Sex Differences in Tool Use Acquisition in Bonobos (Pan paniscus)

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All the great ape species are known tool users in both the wild and captivity, although there is great variation in ability and behavioral repertoire. Differences in tool use acquisition between chimpanzees and gorillas have been attributed to differing levels of social tolerance as a result of differences in social structure. Chimpanzees also show sex differences in acquisition and both chimpanzees and bonobos demonstrate a female bias in tool use behaviors. Studies of acquisition are limited in the wild and between species comparisons are complicated in captivity by contexts that often do not reflect natural conditions. Here we investigated tool use acquisition in a captive group of naïve bonobos by simulating naturalistic conditions. We constructed an artificial termite mound fashioned after those that occur in the wild and tested individuals within a social group context. We found sex differences in latencies to attempt and to succeed where females attempted to fish, were successful more quickly, and fished more frequently than males. We compared our results to those reported for chimpanzees and gorillas. Males across all three species did not differ in latency to attempt or to succeed. In contrast, bonobo and chimpanzee females succeeded more quickly than did female gorillas. Female bonobos and female chimpanzees did not differ in either latency to attempt or to succeed. We tested the social tolerance hypothesis by investigating the relationship between tool behaviors and number of neighbors present. We also compared these results to those reported for chimpanzees and gorillas and found that bonobos had the fewest numbers of neighbors present. The results of this study do not support the association between number of neighbors and tool behavior reported for chimpanzees. However, bonobos demonstrated a similar sex difference in tool use acquisition, supporting the hypothesis of a female bias in tool use in Pan. Am. J. Primatol. 75:917–926, 2013. © 2013 Wiley Periodicals, Inc.

Key words: great apes; termite fishing; social tolerance

INTRODUCTION

Many species of non-human primates use tools in both captivity [chimpanzee: Kohler, 1927; bonobo: Jordan, 1982; orangutan: Galdikas, 1982; sooty mangabey: Kyes, 1988; capuchin: Viscalberghi, 1990; gorilla: Fontaine et al., 1995; golden lion tamarin: Stoinski & Beck, 2001; ring-tailed lemur and brown lemur: Santos et al., 2005; gibbon: Cunningham et al., 2006; vervet: Santos et al., 2006; mandrill: Pansini & de Ruiter, 2011] and the wild [chimpanzee: van Lawick-Goodall, 1970; red colobus: Struhsaker, 1975; bonobo: Kano, 1982; orangutan: van Schaik et al., 1996; capuchin: Phillips, 1998, Boinski et al., 2000; gorilla: Breuer et al., 2005; spider monkey: Rodrigues & Lindshield, 2007; long-tailed macaque: Gumert et al., 2011]. Tool use by great apes is of particular interest for modeling and identifying potential conditions that contributed to the evolution of hominin tool use [Byrne, 2004; McGrew, 1992; van Schaik et al., 1999]. Research on this topic has revealed a great deal of behavioral variation in tool use behaviors both within and between the different ape species [Boesch & Boesch-Achermann, 2000; Galdikas, 1982; Gruber et al., 2010; Goodall, 1986; Kano, 1992; McGrew, 1992; Nishida, 1990; Reynolds, 2005; Whiten et al., 2001]. Observations such as these have resulted in the description of and hypotheses related to material culture in great apes [Hohmann & Fruth, 2003; McGrew, 1992; van Schaik et al., 2003; Whiten et al., 2001].

Addressing these differences, van Schaik et al. [1999] proposed four conditions that favor the evolution of material culture: (1) ecological opportunity, (2) motor dexterity (3), the cognitive ability to...
solve problems, and (4) a high degree of social tolerance as a means to facilitate the social learning of such complex behaviors. In the captive setting, numerous tool use experiments and anecdotal evidence have demonstrated that all four species of great apes possess the motor dexterity and cognitive ability to manufacture and use tools, even though there is great variation in ability and behavioral repertoires (gorillas: artificial fishing [Boysen et al., 1999]; orangutans: digging sticks and rain covers [Galdikas, 1982]; chimpanzees and bonobos: artificial fishing, aimed throwing, play, etc. [Gruber et al., 2010]). Even though chimpanzees and bonobos differ in their abilities to solve physical and social cognitive problems [Herrmann et al., 2010], recent studies also indicate that all of the great apes have a similar understanding of the functional properties of tools [Herrmann et al., 2008].

