8 The social context of chimpanzee tool use

Crickette M. Sanz
Washington University, Department of Anthropology

David B. Morgan
Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo
Wildlife Conservation Society, Congo

Although several animal species exhibit some form of tool use (Shumaker *et al.*, 2011), there are relatively few animals which flexibly use a diverse repertoire of implements on a regular basis within their natural environments. As shown in this volume, hominins, chimpanzees, orangutans, some capuchins and corvids are the exceptions. Van Schaik *et al.* (1999) have suggested that the evolution of material culture in primates is dependent upon the intersection of four primary factors: manipulative skills, cognitive abilities, suitable ecological niches and social tolerance. Although one cannot entirely dismiss the possibility of differences in manipulative skills and cognitive abilities within species, there are intriguing differences in diversity and types of tool use among populations of wild chimpanzees (*Pan troglodytes*) which are not entirely explicable by environmental circumstances, and so have been attributed to social influences (Whiten *et al.*, 1999, 2001; Möbius *et al.*, 2008). With the exception of a few developmental studies, the social context of tool use remains largely unexplored in these apes.

Primates show differing degrees of social cohesion, and varying responses to fluctuations in the availability of resources in their environment. The abundance and distribution of important food resources dictates not only population density, but also social tolerance. Social tolerance varies across species, but may also differ within species (among populations, groups and even individuals). Resource scarcity may incite feeding competition among conspecifics, which could cause primates to avoid spending time in close proximity, whereas bountiful resources may attract conspecifics to forage at the same site. Social tolerance in gregarious foraging could enhance social learning by allowing primates to forage in close proximity to each other, providing a relaxed social atmosphere in which attention may be focused on a task, and enabling subordinate individuals to participate in close proximity foraging without risk of theft or aggression by conspecifics (van Schaik, 2003). The "opportunities for social learning hypothesis" predicts that higher degrees of social tolerance should result in a larger number of customary technical skills exhibited by primates (van Schaik, 2003). An extension of the opportunities for social learning hypothesis is that higher degrees of

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social tolerance could be associated with the transmission of more complex tool behaviors. Pradhan *et al*. (2012) have proposed that variation in sociability accounts for intraspecific and interspecific differences in the simple and cumulative technology of chimpanzees and orangutans. In this chapter we examine the social context of tool use in the chimpanzee population residing in the Goualougo Triangle, which is known to exhibit relatively complex technology. We report on the degree of gregariousness within this wild chimpanzee population, and attempt to elucidate pathways of information transmission within and between communities in this region.

Coussi-Korbel and Fragaszy (1995) have proposed that the degree of social tolerance exhibited by a species and coordination in time and space between conspecifics will not only affect the likelihood of individuals attaining information, but also the type of information that is attained. Species with egalitarian relationships are predicted to have more frequent and extensive behavioral coordination between individuals in both time and space than those with despotic relationships, in which certain individuals may actively avoid others. Individuals may be coordinated in space when an individual approaches a place where another individual previously engaged in a tool task, but is no longer present. In this setting, the naive individual has the opportunity to gain information about the task and potential quality of the site based on physical alterations that persist in the environment. Information may also be gained by interacting with discarded tools. For example, at sites where chimpanzees fish for termites, discarded fishing probes may be found on or around the periphery of the termite nest. Termite-nest puncturing tools may also be found littered around a termite nest or even embedded within the matrix of a nest. These tools persist for several months, and may be reused by subsequent visitors. Another example is the wooden and stone hammers used for nut cracking that are often transported to trees producing nuts, and remain in close proximity to anvils, which may be covered with tell-tale nut shells from previous tool-using bouts (Boesch & Boesch, 1984; Chapter 11). This is also the case for nut-cracking sites of capuchin monkeys (Visalberghi *et al*., 2007; Chapter 10).

