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An experimental, comparative investigation of tool use in chimpanzees and gorillas

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Studies of ape tool use have been conducted in captivity since the early 1900s and in the wild since the 1960s. Chimpanzees are the most prolific tool users among the apes, and are known to use more tools than any other nonhuman animal. In contrast, reports of gorilla tool use are rare both in wild and captive settings. Studies of the processes involved in tool use learning have been limited in the wild by the lack of ability to control several unpredictable variables, and in captivity by tool use opportunities that are often presented in non-naturalistic contexts. We attempted to address both of these limitations by providing naïve subjects with a naturalistic tool use device (built to simulate a termite mound) while housed in a more natural social setting to approximate how learning would occur in the wild. Both gorillas and chimpanzees participated in the experiment to allow comparative analyses of acquisition of tool behaviour and the factors that may affect acquisition. Both species showed low frequencies of interaction with the mound in the baseline condition, before baiting with a food reward. Once baited, chimpanzees both attempted and succeeded to extract the reward more quickly than did gorillas. The number of social group members at the mound was significantly higher for chimpanzees than for gorillas and may have affected skill acquisition. We advocate that comparative approaches to skill acquisition and learning are valuable, but that researchers need to be cognizant of species differences in social structure that may affect results.

Tool use is broadly defined as the movement of a detached object that is used to change the location or condition of another object or organism (van Lawick-Goodall 1970; Beck 1980; but see St Amant & Horton 2008). van Lawick-Goodall's (1970) review of tool use in primates and other vertebrates was the first to document wild chimpanzees not only using tools, but actually making tools by altering objects in their environment to serve a specific purpose. Goodall described a behaviour called 'termite fishing', in which individual chimpanzees fashion pieces of vegetation into an appropriate size to puncture a termite mound and extract the termites that cling to the tool. Since then, researchers have reported a vast tool repertoire for chimpanzees that varies greatly across geographical ranges, genetic populations and ecological systems (reviewed in McGrew 1992), including nut cracking (Boesch & Boesch 1984; Sakura & Matsuzawa 1991; Matsuzawa 1996; McGrew et al. 1997), honey dipping in beehives (McGrew 1992; Stanford et al. 2000; Hicks et al. 2005), pestle pounding (Yamakoshi & Sugiyama 1995; Humle & Matsuzawa 2004), ant dipping (Nishida 1973; Nishida & Hiraiwa 1982) and using leaves as sponges for drinking water (Tutin et al. 1995; Tonooka 2001). Much of this variation cannot be explained by ecological differences, and as a result, primatologists have suggested that differences between populations in tool use indicate the presence of cultures built on processes of social learning (Whiten et al. 1999). Cultural differences have since been reported in other species, including orangutans (van Schaik et al. 2003), capuchin monkeys (Perry et al. 2003) and cetaceans (Rendell & Whitehead 2001).

In contrast to the dense literature on wild chimpanzee tool use, reports of wild gorillas using tools are rare. Breuer et al. (2005) reported two possible forms of tool use in wild western lowland gorillas, *Gorilla gorilla gorilla*. In one observation, an adult female used a branch to test the depth of a pool of water. In a second instance, another adult female used a tree trunk as a buttress while feeding, and later used the trunk as a bridge to cross a swamp. In wild Cross River gorillas, *Gorilla gorilla diehli*, Wittiger & Sunderland-Groves (2007) reported that three male gorillas threw grass during an agonistic encounter with researchers and two other

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gorilla–human encounters involved aimed object throwing by gorillas.

Both gorillas and chimpanzees have been observed using tools in captivity. Chimpanzees have an especially lengthy literature, beginning with Kohler's (1927) seminal observations of chimpanzees stacking boxes and using tools to access food that was out of reach. Since then, chimpanzees have been shown to be adept and creative tool users, using poles to escape from their enclosures (Menzel 1973) and using keys to open doors (Temerlin 1975). However, experimental testing of chimpanzee tool use abilities have most commonly used non-naturalistic conditions such as using rakes to access out-of-reach food (Tomasello et al. 1987; Nagell et al. 1993), using sticks to poke a food reward out of a 'trap-tube' (reviewed in Call, in press) or poking a stick into a device to remove a blockade and release food (Whiten et al. 2005). Extractive tool use, such as 'fishing' for food, has been studied only rarely in captivity, and usually in the context of measuring whether the device provided environmental enrichment sufficient to reduce negative behaviours (Nash 1982; Maki et al. 1989; but see Hirata & Celli 2003). Only one paper that we know of (Paquette 1992) documented the initial discovery and spread of an extractive tool use behaviour in a naïve group (one that had never observed the behaviour) of chimpanzees, using a honey-fishing device.