Although ongoing research is continuing to reveal details and characteristics of tool use in all of the great ape species, chimpanzees remain the most prolific and diverse non-human tool users (e.g.: Bentley-Condit & Smith [2010]), showing the highest degree of behavioral variation and complexity [Boesch & Boesch-Achermann, 2000; Goodall, 1986; McGrew, 1992; Nishida, 1990; Reynolds, 2005; Whiten et al., 2001]. This behavioral variation in tool use across chimpanzee study sites is thought to be the result of distinct cultural differences between groups [McGrew, 1992], suggesting that social learning, facilitated by having a high degree of social tolerance, plays a critical role in acquiring the tool use behaviors present in a group [van Schaik et al., 1999]. Recent research focusing on differences in tool use behavior between chimpanzees and gorillas supports the hypothesis that social tolerance may play an important role during acquisition [Lonsdorf et al., 2009]. A comparative study of tool use acquisition in these two species at the Lincoln Park Zoo (LPZ) measured successful retrieval of bait from an artificial termite mound together with the number of neighbors present during tool use, as a measure of social tolerance [Lonsdorf et al., 2009]. They found that chimpanzees used tools more quickly and had a greater percentage of possible neighbors present than did the gorillas. Later research on chimpanzee tool use acquisition demonstrated that the transmission of novel tool use behaviors (the retrieval of bait from an apparatus called the “Panpipe” at the Yerkes Primate Center) was facilitated by the high social tolerance exhibited by the two model individuals, each of whom were trained to use a different retrieval technique [Horner, 2010]. Higher social tolerance in the chimpanzees at LPZ, therefore, may have facilitated a faster transmission of tool use behaviors than in the gorillas [Lonsdorf et al., 2009]. Lonsdorf et al. [2009] hypothesized that chimpanzees are especially primed for social learning because of the nature of their fission–fusion ranging, where individuals are routinely separated and reunited and must be highly socially tolerant to actively reform social bonds during fusion events.

In addition to the observed differences in tool repertoires between field sites, chimpanzees display significant sex differences in complex foraging behavior. Females use tools to fish for termites more frequently and for longer time periods than do males [McGrew, 1979]. Females are also more efficient at using stone tools to crack open nuts, whereas males hunt for prey and consume meat more frequently [Boesch & Boesch, 1984], although female chimpanzees at Fongoli hunt with tools more frequently than males [Pruetz & Bertolani, 2007]. A study of tool use acquisition in wild chimpanzees at Gombe found that young females spent more time watching their mothers fish for termites, began fishing at an earlier age, and used tools more proficiently than did young males [Lonsdorf, 2005]. Although evidence of tool use from bonobo field sites is sparse [Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982], a recent survey of several captive groups found significant sex differences in tool use behaviors where females used tools more often and showed greater diversity in types of tools used [Gruber et al., 2010]. This raises the question of whether there are sex differences in tool use acquisition in bonobos and whether sex differences in tool behavior are similar or different across the ape species.

Differences in experimental methodology can make direct comparisons among studies and species difficult. This study, therefore, examines the acquisition of tool use behavior in bonobos under a naturalistic setting using a protocol modeled on the experiment comparing tool use acquisition in chimpanzees and gorillas at LPZ [Lonsdorf et al., 2009]. We presented a captive group of bonobos at the Columbus Zoo and Aquarium (CZA) with an artificial termite mound and recorded latency to attempt and to successfully use tools to extract bait. We first predict that, similar to other groups of captive bonobos [Gruber et al., 2010], this group of bonobos will readily use tools. Chimpanzees that fish for termites are selective in the types of tool material used as well as the manner in which the raw material is modified [McGrew et al., 1979]. Chimpanzees often choose woody items in the form of tree and bush branches that are modified through the employment of several behaviors specific to tool-making, such as detachment of raw material, side-branch removal, leave stripping, and bark peeling [McGrew et al., 1979]. Lonsdorf et al. [2009] describe a process of allowing the chimpanzees and gorillas to select tool material from the naturally occurring vegetation within the enclosure at LPZ. The bonobos at CZA were also allowed to select tool material that grew within their enclosure. The task of selecting tool material from natural vegetation, versus being provisioned with tools by the keepers, provided a
novel task for all of the bonobos at CZA. We, therefore, predict that the bonobos at CZA will select tool material and modify that material in a manner similar to what has been described for chimpanzees in both the wild [McGrew et al., 1979] and captive settings [Lonsdorf et al., 2009]. Following Gruber et al. [2010], we predict the bonobos will show similar sex differences in tool use behaviors with females learning to use tools more quickly and using tools more frequently than males. Differences in social tolerance between species have been suggested to explain why a fission–fusion species like chimpanzees use tools more readily than gorillas under identical conditions [Lonsdorf et al., 2009]. Since bonobos are also a fission–fusion species [Kano, 1992; White, 1996] and are, therefore, presumably more socially tolerant than gorillas, we predict that bonobos will be more similar to what has been reported for chimpanzees than for gorillas [Lonsdorf et al., 2009] in both number of neighbors present and tool use behaviors.

