activities as are conspecifics (Ingold, 1996, 1998; Frigaszy, 2003; Nishie, 2008, 2012). Rather, we should view social, material (ecological and genetic), and all other factors as mutually interactive to generate the ongoing processes of activities. During such continual processes, knowledge, as a synthesis of embodied skills for actions and perceptions, is formed through ontogeny and persists through generations. This process-oriented view may encompass the holistic process of culture as a continual practice that is grounded in, not detached from, the *context* in which

all of these factors contribute to the generation and development of embodied knowledge and skills.

This line of reasoning allows us to deal with a much broader range of phenomena in terms of culture, such as social behaviors (Section 38.3.1), feeding habits (Section 38.3.2), play behaviors (Section 38.3.3), and grouping patterns (Section 38.3.4), that have not necessarily been studied as indices of culture in wild chimpanzees. In this respect, we need not seek local

variation in behavioral repertoires as possible candidates for culture, nor must we exclude local variation that is ecologically explicable. This approach resonates with contemporary works in anthropology that focus on the process of practice, in which embodied knowledge and skills are embedded (Ingold, 1998). Thus, it may help us to broaden our perspective and make fair comparisons between human and nonhuman cultures.

References

- Boesch, C. (1995). Innovation in wild chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, 16, 1–16.
- Bonnie, K. E. and de Waal, F. B. M. (2006). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*, 47, 27–34.
- Corp, N., Hayaki, H., Matsusaka, T., et al. (2009). Prevalence of muzzle-rubbing and hand-rubbing behavior in wild chimpanzees in Mahale Mountains National Park, Tanzania. *Primates*, 50, 184–9.
- Fragaszy, D. (2003). Making space for traditions. *Evolutionary Anthropology*, 12, 61–70.
- Hosaka, K. (1995). [Water play.] *Monkey*, 39(2), 20–1. In Japanese.
- Huffman, M. A. and Kalunde, M. S. (1993). Tool- assisted predation on a squirrel by a female chimpanzee in the Mahale Mountains, Tanzania. *Primates*, 34, 93–8.
- Imanishi, K. (1952). [Evolution of humanity.] In [*Man*], ed. K. Imanishi. Tokyo: Mainichi-shinbun-sha, pp. 36–94. In Japanese.
- Ingold, T. (1996). Situating action VI: a comment on the distinction between the material and the social. *Ecological Psychology*, 8, 183–7.
- Ingold, T. (1998). Comments. *Current Anthropology*, 39, 606–7.
- Itani, J. and Nishimura, A. (1973). The study of infrahuman culture in Japan. In *Precultural Primate Behavior*, ed. E. W. Menzel. Basel: Karger, pp. 26–50.
- Itoh, N. (2013). [Dual-rings of mode of coexistence and act choices: Chimpanzee group and emergence of institution.] In [*Practices, Conventions and Institutions: the Evolution of Human Sociality*], ed. K. Kawai. Kyoto: Kyoto University Press, pp. 143–66. In Japanese.
- Itoh, N. and Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates*, 48, 87–96.
- Krützen, M., van Schaik, C., and Whiten, A. (2007). The animal cultures debate: response to Laland and Janik. *Trends in Ecology & Evolution*, 22, 6.
- Laland, K. N. and Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21, 542–7.
- Laland, K. N. and Janik, V. M. (2007). Response to Krützen et al.: further problems with the “method of exclusion”. *Trends in Ecology & Evolution*, 22, 7.
- Lévi-Strauss, C. (1967). *Les Structures Élémentaires de la Parenté*. The Hague: Mouton & Co and Maison des Sciences de l’Homme.
- Marchant, L. F. and McGrew, W. C. (1999). Innovative behavior at Mahale: new data on nasal probe and nipple press. *Pan Africa News*, 6, 16–18.
- Matsusaka, T. and Kutsukake, N. (2002). Use of leaf-sponge and leaf-spoon by juvenile chimpanzees at Mahale. *Pan Africa News*, 9, 6–9.
- Matsusaka, T., Nishie, H., Shimada, M., et al. (2006). Tool-use for drinking water by immature chimpanzees of Mahale: prevalence of an unessential behavior. *Primates*, 47, 113–22.
- McGrew, W. C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C. (2004). *The Cultured Chimpanzee: Reflections on Cultural Primatology*. Cambridge: Cambridge University Press.