Behavioral coordination in time and space requires that two individuals are at the same locality at the same time, and engaging in similar activities. In this setting the naive individual has the possibility to gather information about the substrate, tool action and outcome from an experienced individual. Lonsdorf (2006) and Humle *et al*. (2009) have shown the importance of social learning opportunities in the acquisition of tool-using behaviors of young chimpanzees. Youngsters whose mothers provided more opportunities for tool use in ant dipping showed more advanced skills than those with mothers who provided little opportunity (Humle *et al*., 2009). As no active facilitation was observed in ant dipping, it seems that coordination in space was effective in promoting acquisition of tool-using skills. Further, infants of avid termite-fishing mothers at Gombe were more likely to be proficient tool users themselves (Lonsdorf, 2006). Chimpanzee mothers at Gombe were highly tolerant of their offspring's behaviors, such as reaching toward her tool or termites, stealing tools and investigating the termite mound even when these behaviors seemed to interfere with her food gathering. At the same site, McGrew (1977) documented coaction, which is when a chimpanzee allows another to touch either her hand or part of her tool during use. Coaction has also been identified as a potentially important aspect of social transmission of tool traditions in captive chimpanzees (Horner, 2010).

Social facilitation is an important aspect of the acquisition of tool-using skills (Lonsdorf, 2006; Hopper *et al*., 2007; Humle *et al*., 2009). However, the specific mechanisms of social information transfer and their relative contributions are difficult to determine, particularly in naturally occurring environments. Boesch (1991) compiled observations of social facilitation by chimpanzee mothers in their infant's acquisition of nut-cracking skills in the Taï forest in West Africa. The majority of interactions were characterized as stimulation and facilitation. Stimulation involved the mother leaving the hammer near the anvil, and facilitation occurred when a mother provided tools and/or intact nuts to the infant. The only two instances of active teaching observed among wild chimpanzees were documented in Boesch's (1991) study when a mother intervened to show her infant how to correctly orient an irregularly shaped hammer and in another case the mother demonstrated correct positioning of the nut to her offspring. Mothers were frequently observed to delay their nut cracking while infants ate nuts from her anvil or manipulated her nut-cracking tools, but it is also interesting to note that this behavior changed in relation to the infant's age and skill (Boesch & Boesch-Achermann, 2000). It is advantageous for a mother to allocate only the minimal level of assistance necessary for her offspring to succeed in acquiring the skill. Although the mother eventually benefits through the increasing independence of her offspring, she experiences an immediate cost of relinquishing food resources and/or functional tools to her offspring. In contrast, the recipient of assistance experiences both short- and long-term benefits from this exchange. For young chimpanzees, access to the appropriate materials and opportunity to exhibit a tool behavior seem to be important factors which affect the speed of acquisition and proficiency in using tools.

Active teaching was long considered a derived trait of hominins which emerged after the split from the last common ancestor with chimpanzees (see review in Hoppitt *et al*., 2008). However, recent evidence of teaching from a wide range of taxa, including meerkats and ants, has challenged commonly held notions of social learning and teaching mechanisms (Franks & Richardson, 2006; Thornton & McAuliffe, 2006). Active teaching can be differentiated from other types of socially biased learning by active participation of the instructor. Caro and Hauser (1992) identified teaching in situations in which the instructor modified his/her behavior in the presence of a naive observer, with the specifications that the modification in behavior was at the cost of the instructor and resulted in the observer acquiring information that previously was less accessible. Knowledgeable practitioners may provide opportunities for the learner to practice skills, or they may also coach the individual with encouraging or punishing feedback. To identify the specific mechanisms which underpin the transmission of technological skills and the factors shaping the evolutionary origins of social learning, it is important to carefully examine and compare the social contexts of tool-use acquisition and maintenance within and across species.

Chimpanzee society and tool use

Wild chimpanzees have one of the most expansive and varied distributions of any living primate. Their range extends across equatorial Africa and encompasses habitats ranging from woodland savannahs to dense lowland rainforests. Unlike animal species who live in stable groups, chimpanzees (and other species exhibiting fission-fusion sociality) regularly adjust the size of their foraging parties to available resources. An entire chimpanzee group (referred to as a community) may comprise 20–148 individuals (Mitani, 2006). However, most foraging subgroups consist of fewer than five individuals (Taï: Boesch, 1996; Boesch & Boesch-Achermann, 2000; Gombe: Halperin, 1979; Bossou: Sugiyama, 1984). It has been widely accepted that a combination of ecological, demographic and social factors interact to determine subgroup size and composition (Goodall, 1986; Chapman *et al*., 1995; Boesch & Boesch-Achermann, 2000; Anderson *et al*., 2002; Mitani *et al*., 2002).