METHODS

Ethical Note

This study was conducted with approval at CZA, an Association of Zoos and Aquariums (AZA) accredited institution in Columbus, Ohio, USA. CZA adheres to the welfare and husbandry standards outlined by the AZA. All data were collected using observations of spontaneous behavior. No animals were separated from the group and no social groups were manipulated for the purpose of this study. All data collection methods adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates and were approved by the University of Oregon Institutional Animal Care and Use Committee (IACUC). The authors have no conflict of interest to declare.

Subjects and Housing

All data were collected on the captive group of bonobos housed at CZA. Following Kano’s [1992] age class definitions (infant: 0–1; juvenile: 2–6; adolescent: 7–14; adult: ≥15), the group was composed of four adult males, four adult females, two adolescent females, two adolescent males, one juvenile male, one juvenile female, one infant male, and one infant female (Table I). The bonobos were housed in a complex of areas consisting of two large indoor public viewing exhibits (54.8 m² each) with multiple climbing structures, two off-exhibit indoor enclosures (22.6 m² each), two off-exhibit outdoor enclosures (18.5 m² each) and a large naturalistic outdoor public viewing exhibit (57.9 m × 45.7 m, 2,647.7 m²) with grass, mature trees, and an artificial stream and waterfall. The keepers at CZA managed the bonobos to simulate the species typical fission–fusion process of variable party composition. In the morning, bonobos were allowed access to each other and parties were set based mostly on individual bonobo association preferences rather than parties that were predetermined by the keepers. Most individuals had equal access to each other, but two of the adult males (Jimmy and Donnie) were never allowed to be together because of previous conflicts that had resulted in serious injury. This management process usually resulted in three parties that lasted for 2–3 days, and rarely changed on a daily basis or exceeded 4 days. Each sub-group occupied different public display areas.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Sex</th>
<th>Age (years)</th>
<th>Offspring</th>
<th>No. of trials</th>
<th>Investigate</th>
<th>Attempt</th>
<th>Succeed</th>
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<tbody>
<tr>
<td>Lola</td>
<td>F</td>
<td>7</td>
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<td>Gilda</td>
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<tr>
<td>Unga</td>
<td>F</td>
<td>18</td>
<td>Gander, Jerry</td>
<td>12</td>
<td>4</td>
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<tr>
<td>Ana Neema</td>
<td>F</td>
<td>19</td>
<td>Bila Isia, Gilda, Wilbur</td>
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<tr>
<td>Donnie</td>
<td>M</td>
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<td>Jerry</td>
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<td>JoT</td>
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<td>Maiko</td>
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<td>Gander</td>
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<tr>
<td>Jerry</td>
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<td>Bila Isia</td>
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<tr>
<td>Toby</td>
<td>M</td>
<td>32a</td>
<td>Lola</td>
<td>22</td>
<td>16</td>
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<tr>
<td>Mary-Rose</td>
<td>F</td>
<td>1.5</td>
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<tr>
<td>Susie</td>
<td>F</td>
<td>29a</td>
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<td>16</td>
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<tr>
<td>Lady</td>
<td>F</td>
<td>29a</td>
<td>JoT</td>
<td>16</td>
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<td>Wilbur</td>
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<td>Jimmy</td>
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Note: “aEstimated age for wild-caught individuals; “b latency to attempt and to succeed after first investigation; italicized individuals are under 5 years old and were excluded from data analyses.
During the study period, the bonobos were released into the outdoor exhibit each morning at approximately 0730 hr and were brought back into the indoor enclosures at approximately 1900 hr. The bonobos were rarely brought inside between these hours, except for extenuating circumstances (i.e. dangerous inclement weather or an emergency). Each night the party that occupied the outdoor exhibit was brought into one of the indoor enclosures and the outdoor exhibit remained empty until the following morning. The bonobos were fed each morning and evening at approximately 0730 and 1900 hr. Additional supplemental enrichment feedings were sometimes given throughout the day.