Compared to chimpanzees, tool use studies on captive gorillas are relatively rare and largely anecdotal. These include accounts of lowland gorillas using rakes to access out of reach food as described above for chimpanzees (Chevalier-Skolnikoff 1977; Wood 1984; Fontaine et al. 1995; Mulcahy et al. 2005), using sticks or a blanket to drag an out-of-reach object closer (Natale et al. 1988) and throwing objects to knock food out of inaccessible trees (Nakamichi 1999). Two studies have investigated extractive tool use: Boysen et al. (1999) described western lowland gorillas dipping from an artificial device to extract peanut butter, and Pouydebat et al. (2005) investigated gorillas' ability to manufacture appropriate tools to extract honey from a log with holes bored into it.

Evidence showing that gorillas have successfully used tools in a captive setting suggests that they have the cognitive capacity to use a tool to solve a problem. The question remains as to why gorilla tool use is relatively rarely observed in the wild. Ecological explanations focusing on differences in diet are less convincing given what we now know about the diversity in diets of western lowland gorillas that live sympatrically with chimpanzees, in areas such as the Lope Reserve in Gabon (Kuroda et al. 1996). Breuer et al. (2005) assert that whereas chimpanzees use tools to acquire otherwise inaccessible foods, gorillas may have different ecological pressures influencing tool use within the genus. The authors state that gorillas more often use their own physicality to obtain food from difficult sources that chimpanzees use tools for, such as using fists to access termite mounds, or using their mandibles to crack open hard-shelled nuts. Other possibilities are that gorillas are less likely to investigate and explore novel objects, or that learning is constrained in some manner by gorilla social behaviour. Both chimpanzees and gorillas live in social groups, but there are differences in the composition of the core social group. Gorilla societies are polygynous, with a dominant silverback male and several breeding females comprising a cohesive group; members of this group travel together consistently throughout the day (Watts 1996; Robbins 1999). Chimpanzees live in 'communities' (van Lawick-Goodall 1968) or 'unit-groups' (Nishida 1968) that range in size from 20 to 150 individuals. These communities are multimale and multifemale, promiscuous, and have a male dominance hierarchy in which males form the stable core of the community and defend a group home range (Goodall 1986). Chimpanzee society is termed 'fission–fusion', as members of a community can join or leave travelling parties at any time (Wrangham 1979; Goodall 1986).

Species comparisons of tool use abilities are difficult, as most wild and captive tool use studies have necessarily focused on either single species (chimpanzees: Paquette 1992; gorillas: Pouydebat et al. 2005) or very small numbers of a few species (Visalberghi et al. 1995; Mulcahy et al. 2005). In this study, we presented naïve gorillas and chimpanzees with a naturalistic tool use device, in an identical environment, to investigate species differences in the acquisition of an extractive foraging task. We compared baseline propensity to investigate a novel device, latency to acquire the skill, time spent engaged in the task and social behaviour at the device to test our hypotheses that (1) both species successfully use extractive tools and (2) chimpanzees acquire the skill more quickly and spend more time performing it, which may reflect species differences in social patterns.

METHODS

Subjects and Housing

The study subjects were a group of seven chimpanzees and two groups of gorillas (five and eight members, respectively) housed at the Regenstein Center for African Apes (RCAA) at Lincoln Park Zoo, Chicago, IL, U.S.A. (see Table 1). All animals were captive born. The ape facility was newly constructed in 2004, and during the study the apes rotated through the one exhibit with the testing apparatus so that the housing environment was identical and novel for all groups. The exhibit had an indoor/outdoor design; the indoor exhibit measured 408.42 m^2 and the outdoor exhibit measured 2011.68 m^2. Access to the outdoor yard was temperature dependent, and during the course of the study, all apes had outdoor access at varying times depending on the outdoor weather conditions. The indoor exhibit contained climbing structures of varying heights, deep-mulch bedding and was visible to the general public during daytime hours. Daily meals of fresh produce and biscuits were scattered through the exhibit twice daily, but never within 1 h of testing. Animals were maintained in their social groups and the testing apparatus was presented to the group as a whole without human intervention or demonstration. Offspring under 5 years old ($N = 3$ gorillas, $N = 1$ chimpanzee) are listed in Table 1 but were not included in species comparison analyses to remove potential developmental and associative confounds. No animals were trained to complete the task or demonstrated any portion of the task. In this way, the testing paradigm approximated the natural situation that ape communities that do not habitually termite-fish face in the wild: simply encountering a termite mound with other unskilled members of their social group.

