



Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania

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By the age of 5.5 years, all of the young chimpanzees of Gombe National Park have acquired a skill known as 'termite fishing'. Termite fishing involves inserting a flexible tool made from vegetation into a termite mound and extracting the termites that attack and cling to the tool. Although tool use is a well-known phenomenon in chimpanzees, little is known about how such skills develop in the wild. Prior studies have found adult sex differences in frequency, duration and efficiency of tool-using tasks, with females scoring higher on all measures. To investigate whether these sex differences occurred in youngsters, I performed a 4-year longitudinal field study during which I observed and videotaped young chimpanzees' development of the termite-fishing behaviour. Critical elements of the skill included identifying a hole, making a tool, inserting a tool into a hole and extracting termites. These elements appeared in the same order during the development of all subjects, but females typically peaked at least a year earlier than males in their performance of the skills that precede termite fishing. In addition, young females successfully termite-fished an average of 27 months earlier than young males and were more proficient at the skill after acquisition had occurred. Furthermore, the techniques of female offspring closely resembled those of their mothers whereas the techniques of male offspring did not, suggesting that the process by which termite fishing is learned differs for male and female chimpanzees.

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Chimpanzees use tools for more purposes than any other nonhuman animal (Goodall 1986). The tools used and the behavioural repertoires observed vary greatly across geographical ranges, genetic populations and ecological systems (McGrew 1992). To account for this variation, Whiten et al. (1999) suggested that the population-level variation in chimpanzee behavioural repertoires represents different cultures and that these cultural differences are passed down to individuals from the other members of their community through social learning. The discovery of such extensive cultural differences in chimpanzees raises the question of how these cultural behaviours develop and are maintained in a community.

Due to the number and variety of tools used by many wild chimpanzee populations, young chimpanzees have much to learn about how to make and use tools appropriately. Several scientists have investigated the acquisition of

tool-use skills in captive apes in the context of elucidating the types of social learning employed. The most basic and inclusive definition of social learning is that 'individual B learns some or part of the behaviour from individual A'. Social learning has been further dissected into three broad categories: (1) stimulus enhancement, in which A draws B's attention to the location or object to which the behaviour is directed and B then learns the goal and form of the behaviour on its own; (2) emulation, in which B learns from A the goal of a particular behaviour, but does not reproduce the exact form of A's behaviour; or (3) imitation, in which B learns not only the goal, but some part of the form of the behaviour from A (Whiten & Ham 1992). The distinction between the different types of social learning has been made because these categories are presumed to represent different cognitive capabilities, where stimulus enhancement is the least complex and imitation is the most complex (Visalberghi & Fragaszy 1990; Whiten et al. 2004).

Two separate reviews of primate social learning have suggested that monkeys and apes learn much of their socially learned behaviours through a combination of stimulus enhancement followed by individual trial-and-error

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learning (Fragaszy & Visalberghi 1996; Tomasello 1996). However, what continues to be debated is whether non-human primates have the ability to imitate, and to what degree (Whiten et al. 2004). Tomasello et al. (1987) performed one of the first studies to investigate non-human primate imitation, by testing the ability of 14 captive chimpanzee subjects (ranging in age from 4 to 9 years of age) to learn from a demonstrator how to use a rake as a tool for acquiring food that was out of reach. None of the older individuals learned the skill from the demonstrator, and although the younger individuals learned to pull in food with the rake, none imitated the specific technique used by the demonstrator. As a result, Tomasello et al. concluded that chimpanzees show emulation (use the rake to pull in food) but not imitation. Nagell et al. (1993) extended this research and compared the behaviour of chimpanzees and human children on the rake task. Human children more often imitated the exact form of the behaviour from the demonstrator. In a subsequent experiment, Tomasello et al. (1993b) found that chimpanzees raised by humans ('enculturated' chimpanzees) did not differ in imitative abilities from human children, whereas the imitative abilities of mother-reared captive chimpanzees were much poorer. To further investigate and compare the imitative abilities of chimpanzees versus human children, Whiten et al. (1996) presented a specially designed 'artificial fruit' to eight captive chimpanzees (average age 4.5 years) and 24 human children (ranging from 2 to 4 years old). The fruit had three defences, which had to be removed in one of two ways before it could be eaten. Each subject repeatedly observed one of two alternative methods for removing each defence. Human children showed imitation for two of the three components, whereas chimpanzees showed imitation for one component. In a subsequent experiment (Whiten 1998), chimpanzees were shown one of two alternative techniques for removing each defence and one of two alternative sequential patterns of removing defences. After repeated cycles of demonstration, the subjects showed imitation of the sequence of defence removal.