An artificial termite mound was installed in the outdoor enclosure near Viewing Area 1 (Fig. 1) for the purpose of this study and provided a novel structure and tool related task for this group at CZA. From the known histories of the study group (Table I), all but two individuals (Ana-Neema and Unga) were naïve to an artificial extractive foraging structure. Ana-Neema had previously resided at the Milwaukee Zoo in Milwaukee, WI where she was exposed to an artificial structure and had learned to successfully fish for bait using tools provided by the staff as enrichment. Finding a tool from the naturalistic habitat and modifying it for use on this new device provided this subject with a novel task for the purpose of this study. Unga previously resided at the Planckendael Zoo in Belgium where she was presented with several tool use opportunities, including those involving extractive foraging using devices, but not an artificial termite mound.

**Testing Apparatus and Bait**

An artificial termite mound was constructed from concrete, rebar, wire mesh, and paint (Fig. 2). The mound was constructed by the CZA staff and was fashioned to resemble those naturally occurring in the wild. Eight bait holes were bored into the mound and fitted with removable polyvinyl chloride (PVC) tubes that measured 15.0 cm in length and 4.5 cm in diameter. The mound had a small locked access door.
to allow the staff to remove and replace the bait tubes. The unba
tited mound was installed in the outdoor habitat in front of a large public display window
during November of 2010. The subjects were free to
explore the unba
tited mound both before and after June 29, 2011, the first day of baited trials. All
subjects were considered habituated (i.e. did not display avoidance behavior and readily approached
the apparatus) to the mound before trials began. Beginning June 29, 2011, the mound was baited each
morning by CZA staff during their regular morning check of the enclosure. The baited tubes remained in
the mound throughout the day until the following morning when they were replaced by new tubes with
fresh bait. Bait included honey and/or pureed blue-
berries, raspberries, bananas, and cooked sweet potatoes and carrots. All subjects readily consumed
these food items as part of their regular diet. No tools
or raw material were explicitly provided to the
animals, instead, individuals were allowed to con-
struct tools out of the naturally occurring vegetation
growing in the enclosure (i.e. tree branches, grass, bushes, etc.).

Data Collection and Definitions

Data were collected most days between June 29,
2011 and August 29, 2011. Data collection began
when the first individual was released into the outdoor enclosure in the morning and ended when
the last individual was shut out of the enclosure for
the night. Each day that a subject had exposure to the
ba
tited mound was scored as one trial for that subject.
Individuals within 1 m of the mound were scored as
being within proximity of the mound. All presence
data and behaviors within 1 m of the mound were videotaped and coded by K.J.B. Continuous data
were collected from the videotapes and included frequencies and durations of all predetermined
mound-related behaviors (i.e. investigate, poke, tool
behavior, and fish as defined by Lonsdorf et al. [2009])
for each subject. Attempting the task was defined as
inserting a tool into the bait tubes without accessing
the bait and successful fishing was defined as
inserting a tool into the bait tubes and retrieving
bait [Lonsdorf et al., 2009]. Lonsdorf et al. [2009]
de
defined latency as the number of trials with the
ba
tited mound experienced by each individual before
they attempted the task or successfully fished.

The bonobos at CZA had access to the unba
tited mound for approximately 6 months before the first
baiting and were housed outside of the visual and
auditory range of the mound during baiting. Because
the mound was baited out of sight of the bonobos, no
subjects had visual information that the mound was
baited until they approached and investigated the
structure. The mound was not baited unless observ-
ers were present and the baited mound was observed
for the entire time that bonobos were in the
closures. We recorded latency to investigate the
mound as the number of baited trials until first
investigation. Latency to attempt and latency to
succeed were then recorded as the number of trials
after this initial investigation before they attempted
the task or successfully fished.