Testing Apparatus

The testing apparatus was a hollow, concrete structure (274 cm wide $\times$ 205 cm tall, and 15 cm thick) designed to replicate a natural termite mound found in wild ape habitats. We cut the mound in a vertical cross-section and built it onto a glass viewing wall in the northwest corner of an indoor exhibit so that it protruded 104 cm into the animal space (see Fig. 1a), allowing researchers but not apes visual access to the interior of the mound. We bored eight holes into the mound and fitted each hole with a polyvinyl chloride (PVC) receptacle, onto which tubes (4.5 cm diameter) of various lengths and configurations could be attached. The initial tube length used for this study was 13.5 cm. The eight holes were spaced across the mound surface to allow the apes access to a 'bait' (in this study, ketchup or mustard). The mound also had an access door on the inside, through which an animal caretaker could enter and attach the bait tubes without entering the animal side of the exhibit (see Fig. 1b). Tools for the task were not provided to the apes, but

Table 1
Individual subjects by species, age and sex, and their latency (measured by number of trials) to attempt and succeed at the fishing task

ID	Species/group	Age (years)	Sex	Latency to attempt	Latency to success	Mother name (if in group)
Chuckie	Chimpanzee	5	F	1	1	Kathy
Nana	Chimpanzee	9	F	1	1	
Kathy	Chimpanzee	14	F	1	1	
Cashew	Chimpanzee	19	F	1	1	
Optimus	Chimpanzee	5	M	1	3	
Kipper	*Chimpanzee*	*4*	*M*	*1*	*58*	*Cashew*
Hank	Chimpanzee	14	M	9	13	
Makari	Gorilla 1	17	F	12	12	
Bahati	Gorilla 1	14	F	13	32	
Rollie	Gorilla 1	7	F	34	41	
Azizi	*Gorilla 1*	*1*	*M*	*45*	—	*Makari*
Susie	*Gorilla 1*	*4.5 m*	*F*	—	—	*Bahati*
Mumbali*	Gorilla 1	8	F	—	—	
Tabibu	Gorilla 1	12	F	—	—	
Jojo	Gorilla 1	24	M	—	—	
Kwan	Gorilla 2	17	M	1	1	
Kowali	Gorilla 2	24	F	1	20	
Madini	Gorilla 2	8	F	2	7	
Bulera	Gorilla 2	17	F	12	25	
Amare	*Gorilla 2*	*1*	*M*	—	—	*Kowali*

Individuals under 5 years old are in italics to indicate that they were removed from analyses of species comparisons.

* This individual exited the study after 20 bait trails because of illness and subsequent death.

rather, individuals were able to fashion tools from natural vegetation (hay, trees, branches, etc.) found in the indoor or outdoor exhibits.

Bait Schedules and Conditions

Data for this study were collected during June 2004–November 2006, during which time, each of three ape groups rotated through the exhibit containing the mound. The first month that any group was in the exhibit was conducted as a 'baseline' phase, in which we did not bait the mound, but the groups had free access to the unbaited mound. Video data were collected on weekdays, except when either exhibit maintenance prevented access to the exhibit or holidays fell on a weekday. To determine an appropriate bait substance, we conducted a palatability test with each group using different substances and found that all test subjects readily consumed ketchup and mustard. These substances were approved by veterinary staff and had the added benefit of not attracting stinging insects to the testing apparatus, as would sweeter substances such as honey or jelly. During the 'bait' phases, we baited the mound every other day (Monday–Friday) at randomized times between 1100 and 1400 hours, on the hour, by filling the tubes with approximately 5 cm (266 ml) of the bait substance and attaching the tubes from the inside of the mound. The bait substance used on a particular day was determined by a fixed schedule, and the substance and bait time for each progressive day of the study was identical for all groups. Each bait day was followed by a control day, in which the mound was unbaited, but behavioural data were collected in the same manner as on the bait day. To collect video data, we used a stationary, ceiling-mounted security camera to film the entire mound and a 1 m perimeter around the mound from 0900 to 1530 hours daily during both baseline and bait phases. The security camera was connected to a time-lapse VCR (Panasonic AG-RT650) that was pre-set to record each 6.5 h daily session.

