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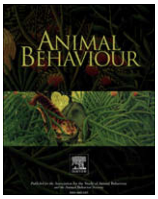

An experimental, comparative investigation of tool use in chimpanzees and gorillas

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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 × 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