A tool use bout was defined as the time during
which an individual continuously fished or attempted
to extract bait. When an individual left 1 m proximity
of the mound, or stopped tool use behaviors for more
than 30 s but remained within 1 m proximity of
the mound, the bout was scored as finished. To
compare the time spent fishing between individuals,
we first summed the duration of each successful
fishing bout for each individual and then divided this
total time by the number of trials for that individual
to control for variation in number of trials (Table I).
To compare rate of fishing between individuals, we
first calculated the total number of bouts and then
divided this number by the total number of trials for
that individual to again control for variation in
number of trials.

Each group member within 1 m of the mound was
scored as a “neighbor” [Lonsdorf et al., 2009] for each
focal individual on each day during each bout. The number of neighbors was recorded for each individual
that was within 1 m of the mound, regardless of
whether or not that individual, or their “neighbors,”
were engaged in mound related behaviors. Group
composition in the outdoor enclosure at CZA was
variable (see “Subjects and Housing Section”) and,
following Lonsdorf et al. [2009], we controlled for
differences in group sizes by calculating the number
of neighbors as a percentage based on presence data
(number of neighbors/number of group members in
the enclosure − 1). The percentage of neighbors was
calculated for all individuals for all approaches to
within 1 m proximity of the mound including fishing
behavior, attempts to fish, and non-fishing approaches.

Data Analyses

Frequency data were compared using G tests of
Goodness of Fit with Williams correction applied
[Sokal & Rohlf, 2012] and ANOVAs were used to test
for significant differences in means [Sokal &
Rohlf, 2012]. All data were tested for fit to the
assumptions of ANOVAs, including normality, and
no transformations were required. Data on individual
chimpanzee and gorilla latencies to attempt and to
succeed published in Table I of Lonsdorf et al. [2009]
were used for comparison with the bonobo data
collected on mean latencies to attempt and to succeed
for the purpose of this study. In addition, we obtained
N’s, means, and standard errors for percentage of
possible neighbors for chimpanzees and gorillas
during baited trials using Figure 3 from Lonsdorf
et al. [2009]. We made the assumption that, although
the enclosures at CZA and LPZ differed in size, each
of the groups had equal access to their respective artificial termite mounds. Where there were significant differences among the three species, we used a priori orthogonal multiple comparisons [Sokal & Rohlff, 2012] to first compare gorillas to the Pan genus (both chimpanzees and bonobos) as a single unit and then to compare bonobos to chimpanzees. Following the data analysis methodology in Lonsdorf et al. [2009], all individuals from all three species that were under 5 years at the time of data collection were not included in the analysis and results. Analyses were run using SAS® and BIOMstat (version 3.3).

RESULTS

Group Results

The first individual to both attempt and successfully fish was a naïve juvenile female, Lola, who investigated the mound, manufactured a tool, attempted, and successfully fished on the first baited trial presented to the bonobos. Group mean latency to investigate the mound was 3.00 ± SE 1.335 trials. Seven individuals (four females and three males) investigated the mound on their first trial, and seven individuals (four females and three males) investigated the mound after their first trial (range = 2–16 trials, mean = 4.86 trials, Table I). Two adult males, Jimmy and Maiko, never investigated the mound during the study period and although Maiko successfully learned to fish for bait, he was never observed to investigate the mound. Group mean latency to attempt after investigation was 4.300 ± SE 1.291 trials (range = 1–11, N = 10, individuals <5 years excluded: N = 2), although some individuals never attempted the task (N = 3, one male and two females, individuals <5 years excluded: N = 1). Group mean latency to succeed after investigation was 5.67 ± SE 2.121 trials (range = 1–20, N = 9, individuals <5 years excluded: N = 1) trials.

After 60 days, 62.5% (N = 10, including one individual <5 years) of the subjects had successfully performed fishing behavior (Table I). Of these subjects, 50.0% (N = 5) successfully modified raw materials into tools and 50.0% (N = 5) only used material that had been modified by another individual or material that did not require modification to be successfully used as a tool (i.e. straight piece of woody material with no side branches or leaves, etc.). A total of 901 tool use bouts were recorded, of which 99.7% (N = 898) included tools made from woody material (tree and bush branches). Other tools used included grass, leaves, and wood–wool nesting material.