Video Scoring and Analyses

To analyse behaviour at the mound, we scored individual subjects' behaviour for each baseline, bait and control day. We scored the entirety of each 6.5 h tape session using continuous data collection for each group member. For example, if a social group contained seven individuals, continuous data was collected for all seven group members throughout the 6.5 h session. We recorded frequencies and durations of all instances of 16 behaviours for each subject, including tool use behaviours (Fish, Poke, Investigate and Tool Behaviour; see Table 2) and non-tool-use behaviours, such as Inactive, Play, Groom, Feed, and so forth. Videotapes were

Figure 1. Artificial termite mound as viewed from (a) the subjects' side and (b) the inside, which was visible to researchers, the public and animal care staff, but not to study subjects.

Table 2
Ethogram of tool-related behaviours

Behaviour	Description
Fish	Direct contact with a hole on the mound using a tool
Poke	Poke or prod at the baited hole using fingers; no tool involved
Investigate	Inspect the mound using visual or olfactory senses. No tool involved; no poking or prodding with fingers involved. The face must be oriented to and within 5 cm of the mound for 3 s or more
Tool Behaviour	Interact with tool/tool use material. Includes mouthing or modifying tools, or otherwise manipulating tool use material, but not contacting the mound with the tool

evaluated by four different researchers that had been trained on the same protocol and that had passed an interobserver reliability test (≥85% agreement) before commencing scoring.

For assessing baseline investigation of the mound, we scored individual frequencies of specific behaviours within 1 m of the mound for the first month that each ape group was in the exhibit, resulting in 17 baseline days of data. We scored the target behaviours from the video data and then compared between species using the Mann–Whitney *U* test in SYSTAT version 11.0 (SYSTAT Software, Inc., Chicago, IL, U.S.A.).

Upon the start of bait trials, we determined the latency to attempt the task (without accessing the bait substance) and latency to succeed in the task, defined as inserting a tool into the mound and retrieving the bait substance. Latency was measured in terms of the number of bait trials presented. We used the first 15 bait trials to represent the initial opportunity for discovery and acquisition of this foraging task by naïve individuals. However, some individuals made their first attempt to fish outside this time period (after the 15th bait day) and these are indicated in Table 1.

To compare the percentage of time that each species spent in 'termite-fishing behaviours' (hereafter 'fishing'), we first computed the daily duration for relevant behaviours (Fish, Poke, Investigate and Tool Behaviour) for the time period in which the bait tubes were available. These individual, daily percentage durations were then averaged over sets of five consecutive bait days to create a series of three phases over the first 15 baits. We analysed species and phase differences using analysis of variance (ANOVA) in SYSTAT version 11.0.

To evaluate social behaviour at the mound, we scored the number of group members or 'neighbours' present within 1 m of the mound for each individual subject on each day. We calculated a percentage of possible neighbours (number of neighbours/number of individuals in the group − 1) to control for group size differences. The average number of neighbours per condition (bait versus control) was calculated separately for related and unrelated dyads to account for high levels of association between mother–infant pairs. We analysed species and condition differences using the ANOVA test in SYSTAT. Within-condition tests were conducted using the Mann–Whitney *U* test in SYSTAT.

Supplementary Behavioural Data Collection

As a part of an ongoing behavioural monitoring programme conducted since July 2004, behavioural data was collected by trained research staff on each of the ape groups housed at RCAA. Data was collected from 1000 to 1700 hours on most weekdays for each ape. During 10 min focal follows, observers entered data on behaviour and social proximity every 30 s into a computerized observation module (Noldus Observer, Noldus Information Technology, Wageningen, The Netherlands) programmed with a 36-item ethogram. To better understand general object use, we extracted object manipulation data from the behavioural monitoring data set. We defined object manipulation as the examination of any nonfood enrichment item, structural elements within the exhibit, or bedding materials, but excluding tool use. For each adult subject, we used these data to calculate a proportion of time spent manipulating objects. We also used these data to gain a measure of social proximity throughout the exhibit to better understand social dynamics outside the context of the termite mound. Proximity was defined as time in which the focal subject was touching or within 1 m of a conspecific. Species were compared using the Mann–Whitney *U* test.