Every population of wild chimpanzees has also been documented to exhibit at least one type of tool-using behavior, and several groups have a diverse repertoire of tool types (McGrew, 1992; Sanz & Morgan, 2007). Technological repertoires shown by a particular community range from 6 to 22 different tool types (Sanz & Morgan, 2007). The composition of these tool kits differs between populations, and sometimes adjacent groups (McGrew & Collins, 1985; McGrew, 1992; Boesch, 2003; Sanz & Morgan, 2007). Although ecological factors shape some of the differences between groups, other behaviors have been identified as putative cultural variants which presumably rely on social transmission to be maintained at a habitual or customary level within chimpanzee society (Whiten *et al*., 1999, 2001).

The structural dynamics of fission-fusion societies pose specific challenges to the maintenance of behavioral variants through social transmission. The entire membership of a chimpanzee community is rarely, if ever, assembled in the same locality, but rather comprises several subgroups which vary in size and composition throughout the day. Van Schaik (2003) used time spent in a social subgroup (or party) as a proxy for opportunities for social learning, and found that time spent in foraging parties was positively related to the number of feeding tools and putative cultural variants exhibited within a chimpanzee community. Although vertical transmission (between mother and her offspring) is the most frequent means of skill transmission, van Schaik (2003) claims that horizontal transmission (between mature individuals) provides the only plausible explanation for variation across populations in the size of a population's tool kit or cultural repertoire. Social intersections at some types of tool-using sites may be rare and particularly uncommon among certain individuals, such as adult females residing in the peripheral areas of the group's range. However, there are tool-harvested resources such as nuts which may attract large parties of mixed age and sex composition to the same locality within a community range (Boesch & Boesch-Achermann, 2000).

Within fission-fusion societies, individuals may exhibit preferences for associating with particular conspecifics more than others. Individual identity or pre-existing relationships may also have an effect on whether or how information is transmitted within a group (Coussi-Korbel & Fragaszy, 1995). Frequent association and close proximity among certain individuals is more likely to promote information transfer than among loose associates. The specific type of interaction between individuals is also likely to affect the type and amount of information transferred. Some types of tool-using skills are relatively simple and therefore more likely to be invented by individuals with little or no social input. Leaf sponging is a behavior with relatively few components (Sanz &

Morgan, 2010) which has been invented by captive chimpanzee populations provided with the appropriate materials and setting (Kitahara-Frisch & Norikoshi, 1982). In contrast, more complex technical skills may require more specific input about raw materials, tool manufacture, tool actions and results. Acquisition of more complex skills may require exposure or proximity to a model, as has been shown in captive studies (Hopper *et al*., 2007).

Until recently it was widely held that chimpanzee tool use was characterized by a direct relationship between a single tool and its goal. Several study populations have now been reported to exhibit hierarchically structured use of multiple tools and flexibility in using a tool for multiple goals (Sanz & Morgan, 2007, 2010; Boesch *et al*., 2009). Further, some tools have specific design features, such as material selectivity or pre-modification of tool form, which increase the complexity of the task (Sanz *et al*., 2009; Sanz & Morgan, 2010). The chimpanzee population in the Goualougo Triangle located in northern Republic of Congo exhibits a wide range of tool-using behaviors, several of which involve the regular use of tool sets – multiple tools used in sequence to accomplish a task. In contrast to previous reports of the rarity of tool sets, these behaviors are habitual in termite (Sanz *et al*., 2004), driver ant (Sanz *et al*., 2010) and honey gathering (Sanz & Morgan, 2009) contexts within this chimpanzee population, and possibly across the range of the central subspecies (*Pan troglodytes troglodytes*).

In this chapter we review the social settings in which tool use occurs within the Goualougo Triangle chimpanzee population, whose members regularly exhibit complex tool-using behaviors. We compare different tool-using contexts to determine if coordination in space, time and social interactions provides varied opportunities for social transmission of tool-using skills. Social networks at tool sites are also examined to determine if the observed degree of social contact could facilitate horizontal transmission within and between groups. In particular, we are interested in identifying the potential means by which the relatively complex tool-using behaviors of these chimpanzees have been so effectively maintained over both time and space. Insights from these wild apes will enable us to better understand the mechanisms underlying the large-scale similarity of technology among our hominin ancestors.

Methods

Study site

The Goualougo Triangle is located within the southern portion of the Nouabalé-Ndoki National Park (16°51′–16°56′ N; 2°05′–3°03′ E) in northern Republic of Congo. The study area is composed of evergreen and semi-deciduous lowland forest, with altitudes ranging between 330 m and 600 m. The climate can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones. Rainfall and temperature were recorded daily at the Goualougo Triangle base camp. Rainfall was 1650 mm in 2007 and 1676 mm in 2008. The average minimum and maximum temperatures were 21.5°C and 24.2°C in 2007, and 21.5°C and 24.1°C in 2008.