Sex Differences in Bonobos

There was a significant sex difference in mean latency to attempt to use tools to fish in this bonobo group. Females attempted the task after fewer trials (mean = 1.80 ± SE 0.583 trials, N = 5, individuals <5 years excluded: N = 1) than did the males (mean = 6.80 ± SE 2.010 trials, N = 5, individuals <5 years excluded: N = 1, ANOVA: F = 5.71, df = 1.8, P < 0.05, Fig. 3). There was also a significant sex difference in mean latency to succeed in this bonobo group, where females succeeded in fishing after significantly fewer trials (mean = 1.80 ± SE 0.583 trials, N = 5, individuals <5 years excluded: N = 1) than did the males (mean = 10.50 ± SE 3.524 trials, N = 4, ANOVA: F = 7.56, df = 1.7, P < 0.05, individuals <5 years excluded: N = 1). There was no significant difference in the number trials experienced by males and females (F = 0.66, df = 1.14, P = 0.4301, Table I). Females engaged in significantly more fishing bouts than did the males (488 female bouts, 74 male bouts, Goodness of Fit: G = 325.737, P < 0.001). There was no significant difference in the mean duration of bouts per trial between females (mean = 408.6 ± SE 159.7 sec/trial) and males (mean = 223.2 ± SE 194.3 sec/trial, ANOVA: F = 0.55, df = 1.11, P = 0.472).

Sex Differences Across Species

The comparison of results for males and females among the three ape species (excluding individuals under 5 years old) demonstrated that there were no significant differences among the species in mean latency to attempt or to succeed in males (attempt—ANOVA: F = 0.64, df = 2.5, P = 0.5636; succeed—ANOVA: F = 0.73, df = 2.4, P = 0.5364) or in latency to attempt in females (ANOVA: F = 3.61, df = 2.12, P = 0.0593, Table II). There were significant differences among the species in latency to succeed in females (ANOVA: F = 12.34, df = 2.12, P < 0.005). The multiple comparisons within this statistically significant ANOVA show that there was no
significant difference within Pan, between female bonobos and female chimpanzees, in latency to succeed \((F = 0.02, \text{ df} = 1, P = 0.8864)\), but there was a significant difference between female gorillas and female Pan in latency to succeed \((F = 24.63, \text{ df} = 1, P < 0.001)\).

### Numbers of Neighbors

We recorded the number of neighbors for 1,192 observations of 15 focal animals engaged in all mound-related behaviors. We tested for differences in the number of neighbors during mound related behaviors by focal bonobos in this group using a Nested ANOVA. There were significant differences in number of neighbors between individuals \((F = 10.61, \text{ df} = 13,1177, P < 0.0001)\) but there was no significant sex difference in number of neighbors \((F = 0.21, \text{ df} = 1,13, P = 0.6521)\). There was, however, a significant difference in mean number of neighbors present between bonobos (CZA), chimpanzees (LPZ), and gorillas (LPZ) \((\text{ANOVA: } F = 25.793, \text{ df} = 2,26, P < 0.001, \text{ Table III})\). Bonobos had the fewest mean percentage of possible neighbors present at the mound.

### DISCUSSION

The results presented in this study confirm previous studies and our prediction that bonobos possess the motor dexterity and cognitive ability to manufacture and use appropriate tools. Although recent studies also indicate that all of the great apes have a similar understanding of the functional properties of tools [Herrmann et al., 2008; but see Herrmann et al., 2010], other studies have suggested that species as well as sexes may show differing levels of propensity or aptitude in constructing and using tools [Gruber et al., 2010; Lonsdorf et al., 2004; Lonsdorf et al., 2009; McGrew, 1992; Reynolds, 2005; Whiten et al., 2001]. We found that, comparable to the chimpanzees at LPZ, several individuals in this group of bonobos rapidly became proficient in manufacturing tools and extracting bait from the artificial termite mound. Tools were mostly constructed out of woody material harvested primarily from the nearby trees and bushes within the naturalistic outdoor enclosure. Tool construction was remarkably similar to what has been described for termite fishing in wild chimpanzees [McGrew et al., 1979], including detachment of raw material, side branch removal, leaf stripping, and bark peeling. Both the individual that constructed the tool as well as other members of the group often reused tools that were constructed out of woody branch-type material. On several occasions, individuals were observed carrying tools away from the mound and returning some time later with the same tool to begin another fishing bout.