Ethical Note

This research project and the procedures for baiting the termite mound were approved by the Lincoln Park Zoo Research Committee, which is the governing body for all animal research at the institution. No social group manipulations occurred, and exhibit rotations were conducted as part of normal husbandry routine. Bait substances, amount and frequency were reviewed and approved by veterinary and nutrition staff. Data collection was observational and no modifications were made to standard animal care routines.

RESULTS

Baseline Investigation of the Mound

Overall, frequencies of performing fishing behaviours at the mound during the baseline period were low for both species (see Table 3). Chimpanzees were significantly more likely to Fish (Mann–Whitney *U* test: $U = 50$, $N_1 = 6$, $N_2 = 10$, $P = 0.004$) than gorillas, which showed no instances of fishing behaviour during the baseline period. Four of the six independent chimpanzees fished during baseline, with 1, 3, 4 and 13 instances, respectively. We found no difference in frequencies of Investigate ($U = 38$, $N_1 = 6$, $N_2 = 10$, $P = 0.290$), Poke ($U = 28.5$, $N_1 = 6$, $N_2 = 10$, $P = 0.860$) and saw no instances of Tool Behaviour (manipulation without contacting the mound) during the baseline phase in either species.

General Object Manipulation

When comparing individuals 5 years and older, the behavioural monitoring data showed that chimpanzees spent significantly more of the observation period engaged in general (non-tool-use) object manipulation than did gorillas (8.3% versus 2.4%; $U = 54$, $N_1 = 6$, $N_2 = 10$, $P < 0.00$).

Latencies to Attempt and Succeed

Once the mound was baited, individual chimpanzees and gorillas had different latencies to attempt and succeed in fishing (Table 1). All chimpanzees except for the alpha male attempted to fish on the very first trial. All four female chimpanzees succeeded on the first day, followed in succeeding days by the 5-year-old male (Optimus), the 14-year-old alpha male (Hank) and finally, the youngest member of the group (4-year-old male Kipper). Gorillas showed much more variability in latencies to attempt and succeed in the task: some individuals attempted and succeeded in the task

Table 3
Comparison of fishing behaviours performed at the mound by chimpanzees and gorillas during 17 days of baseline data collection

	Fish	Poke	Investigate	Tool behaviour
Chimpanzees	3.00 (±4.93)	0.86 (±1.55)	2.00 (±1.26)	0 (NA)
Gorillas	0 (NA)	1.60 (±2.72)	0.50 (±1.08)	0 (NA)

Values are mean frequencies ± SE.

on the first day (17-year-old silverback Kwan) and some individuals never attempted the task even after 60 bait trials. It is noteworthy that in the gorillas, the highest-ranking female in each group (Makari for group 1 and Kowali for group 2) were the first animals to attempt the task.

Fishing Behaviours

Chimpanzees performed significantly more fishing behaviours during the first 15 bait trials than gorillas (ANOVA: $F_{1,42} = 45.69$, $P < 0.001$; Fig. 2). Although both species showed a significant increase in time spent fishing across phases ($F_{2,42} = 6.93$, $P = 0.003$), chimpanzees showed a greater increase than gorillas ($F_{2,42} = 4.59$, $P = 0.016$).

Social Behaviour at the Mound

The average percentage of possible neighbours present at the mound with a focal subject was significantly greater for chimpanzees than for gorillas (ANOVA: $F_{1,28} = 19.34$, $P < 0.001$). There was also a significant effect of condition (bait or control) on social behaviour of both species ($F_{1,28} = 13.53$, $P = 0.001$), and a significant interaction between species and condition ($F_{1,28} = 4.37$, $P = 0.046$). On average, all focal subjects had more neighbours at the mound on bait days versus control days, and, overall, chimpanzees had more neighbours than gorillas. In addition, the significance of the interaction suggests that the effect of increasing numbers of neighbours during the bait condition was more pronounced in chimpanzees than in gorillas. We further analysed differences in the number of neighbours during the bait condition only. Since the chimpanzee and gorilla groups all had nursing mother–infant pairs, we calculated the differences in the number of neighbours for focal subjects by first including and then excluding dependent offspring neighbours from our analysis. Within the bait condition, focal chimpanzees had significantly more neighbours at the mound than did gorillas, regardless of whether mother–infant dyads were included (Mann–Whitney U test: $U = 53$, $N_1 = 6$, $N_2 = 10$, $P = 0.012$) or excluded ($U = 57$, $N_1 = 6$, $N_2 = 10$, $P = 0.003$; Fig. 3).