Data collection

Direct observations of the chimpanzees in the Goualougo Triangle have been ongoing since February 1999. Chimpanzee tool-using behaviors have been documented by direct observation throughout this time and by remote video monitoring since 2003 (for description of these methods, see Sanz *et al.*, 2004). For all observations of tool-using behavior, we recorded the identification of the chimpanzee, type of object used, target of object, actions, context and/or goal of the tool-using behavior and the outcome. In addition, chimpanzee tool assemblages were also collected at termite and ant nests by several field teams conducting daily reconnaissance walks, and during monthly phenology circuits. We recorded the location, materials used to make the tool, length, width and any modifications to each tool.

We also examined the size and composition of subgroups engaging in feeding on particular types of food resources (termites, leaves, fruits). These measures serve as a proxy for social tolerance, or opportunities for social learning (van Schaik, 2003).

Dyadic association indices

Matrices of dyadic associations were calculated based on direct and remote video observations of sexually mature males and females. Associations were scored as presence of an individual in the same party. Association was quantified as:

$$\frac{x}{x + y_a + y_b},$$

where x is the number of sightings that include both chimpanzees, y_a is the number of sightings that included chimpanzee a but not chimpanzee b, and y_b is the number of sightings that included chimpanzee b but not chimpanzee a (Cairns & Schwager, 1987; Ginsberg & Young, 1992).

Network analysis

Matrices of association indices were treated as weighted networks (Newman, 2004; Barthélemy *et al.*, 2005; Boccaletti *et al.*, 2006). Binary networks consider ties between individuals (edges) as present or not, whereas weighted networks show heterogeneity in the connections between nodes. Typical analyses of social networks include measures of which individuals are best connected and how individuals are connected within a network (Newman, 2003). We adopted the standard measure of clustering coefficient to assess the degree to which individual nodes (in this case chimpanzees) tend to cluster together within a social network. More specifically, the clustering coefficient calculates the probability that adjacent nodes of a particular node are connected. This is based on the premise that two associates of a particular individual have a greater probability of knowing one another than two individuals chosen at random from a population. The weighted clustering coefficient takes into account that associations with some neighbors are more important than others (Holme *et al.*, 2007). Network analyses were performed using SOCPROG 2.3 (Whitehead, 2006).

Results

Coordination in space

Tool traces were frequently recovered from tool-using activities that occurred on the ground, such as termite and ant gathering. Tools were also occasionally recovered from sites where chimpanzees were observed to gather honey, which most often occurs in the forest canopy. However, individuals often placed their tools on branches in the high canopy, which prohibited tool collection by the authors. Because of this, the remainder of our investigations of coordination in space focus only on ant dipping and termite fishing. During circuits of active termite nests, we recovered an average of 3.0 fishing probes ($n = 685$ tool assemblages, range = 1, 30) and 4.1 puncturing sticks ($n = 94$ tool assemblages, range = 1, 32) per site. These assemblages often consisted of tools of different ages, indicating repeat visitation to the tool-using site. We also collected 284 tool assemblages (totaling 1060 tools) at ant nests in the Goualougo Triangle (Sanz *et al.*, 2010). The average number of ant-gathering tools recovered at each site was 3.7 tools ($n = 284$, range = 1, 18). Thirty-six percent of these assemblages recovered at ant nests contained two types of tools: nest-perforating tools and ant-dipping probes. Although we have documented seasonal peaks in some types of tool use (Chapter 3; Sanz *et al.*, 2010), there were ample possibilities for chimpanzees to encounter tool sets at termite nests throughout the year. Due to the high degree of material selectivity and modification of tools exhibited in tool manufacture by this chimpanzee population, their tools were easily distinguishable from other detached vegetation around insect nests (see Figure 8.1).

Coordination in time and space

The average number of individuals in chimpanzee parties at termite nests was 2.23 ± 1.57 individuals ($n = 388$, range = 1, 14), smaller than parties observed in other contexts (4.98 ± 4.19, $n = 606$). This difference was significant for both males and females compared across the two settings ($\text{Wilcoxon}_{\text{Males}}$ $Z = -3.011$, $p = 0.002$; $\text{Wilcoxon}_{\text{Females}}$ $Z = -4.107$, $p < 0.001$). However, party sizes in termite gathering were actually of intermediate size in comparison to party sizes in other foraging contexts (Figure 8.2). Party sizes were larger when feeding on leaves, fruits or flowers, and smaller when feeding on meat, bark or pith.