Following Lonsdorf et al. [2009], “investigation” of the mound was defined as using visual and olfactory senses to examine the contents of the bait holes in order to identify when subjects were first clearly aware that the termite mound contained bait. This definition appeared appropriate for most individuals, except for one. Maiko, a low-ranking male, did not investigate the mound under this definition, but was in the vicinity of fishing individuals on several occasions prior to his first attempt. In this single case, it appears that Maiko used information from observing the behaviors of other group members to identify that the mound contained bait. Also following Lonsdorf et al. [2009], “attempt” was defined as non-successful use of tools, however, all of the bonobos except Maiko frequently poked at the holes in the termite mound with their fingers before their first attempt to use tools to extract bait. It is possible, therefore, that Maiko learned to successfully fish by observing other group members from a distance rather than through a standard method of trial-and-error that involved very close proximity to group members that were fishing and frequently poking. It is not surprising that, because the bonobos were tested within social groups, a low-ranking male would not approach the mound while multiple individuals were engaged in mound related behaviors surrounding a high-value food source. Maiko’s behavior highlights the importance of conducting research within the social context in order to observe potential variation in behavioral strategies.

### TABLE II. Latencies to Attempt and to Succeed for Males and Females in Chimpanzees\(^a\), Gorillas\(^a\), and Bonobos

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th></th>
<th></th>
<th>Females</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>N</td>
<td>Mean</td>
<td>SE</td>
<td>N</td>
</tr>
<tr>
<td>Attempt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>5.00</td>
<td>4.00</td>
<td>2</td>
<td>1.00</td>
<td>0.00</td>
<td>4</td>
</tr>
<tr>
<td>Gorilla</td>
<td>1.00</td>
<td>0.00</td>
<td>1</td>
<td>12.33</td>
<td>4.85</td>
<td>6</td>
</tr>
<tr>
<td>Bonobo</td>
<td>6.80</td>
<td>2.01</td>
<td>5</td>
<td>1.80</td>
<td>0.58</td>
<td>5</td>
</tr>
<tr>
<td>Succeed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>8.00</td>
<td>5.00</td>
<td>2</td>
<td>1.00</td>
<td>0.00</td>
<td>4</td>
</tr>
<tr>
<td>Gorilla</td>
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<td>0.00</td>
<td>1</td>
<td>22.83</td>
<td>5.15</td>
<td>6</td>
</tr>
<tr>
<td>Bonobo</td>
<td>10.50</td>
<td>3.52</td>
<td>4</td>
<td>1.80</td>
<td>0.58</td>
<td>5</td>
</tr>
</tbody>
</table>

\(^a\)Note: Data for chimpanzees and gorillas from Lonsdorf et al. [2009].

### TABLE III. Mean Percentage of Number of Neighbors for Chimpanzees\(^a\), Gorillas\(^a\), and Bonobos

<table>
<thead>
<tr>
<th></th>
<th>Mean (%)</th>
<th>SE</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees</td>
<td>75.81</td>
<td>5.58</td>
<td>6</td>
</tr>
<tr>
<td>Gorillas</td>
<td>36.28</td>
<td>6.05</td>
<td>10</td>
</tr>
<tr>
<td>Bonobos</td>
<td>21.71</td>
<td>3.44</td>
<td>13</td>
</tr>
</tbody>
</table>

\(^a\)Note: Data for chimpanzees and gorillas from Lonsdorf et al. [2009].
As has been observed in chimpanzees [Lonsdorf, 2005; McGrew, 1979], there were similar significant sex differences in tool use behaviors in this group of bonobos. We found that the female bonobos were much quicker to attempt to use tools and successfully fished more quickly than did the males. This result is similar to the description of the acquisition of termite fishing in chimpanzees [Lonsdorf, 2005]. Although Lonsdorf [2005] observed learning in young chimpanzees, whereas we measured tool acquisition in bonobos ranging in age from 6 months to 32 years, the result that mean time to acquisition in females was significantly shorter than in males is similar to what we observed in the bonobos. In addition, once successful, the female bonobos returned to the artificial termite mound and fished significantly more frequently than did the male bonobos. Together our results support previous research demonstrating a female bias in tool use in Pan [Gruber et al., 2010].