General Species Differences in Social Proximity

Using behavioural monitoring data, we examined the proportion of time that each subject spent in social proximity.

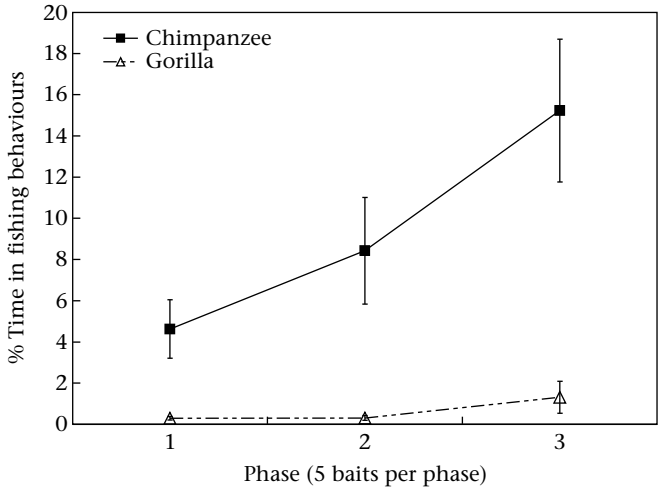

Figure 2. Comparison of the percentage of time that chimpanzees and gorillas spent engaged in fishing behaviours during baited trials. Bait trials were lumped in groups of five to give three separate phases encompassing the first 15 baits.

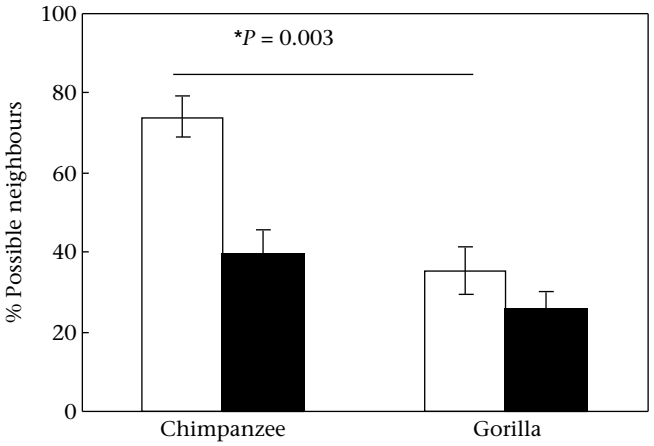

Figure 3. Comparison of sociality at the mound by chimpanzees and gorillas during baited (open bars) and unbaited (solid bars; control) trials. Mother–offspring dyads were excluded from this analysis. Values are means ± SE.

Chimpanzees spent significantly more time in proximity to conspecifics (38.8%) than did gorillas (14.9%) (Mann–Whitney U test: $U = 57$, $N_1 = 6$, $N_2 = 10$, $P = 0.003$).

DISCUSSION

We have taken a comparative approach to investigate the acquisition of a tool use task in chimpanzees and gorillas. Because of the group-housed nature of the study subjects, the task was presented to the entire social group and animals were not separated individually to interact with the apparatus. Rather, we attempted to replicate the situation of a naïve social group of apes coming upon a termite mound in their natural habitat. As such, this experiment was not explicitly designed to test whether individuals could learn the task individually, and therefore, it was not a direct test of social-learning abilities. All seven chimpanzees and seven of 13 gorillas eventually learned to perform a fishing task that required locating tool material, fashioning it into an appropriate size, and using it to retrieve a food reward from an artificial termite mound. In the discussion below, we examine species differences in initial investigation of the device, object manipulation and social behaviour as factors that may influence the differences in acquisition observed.

The propensity to investigate a novel object may have implications for the invention and discovery of new behaviours (Kummer & Goodall 1985). Therefore, we first investigated whether the two species' interactions with the mound differed before the mound was used as a food-delivery device. The overall frequency of interacting with the mound during the baseline period was extremely low for both species. The behaviour with the highest frequency was Fish for chimpanzees, which occurred three times on average over the entire 17-day period of baseline data collection (see Table 3). This rate was significantly higher than that for gorillas, which showed no fishing during the baseline period. We also performed a more general analysis of object manipulation and found that chimpanzees were significantly more likely to engage in these non-tool-use manipulations than gorillas. While object manipulation is not equivalent to either tool use or investigation of novel objects, it may be considered a precursor to the tool-use task studied here. When combined, these results provide some support for the idea that chimpanzees have a greater predisposition for tool use. Whether gorillas are less likely to explore other novel devices or exhibit elements requires further investigation.