Our results indicate ample opportunity for vertical transmission among these apes, as parties visiting termite nests were most often composed of mothers with their dependent offspring (37% of parties). Lone individuals were the next most frequent visitors to termite nests, accounting for 32% of visitation. Adult parties and mixed parties of different age and sex classes accounted for only 12% of parties at termite nests. Small parties consisting of only mothers or a lone individual raises the question about the possibility of horizontal transmission in tool-using contexts. However, graphical analysis of dyadic association indices at termite nests showed a high degree of social connectivity among mature individuals within the Moto community, despite the rarity of adult-only and mixed-party associations (Figure 8.3). The association network of adult parties

Figure 8.1 A subterranean termite nest with discarded puncturing tools. These stick tools persist for several months and may be used by different individuals who visit the nest after the tools have been deposited.

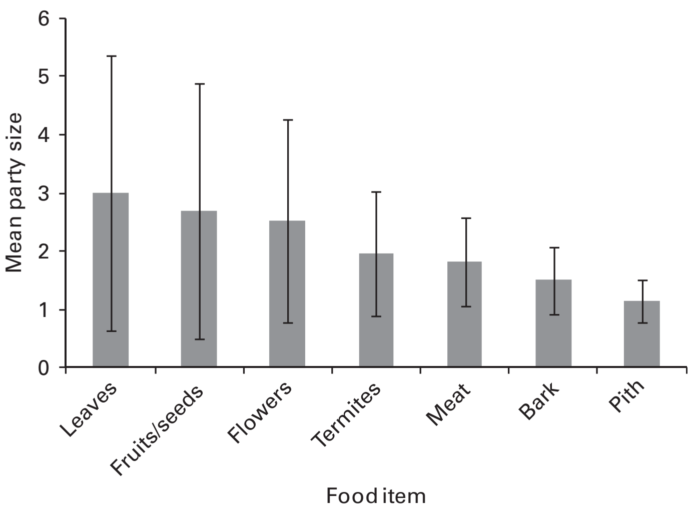

Figure 8.2 Chimpanzee party sizes across different foraging contexts. The number of individuals visiting termite nests is often smaller than those foraging on fruits or leaves.

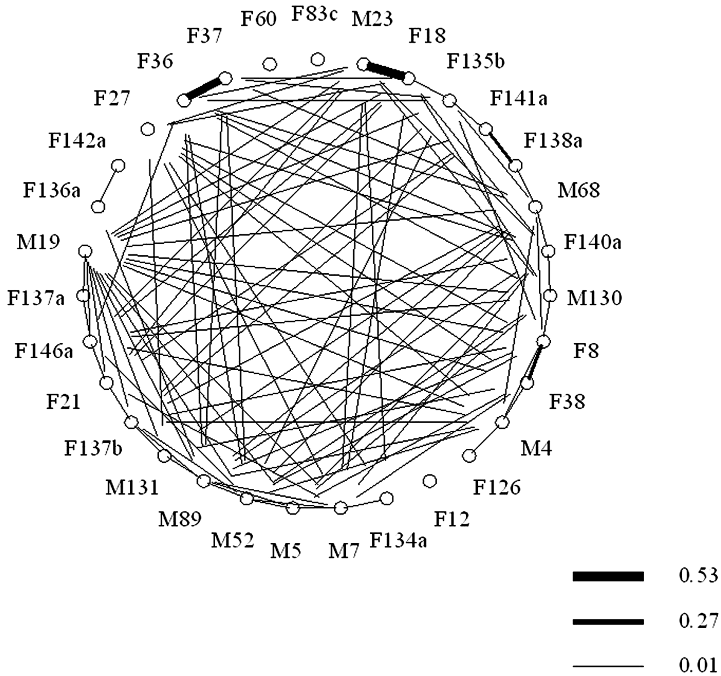

Figure 8.3 Associations of mature individuals in the Moto community at termite nests. Line weights depict strength of association between two individuals.

Table 8.1 Social clustering of chimpanzees in termite fishing and in other contexts, compared with social networks of dolphins and humans.