In contrast to the relatively large number of studies of social learning in captivity, few studies have examined the development of a naturally occurring tool-use pattern in the wild. McGrew (1977) provided a descriptive account of chimpanzee infant behaviour during ant-dipping attempts by their mothers using a cross-section of individuals at different ages. Boesch (1991) recounted observations of a mother actively facilitating her offspring's attempt to crack nuts open with stones. Matsuzawa (1994), Inoue-Nakamura & Matsuzawa (1997) and Biro et al. (2003) reported on a series of experiments that investigated development and acquisition of stone tool use in the wild chimpanzees of Bossou, Guinea. Their observations took place in an outdoor laboratory prepared by the researchers, who also provided the stones and nuts to be used. No previous studies have investigated the longitudinal development and learning processes of a tool-use behaviour in unmanipulated wild chimpanzees.

Theoretical scientists often assume that all individuals in a population are equally likely to learn new information

(Reader & Laland 2000). However, this seems overly simplistic for a species like chimpanzees in which males and females lead vastly different adult lives. More probable is that natural selection has shaped chimpanzee behavioural development such that male and female offspring start to learn and develop sex-specific behaviour at a very young age. Several study sites have reported sex differences in adult tool-use and foraging behaviours. For example, adult female chimpanzees at Gombe termite-fish more often and for longer periods than adult males, whereas males hunt more often than females (McGrew 1979). In the Tai forest, adult females are more efficient when cracking open nuts with stone tools than are males (Boesch & Boesch 1981).

In a comprehensive literature review of sex differences in socially learned tasks, Choleris & Kavaliers (1999) found that the sex of subjects is usually not reported or not analysed in primate learning studies and put out a 'call' for more studies to address this issue. Kawai (1965) provided a systematic description of the best-known and earliest example of sex differences in skill acquisition in Japanese macaques, *Macaca fuscata*. On two separate occasions, a young female Japanese macaque invented new behaviours: washing sweet potatoes and throwing wheat into water to separate wheat grains from sand grains. In both cases, the behaviour spread to and was adopted by male and female juveniles and adult females, but not by adolescent or adult males. Hiraiwa-Hasegawa (1989) reported sex differences in the behavioural development of wild chimpanzees, with young females spending more time ant fishing and nest making than males at all ages investigated. However, the course of development of those skills was not followed. Other studies have either failed to find sex differences (Bugnyar & Huber 1997) or did not report the sex of the animals (Nagell et al. 1993; Tomasello et al. 1993b). In a study of the development of stone tool use in the chimpanzees of Bossou, Guinea, the researchers were unable to test for sex differences in development due to the small community size, which only allowed them to observe three infants (Inoue-Nakamura & Matsuzawa 1997). In a later summary of the studies at Bossou, Biro et al. (2003) presented data on individuals acquiring nut cracking at Bossou, Guinea. Although the authors did not test for sex differences, the age of acquisition of nine individuals can be inferred from the table presented in the paper. The average age of acquisition was 5 years for the three males studied and 4.2 years for the six females studied. The developmental course of these individuals was not reported. In a study of the ontogeny of a complex fruit-processing skill in wild chimpanzees, Corp & Byrne (2002) did not report testing for sex differences.