Once the mound was baited with a food reward, individuals of both species solved the problem of how to access the food in the

mound using a tool. All but one of the chimpanzees attempted on the very first day of baiting (Table 1). Gorillas showed much more variability across individuals: one attempted and succeeded on the first day, whereas five individuals never attempted to access the food over the course of the study. While two of these individuals were very young (<2 years), the remaining three gorillas were all at least subadults (>8 years), suggesting that age alone cannot explain individual variance among gorillas. For the first 15 bait trials, representing the initial acquisition period, chimpanzees spent a greater percentage of time engaged in fishing behaviours than gorillas (Fig. 2). This difference was significant for the effects of species and phase alone, and also for the species-by-phase interaction, suggesting that while both species increased the percentage time they spent fishing over the three phases, chimpanzees fished more overall and increased their fishing time more as the phases progressed.

van Schaik et al. 's (1999) socioecological model for the evolution of material culture consists of four criteria that determine the invention and propagation of an extractive foraging behaviour such as termite fishing: (1) ecological opportunities, (2) motor dexterity (3), cognitive abilities and (4) social tolerance. This was one of the first descriptions of the importance of social tolerance for the evolution of cultural behaviours. van Schaik (2003) subsequently compared the size of particular chimpanzee communities' tool-kits in relation to a measure of social tolerance (percentage of time spent in parties) and found a strong positive correlation. In a parallel analysis for orang-utans, he found that within-group variation in the degree of tool use was correlated with exposure to other individuals in a relaxed foraging context. Whether discussing individual or social learning of a task at a particular location (as in present study), it is intuitive that social tolerance is of paramount importance. However, empirical evidence of the importance of social tolerance is limited. Bonnie & de Waal (2006) found that affiliation within a dyad was one of the key predictors of transmission of a behaviour known as the grooming hand-clasp in chimpanzees. Similarly, Horner, (in press) described the importance of social tolerance among chimpanzees used as demonstrators in diffusion–chain studies of cultural transmission. More recently and outside the primate taxon, Schwab et al. (2008) found that affiliate relationships among kin enhanced the performance of common ravens, *Corvus corax*, in a social learning task.

In our experiment, we did not explicitly test whether social learning occurred, because we did not test animals individually to control for trial-and-error learning. However, application of van Schaik et al.'s (1999) four criteria is still quite informative. Chimpanzees and gorillas in our study showed both the cognitive capacity and the motor dexterity necessary to solve the problem. We controlled ecological influences as much as possible by exposing animals to the exact same exhibit, apparatus and testing conditions. As discussed above, we found some evidence for species differences in investigative behaviours that merits further investigation. That leaves us to investigate species differences in social tolerance by considering similar metrics to the 'time spent in parties' used by van Schaik (2003). As the most basic form of social tolerance is proximity, we used two measurements: the first was percentage of time spent in proximity at the termite mound itself, and the second was a more general measure of sociality from proximity data in behavioural monitoring records. At the termite mound, group size differed significantly between the species (Fig. 3). Our analyses showed that regardless of whether the mound was baited, chimpanzees had more neighbours at the mound than did gorillas. Both species had significantly more neighbours at the mound when the mound was baited versus unbaited (control condition), but the number of neighbours was significantly greater for chimpanzees than for gorillas. Since the baited condition was the one most likely to facilitate task learning, we further compared the average number of neighbours within this condition, and found that chimpanzees had significantly more neighbours whether or not mother–infant dyads of both species were included in the analysis. When mother–infant dyads were excluded, chimpanzees had approximately 74% of group members present during bait trials, while gorillas on average had approximately 35% of the group members at the mound. This finding was strongly affected by the dominant female gorillas in each group, which were the first to attempt the task, were consistently found at the mound on bait days, and were observed barking at other individuals in proximity to the mound. Although subordinate gorilla group members had the same access to the mound, they rarely approached it. The lack of time spent by the subordinate individuals at the mound invariably gives them less time to explore the mound and attempt the task, whether individually or socially. We did not observe the same rank effects or avoidance of the mound by subordinate individuals in chimpanzees. The results for social proximity in the exhibit as a whole parallel those found at the termite mound, where we found that individual gorillas were far less likely to be in close proximity to conspecifics than were chimpanzees. Gorillas spent 14.9% of their time within 1 m of groupmates, whereas chimpanzees spent 38.8% of their time close to each other. These differences in tolerance of close proximity could explain not only the species differences in time spent in fishing behaviours (Fig. 2), but also the high variability observed in latencies to attempt and succeed in gorillas.