- McGrew, W. C. and Tutin, C. E. G. (1978). Evidence for a social custom in wild chimpanzees? *Man*, 13, 234–51.
- McGrew, W. C., Marchant, L. F., Scott, S. E., and Tutin, C. E. G. (2001). Intergroup differences in a social custom of wild chimpanzees: The grooming hand-clasp of the Mahale Mountains. *Current Anthropology*, 42, 148–53.
- Nakamura, M. (2002). Grooming-hand-clasp in Mahale M group chimpanzees: implication for culture in social behaviors. In *Behavioural Diversity in Chimpanzees and Bonobos*, ed. C. Boesch, G. Hohmann, and L. F. Marchant. Cambridge: Cambridge University Press, pp. 71–83.
- Nakamura, M. (2003). [Questions about chimpanzee culture studies.] *Ecosophia*, 12, 55–61. In Japanese.
- Nakamura, M. (2010a). Ubiquity of culture and possible social inheritance of sociality among wild chimpanzees. In *The Mind of the Chimpanzee*, ed. E. V. Lonsdorf, S. R. Ross, and T. Matsuzawa. Chicago, IL: The University of Chicago Press, pp. 156–67.
- Nakamura, M. (2010b). Poke-type social scratching persists at Mahale. *PanAfricaNews*, 17, 15–17.
- Nakamura, M. and Itoh, N. (2008). Hunting with tools by Mahale chimpanzees. *Pan Africa News*, 15, 3–6.
- Nakamura, M. and Nishida, T. (2006). Subtle behavioral variation in wild chimpanzees, with special reference to Imanishi's concept of *kaluchua*. *Primates*, 47, 35–42.
- Nakamura, M. and Uehara, S. (2004). Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: implications for chimpanzee social custom. *Current Anthropology*, 45, 108–14.
- Nakamura, M., McGrew, W. C., Marchant, L. F., and Nishida, T. (2000). Social scratch: another custom in wild chimpanzees? *Primates*, 41, 59–71.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. *Primates*, 9, 167–224.
- Nishida, T. (1973). The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. *Journal of Human Evolution*, 2, 357–70.
- Nishida, T. (1980a). Local differences in responses to water among wild chimpanzees. *Folia Primatologica*, 33, 189–209.
- Nishida, T. (1980b). The leaf-clipping display: a newly-discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution*, 9, 117–28.
- Nishida, T. (1983). Alloparental behavior in wild chimpanzees of the Mahale Mountains, Tanzania. *Folia Primatologica*, 41, 1–33.
- Nishida, T. (1987). Local traditions and cultural transmission. In *Primate Societies*, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker. Chicago, IL: The University of Chicago Press, pp. 462–74.
- Nishida, T. (1994). Review of recent findings on Mahale chimpanzees: implications and future research directions. In *Chimpanzee Cultures*, ed. R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne. Cambridge, MA: Harvard University Press, pp. 373–96.
- Nishida, T. (1997). Sexual behavior of adult male chimpanzees of the Mahale Mountains National Park, Tanzania. *Primates*, 38, 379–98.
- Nishida, T. (2003). Individuality and flexibility of cultural behavior patterns in chimpanzees. In *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*, ed. F. B. M. de Waal and P. Tyack. Cambridge, MA: Harvard University Press, pp. 392–413.
- Nishida, T. (2012). *Chimpanzees of the Lakeshore: Natural History and Culture at Mahale*. Cambridge: Cambridge University Press.
- Nishida, T. and Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution*, 11, 73–99.
- Nishida, T. and Uehara, S. (1980). Chimpanzees, tools, and termites: another example from Tanzania. *Current Anthropology*, 21, 671–2.
- Nishida, T. and Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *African Study Monographs*, 3, 109–30.
- Nishida, T. and Wallauer, W. (2003). Leaf-pile pulling: an unusual play pattern in wild chimpanzees. *American Journal of Primatology*, 60, 167–73.
- Nishida, T., Wrangham, R. W., Goodall, J., and Uehara, S. (1983). Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *Journal of Human Evolution*, 12, 467–80.
- Nishida, T., Kano, T., Goodall, J., McGrew, W. C., and Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, 107, 141–88.