Taxa	Network	Clustering coefficient	Reference
Human	High-energy physics coauthors	0.73	Newman, 2001
Human	Company directors	0.59	Newman *et al.*, 2002
Human	Computer science coauthors	0.50	Newman, 2001
Human	Theoretical physics coauthors	0.43	Newman, 2001
Dolphin	Moray Firth dolphin associations	0.41, 0.58	Lusseau *et al.*, 2006
Dolphin	Doubtful Sound dolphin associations	0.30	Lusseau, 2003
Chimpanzee	Chimpanzee associations at termite nests	0.26	This study
Chimpanzee	Chimpanzee associations – contexts other than termite nests	0.19	This study
Human	Movie actors associations	0.08	Newman *et al.*, 2002
Human	Biomedical research coauthors	0.07	Newman, 2001

and mixed parties visiting termite nests was relatively dense, with most individuals showing several connections with other mature individuals within the community.

As shown in Table 8.1, clustering coefficients were higher in termite gathering than other feeding contexts, which indicates that although party sizes were relatively small in termite gathering, there was a higher degree of social connectedness and more potential pathways of horizontal transmission than in other feeding contexts. Network analytic measures also provide a means of comparing the degree of connectivity across species and different types of social networks; for example, the clustering coefficients of this chimpanzee population were within values reported from human and dolphin social networks.

We also found that chimpanzees from different communities spatially overlapped in their use of termite nests located in the boundary areas of their community ranges. However, apes from adjacent social groups were never observed to use the same site at the same time. In addition to female dispersal between groups, spatial overlap in tool site use extends the possibility of horizontal information transfer between groups via local or stimulus enhancement. Males were observed to inspect fresh tools found at termite nests within boundary areas (Supplemental Video #8.1), which is a behavior rarely observed in the core area of the range.

Social facilitation

We observed several different types of social interactions during tool-using episodes which could facilitate the transfer of information between individuals. First, individuals tolerate others in close proximity. In addition, immature chimpanzees often approached their mothers to observe their behavior. We rarely observed mothers allowing youngsters to gather termites directly from their tools. However, several females transferred tools and productive work sites to their offspring. During 101 hours of video-recorded tool use at termite nests, a total of 33 tool transfers were observed (Supplementary Video #8.2). Three types of tools (fishing probes, perforating twigs and puncturing tools) are used by the chimpanzee population to gather termite prey (Sanz *et al*., 2004). Fishing probes or materials to manufacture fishing probes accounted for 97% of observed tool transfers, with only one exchange involving a puncturing tool and no observations of social exchanges involving perforating tools. More than half of the observed tool transfers (18 of 33 transfers) also involved gaining access to a termite tunnel for fishing. Coaction was also observed in this chimpanzee population.

Discussion

In this study we found that the social context of chimpanzee tool use is rich in opportunities for social learning which may serve to stimulate and maintain complex technologies within and between social groups across space and over time. Chimpanzees are not only gregarious, but highly tolerant of conspecifics at tool-using sites. While vertical transmission is likely to be the most common means of social information transfer within social groups, we also documented ample opportunities for indirect and direct transfer of information among mature conspecifics within and between chimpanzee communities in the Goualougo Triangle. While contact with tool traces or noticeable changes in the tool site substrate may suffice to maintain simple forms of tool use, the association of individuals at tool sites and transfer of tools are also likely contributors to the maintenance of the complex tool traditions exhibited by chimpanzees in this region. Future comparative studies could be conducted to determine whether the degree of spatial and temporal overlap at tool sites differs among chimpanzee populations, and if this is related to the diversity or complexity of their tool traditions.

Mother–offspring parties (mother with her dependent offspring) were the most frequently observed party composition at termite nests in the Goualougo Triangle. In addition to dependent offspring, mothers were often accompanied by their mature (subadult, adult) offspring. In addition to association within subgroups, mothers and offspring engaged in social interactions which sometimes involved transfer of tools or sharing of work sites. Parties containing multiple mothers and their offspring were also observed at tool sites. Although the kin relationships among adult females in the Goualougo Triangle population are not yet known, all mature subadult females in the main study communities have dispersed from their natal groups. This situation obviously differs from Gombe, where female chimpanzees often visit termite nests with their mature maternal kin (Lonsdorf, 2006). Within that chimpanzee population, it is not uncommon to have a mother visiting a termite nest with her daughters' families. The demographics of chimpanzee communities and patterns of female dispersal have implications for the transmission and prevalence of information within and between communities, which could dramatically affect patterns of tool-using skills. Opportunities for immature chimpanzees in the Goualougo Triangle to interact with competent tool users other than their mother arose in mixed parties, female parties and consortships. Similar to mothers, we found that mature individuals were highly tolerant of younger chimpanzees who occasionally approached to watch or even interfered with other individuals' tool-using activities. However, the number of individuals converging at termite nests was relatively low compared to other feeding contexts, such as leaf and fruit food sources.