Although socially living individuals may innovate numerous behavioural solutions to ecological challenges, these behaviours may not be transmitted without a degree of social tolerance between group members. Gorillas live in social groups, but published reports suggest a low frequency of affiliative behaviours and relative intolerance of others. In a study of postpartum proximity measures, Stoinski et al. (2003) reported that captive gorillas rarely spent more than 10% of their time within 1 m of the other group members. In wild female mountain gorillas, rates of affiliation (defined by play, grooming and contact) among females were low (Harcourt 1979; Stewart & Harcourt 1987), and individuals other than dependent offspring were not permitted nearby during feeding (Byrne 1999). In the first field study conducted on western lowland gorillas, no grooming between any adults was observed and rates of affiliation among females and between adult males and females was so low as to preclude statistical analysis (Stokes 2004). This is in stark contrast to chimpanzees, which spend significant amounts of time grooming kin and nonkin (Goodall 1986; Nakamura, in press) and a large percentage of time in foraging parties (van Schaik 2003). Chimpanzees are also tolerant of others' proximity during tool-using behaviours such as termite fishing (wild chimpanzees: Lonsdorf 2006) or honey dipping (captive chimpanzees: Hirata & Celli 2003). The fission–fusion social structure of chimpanzees, with regular making and breaking of social contacts with other members of the group, possibly necessitates a more active cementing of bonds when individuals reunite. This may result in behaviours such as grooming and close proximity during tool use behaviours that would facilitate learning of the task by unskilled individuals. Gorillas do not show such regular changes in party size and composition, so they may have less need to reaffirm social bonds and, therefore, less to gain from developing social skills needed to hone tolerant relationships.

In this comparative analysis of tool use in gorillas and chimpanzees, we attempted to approximate a natural tool-use task, and provide an identical task, situation and environment to the testing groups. Despite this, we found significant species differences in the speed of acquisition of group members and the frequency of performing the task. We found evidence for species differences in the propensity to investigate the termite mound during a baseline

stage as well as significant differences in general object manipulation. Additionally, we found evidence for species differences in tolerance for close proximity of group members; chimpanzees had higher tolerance both at and away from the termite mound. Together, these results suggest that chimpanzees may be better equipped to acquire knowledge that is socially transmitted. Whether individual or social learning is necessary to learn the task, access to the device is critical, and our observations suggest that, in gorillas, subordinate individuals may be socially constrained from accessing the termite mound. Support for the importance of social tolerance has also been reported for wild orang-utans in which the Sumatran species are more social than their Bornean counterparts and show a greater diversity of tool use and other cultural behaviours (van Schaik 2003; van Schaik et al. 2003).

Our results provide another important piece to the rather limited literature on gorilla tool use and social learning. While we cannot discount the importance of ecological requirements and/or less need for tool use in gorillas because of their physicality, a more complete picture of gorilla social learning is certainly needed. Byrne & Russon (1998) argued that the complex processing of nettles shown by mountain gorillas is probably learned by imitation of the programme or sequence of behaviours required for plant defence removal. However, Tennie et al. (2008) recently tested this hypothesis in multiple captive gorilla populations and concluded that genetic predispositions and individual learning are more critical for the appearance of the behaviour than are social learning processes. In an experimental investigation of gorilla imitation, Stoinski et al. (2000) found a tendency for gorillas to copy a human model's method of plant defence removal on an artificial fruit. A logical next step is to see whether gorillas will perform as well when they have to learn from a conspecific demonstrator. For this discussion, bonobos remain an enigma in that they show less diversity of tool use behaviours in the wild despite high levels of social tolerance (Hohmann & Fruth 2003) and have well-developed tool use abilities in captivity (Toth et al. 1993). However, most field observations of bonobos have come from a limited number of study sites with less overall observation time than that for other ape species. As bonobo field studies continue and expand to additional sites, and we understand more about ecological differences, more information on social learning and tool use in this species may become available. As learning studies progress, comparative approaches will be increasingly valuable and it will be critically important within and across taxa to take into account both individual-level and group-level variation in social structure and tolerance.

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