The observed sex differences in this group of bonobos highlight important variations in tool use aptitude and propensity across the ape species and between the sexes. When comparing our results with those published by LPZ, we found that there was no significant difference among the males of the three species in latency to attempt or to succeed. Although caution must be applied when considering small sample sizes, the males in these groups of chimpanzees, bonobos, and gorillas demonstrated similar aptitudes in tool use acquisition. Further research is needed to determine if these results accurately reflect aptitude among the males and the degree to which propensity to use tools affects successful acquisition in males. There were also important similarities and some differences among the females of the three species. Females from all three species had similar mean latencies to attempt to use tools to extract bait suggesting that female chimpanzees, bonobos, and gorillas share a similar propensity to use tools. However, while chimpanzee and bonobo females also had similar latencies to successfully use tools, the two Pan species were significantly quicker to succeed than were the gorilla females. Our results demonstrate similarity between chimpanzees and bonobos in these attributes of tool use acquisition, and verify a key difference in tool use aptitude between the Pan genus and gorillas.

Differences in ecological constraints have been suggested to explain why chimpanzees and gorillas differ in their tool using abilities [Breuer et al., 2005]. Chimpanzees use tools to extract resources that are otherwise difficult to attain, whereas gorillas are more able to use physical strength to acquire hard to obtain food items [Breuer et al., 2005]. Lonsdorf et al. [2009] reported significant differences in propensity to investigate the artificial termite mound at LPZ. Prior to baiting the structure, the chimpanzees engaged in mound-related behaviors significantly more frequently than did the gorillas. In addition, the chimpanzees were faster to use tools to successfully retrieve bait and had a greater percentage of possible neighbors present than did the gorillas. Lonsdorf et al. [2009] suggested that social tolerance, as measured by number of neighbors present, might impact the social learning necessary for successful tool use acquisition. The authors concluded that differences in tool use behavior among species may, therefore, be related to differences in social structure as party or group sizes, stability, and social dynamics can differ significantly both within and between species. We tested this hypothesis with the inclusion of number of neighbors data from the CZA bonobos during their first 60 days of exposure to the baited termite mound. Bonobos also exhibit a fission-fusion social system and previous studies have demonstrated that they have a high degree of social tolerance in the form of lower aggression, higher cohesion, and greater cofeeding during food sharing opportunities compared to chimpanzees [Hare et al. 2007; Kano, 1992; White, 1996]. Because we found that bonobo females, like chimpanzee females, were faster than gorilla females to succeed in this tool use experiment, we expected that the mean percentage of number of neighbors in bonobos to be similar to the number reported in chimpanzees. Instead, we found that the bonobos had the lowest mean percentage of number of neighbors than either chimpanzees or gorillas after controlling for differences in group and party sizes. Our data, therefore, do not support the hypothesis that this measure of social tolerance is a facilitator of the transmission of tool use behaviors in bonobos. However, it is possible that differences in the social management of the groups, at CZA fission–fusion is simulated whereas at LPZ all the chimpanzee and gorilla groups are stable, may have impacted the results.

It is interesting that, given the sex differences in the bonobos in latency to attempt and to succeed, we found no significant difference between the sexes in social tolerance at the mound as measured by the number of neighbors present. There were, however, significant individual differences indicating that some males and females were more social than others. For example, the adult male that fished the most frequently and for the longest duration per bout (Maiko) rarely fished at the mound when any other individuals were present, exhibiting a preference to fish alone. Maiko also seemingly learned to fish by observing others from a distance. One female (Unga), in contrast, rarely fished alone, and when approaching the mound, would often loud call to out-of-sight members of her party who would then join her at the mound a short time after. This further suggests that the social tolerance hypothesis does not universally function at the individual level in this bonobo group. Observations of this group, in contrast, suggest to us that there may be inter-individual differences in
Bonobo Sex Differences in Tool Use / 925

Bonobo Sex Differences in Tool Use

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References


Am. J. Primatol.