Social facilitation was observed in the form of tool transfers between individual chimpanzees. These were often a result of requests from younger individuals toward their mothers or older siblings. The active transfer of raw materials and manufactured tools from one individual to another is seemingly unique among primates. Such transfers indicate sensitivity to another individual's request or need for a tool, and that the giver is willing to assume the immediate costs of reduced foraging and increased energy expended to locate another tool. Leaving the foraging party at a termite nest to procure tool materials may also place an individual at greater risk of leopard predation. Studies of captive populations have shed light on tool transfers by chimpanzees in controlled circumstances (Yamamoto *et al*., 2009), but studies of natural populations are necessary to inform us of the ecological and social constraints within which tool use has evolved. Further systematic research is needed on the type of tool transfers (reactive versus proactive) and their prevalence with relation to group demographics in wild populations.

Transfer of information between social groups is an important and often overlooked aspect of the transmission of advantageous foraging strategies, particularly those involving tools. Foraging in boundary areas of a community range is often difficult to detect because it is done discreetly, so as not to draw the attention of neighboring conspecifics. However, our remote video recordings of chimpanzee visitation to termite nests revealed that individuals from different communities visited the same termite nests. Visits of different community members to a particular termite nest did not occur simultaneously, but rather were separated in time (sometimes less than an hour apart). Tools left at tool-use sites and changes to the tool-using substrate provided clues that chimpanzees have previously visited the site. We observed individuals arriving at a termite nest inspecting the fresh and recent tools left behind by conspecifics. This indirect interaction could be one potential means of facilitating transmission of technological information between groups. Further research on the degree of overlap at tool sites between chimpanzee communities, and its impact on promoting conformity in tool traditions over large spatial scales, is needed.

Fission-fusion sociality is an adaptation which enables organisms to flexibly respond to variable ecological and social circumstances. Chimpanzees form subgroups within their community range that are of optimal size and composition for the task at hand, such as foraging at a fruiting tree or conducting a boundary patrol along their territory's frontier. However, the fluidity of this social structure poses a challenge for information transfer within a social group. All of the group members of the community never assemble at a particular location, and so information must be transmitted within smaller party associations. The naturalistic context of tool use in wild chimpanzee communities provides an opportunity to study the means by which individuals maintain technological traditions. The majority of human hunter-gatherers also live in patrilocal fission-fusion societies, and so we can infer that the last common ancestor may have lived in a similar social setting.

Potts (2004) has suggested the fluctuations in the spatial distribution and temporal availability of particular food resources (fruits) and habitats (forests) since the Miocene are reflected in the evolutionary trajectory of great ape ecology, sociality and cognition. It is further suggested that the flexibility and adaptability of great apes may have provided a selective advantage in fluctuating paleoenvironments. Environmental changes can result in shifting ecological pressures (such as interspecific feeding competition) and/or emergence of opportunities which favor the invention of new technology among wild apes. Population size and distribution are also related to the likelihood of the invention and accumulation of socially transmitted information among hominins. The clade of living hominoids provides us with an opportunity to identify shared and derived traits related to the acquisition and maintenance of technological skills.

Identifying the specific social and environmental circumstances that either promote or suppress specific learning mechanisms and outcomes in natural populations will provide a deeper understanding of the evolutionary forces which have shaped the technological sophistication of our own species. Research is currently underway to document the development of complex tool-using skills in the chimpanzees of the Goualougo Triangle and compare their acquisition of tool-using skills to other wild chimpanzee populations. We also advocate research efforts to document the tool traditions of additional populations, as our understanding of the breadth of behavioral diversity has expanded with the study of additional chimpanzee communities. Climate change and anthropogenic disturbances are two factors which are likely to affect the ecological and social contexts of wild ape tool use in the future (van Schaik, 2001). As a result, the natural cultures of wild apes may be even more endangered than the individuals who harbor this knowledge.

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