- Nishida, T., Mitani, J. C., and Watts, D. P. (2004). Variable grooming behaviors in wild chimpanzees. *Folia Primatologica*, 75, 31–6.
- Nishida, T., Matsusaka, T., and McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: A review. *Primates*, 50, 23–36.
- Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., and McGrew, W. C. (2010). *Chimpanzee Behavior in the Wild*. Tokyo: Springer.
- Nishie, H. (2008). [Chimpanzee culture and sociality: reconsidering “the metaphor of transmission of knowledge”.] *Primate Research*, 24, 73–90. In Japanese with English abstract.
- Nishie, H. (2011). Natural history of *Camponotus* ant-fishing by the M group chimpanzees at the Mahale Mountains National Park, Tanzania. *Primates*, 52, 329–42.
- Nishie, H. (2012). [Chimpanzee Culture and Sociality.] Doctoral Dissertation. Kyoto: Kyoto University. In Japanese.
- Sakamaki, T. (1998). First record of algae-feeding by a female chimpanzee at Mahale. *Pan Africa News*, 5, 1–3.
- Sakamaki, T., Nakamura, M., and Nishida, T. (2007). Evidence of cultural differences in diet between two neighboring unit groups of chimpanzees in Mahale Mountains National Park, Tanzania. *Pan Africa News*, 14, 3–5.
- Shimada, M. (2002). Social scratch among chimpanzees in Gombe. *Pan Africa News*, 9, 21–3.
- Sperber, D. (1982). *Le Savoir des Anthropologues*. Paris: Hermann.
- Takahata, Y. (1982). Termite fishing observed in M group chimpanzees. *Mahale Mountains Chimpanzee Research Project Ecological Report*, 18.
- Takahata, Y., Hiraiwa-Hasegawa, M., Takasaki, H., and Nyundo, R. (1986). Newly acquired feeding habits among the chimpanzees of the Mahale Mountains National Park, Tanzania. *Human Evolution*, 1, 277–84.
- Takasaki, H. (1983). Mahale chimpanzees taste mangoes: toward acquisition of a new food item? *Primates*, 24, 273–75.
- Uehara, S. (1982). Seasonal change in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatologica*, 37, 44–76.
- de Waal, F. B. M. (1999). Cultural primatology comes of age. *Nature*, 399, 635–6.
- de Waal, F. B. M. (2001). *The Ape and the Sushi Master*. New York: Basic Books.
- de Waal, F. B. M. and Seres, M. (1997). Propagation of handclasp grooming among captive chimpanzees. *American Journal of Primatology*, 43, 339–46.
- Washburn, S. and Benedict, B. (1979). Non-human primate culture. *Man*, 14, 163–4.
- Whiten, A., Goodall, J., McGrew, W. C., et al. (1999). Cultures in chimpanzees. *Nature*, 399, 682–5.
- Whiten, A., Goodall, J., McGrew, W. C., et al. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138, 1481–516.
- Wrangham, R. W., de Waal, F. B. M., and McGrew, W. C. (1994). The challenge of behavioral diversity. In *Chimpanzee Cultures*, ed. R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne. Cambridge, MA: Harvard University Press, pp.1–18.
- Zamma, K. (2002). Leaf-grooming by a wild chimpanzee in Mahale. *Primates*, 43, 87–90.
- Zamma, K. (2006). A louse egg left on a leaf. *Pan Africa News*, 13, 8–10.