The chimpanzees of Gombe National Park, Tanzania display a socially learned feeding behaviour, called 'termite fishing', that involves inserting flexible tools of vegetation into a termite mound and extracting the termites that attack and cling to the tool. I performed a longitudinal field study during which individually identified chimpanzees under the age of 11 years were observed and videotaped during termite-fishing sessions in up to four consecutive years. Here I describe the critical

elements required for successful termite fishing and the timing and order in which these are acquired by young individuals. In addition, due to the evidence from previous studies of an adult sex difference in tool-use behaviour and efficiency, I use results presented here and in Lonsdorf et al. (2004) to test the prediction that young females and young males may show differences in both the speed of acquisition of this skill and the process by which it is learned.

METHODS

Study Site and Data Collection

Gombe National Park, Tanzania is a small (35 km²) park, located on the western border of Tanzania and is home to three communities of chimpanzees. Individuals from the Kasekela community, which has been studied for more than 40 years, were observed for this study. The chimpanzees termite-fish year-round, but their efforts become intensely concentrated at the start of the rainy season, from October to December (Goodall 1986). For this study, the author and a Tanzanian research assistant (K. John) collected data over a 4-year period at Gombe National Park, during October–December in 1998 (35 days), 1999 (41 days), 2000 (43 days) and 2001 (44 days) on a total of five mothers and 14 offspring that were under the age of 11 years (8 males, 6 females). We chose a cutoff of 11 years for offspring age because in chimpanzees, 10 years of age roughly correlates with first oestrus in females and puberty in males and is the time when offspring start spending a significant amount of time away from their mother (Pusey 1983). Therefore, the number of offspring observed in each year varied as a result of new births and some offspring ageing to 11 years.

All-day focal animal follows (Altmann 1974) were performed over the four termite-fishing seasons on the females and their offspring. During follows, the start of a termite-fishing session was defined as when a mother approached and contacted a termite mound. When a termite-fishing session occurred, I selected a focal target from a randomized sequence generated for each family (mother and offspring) and videotaped the target animal for a 15-min bout before moving on to the next individual in the sequence. Since mothers were presumed to have already achieved their adult termite-fishing technique, the random order was created such that offspring were sampled twice as often as mothers. If the family left the mound before the end of the 15-min bout, the bout was continued during the next session. If the entire family was sampled and the session was still continuing, I started again at the beginning of the random sequence. This sampling methodology was used in an effort to equalize the amount of data collected on individuals, and to avoid biasing the sample by only recording individuals highly motivated to termite-fish. During the 15-min videotaped samples, I narrated into the recorder data on (1) other individuals at the mound, (2) discarding and choosing of new tools, (3) estimated length of tools used, (4) social interactions at the mound, (5) apparent success/failure of

the individual in acquiring termites and (6) approximate number of termites acquired per dip. Following this methodology, I collected over 67 h of video footage from termite-fishing sessions.

Videotape Analyses

I transferred all videotaped data to a digital format and copied them onto compact discs to facilitate analyses using the Observer Video-Pro by Noldus Information Technology (Wageningen, The Netherlands), a software package for behavioural analysis. After studying the video footage and an unpublished glossary of termite-fishing behaviours (W. McGrew, personal communication), I created a list of over 50 target behaviours (see Table 1) and used the Observer to score and calculate exact durations and frequencies of these behaviours. Behaviours were scored as 'states' when duration was of interest and as 'events' when frequency was of interest and divided into termite-fishing behaviours and non-termite-fishing behaviours. Termite-fishing behaviours included both the critical components required for successful termite fishing, such as inserting a tool into a termite tunnel, and social behaviours such as watching another termite-fish. Non-termite-fishing behaviours included nursing, sleeping and playing. For nonvisible behaviours (e.g. the view of the focal animal was blocked), the behaviour 'can't see' was scored. The percentage of time spent engaged in each behaviour was rescaled by removing the time in which the individual's activities were not visible.

To measure proficiency, I generated a weighted average by categorically measuring the number of termites captured and multiplying the number of dips scored in a particular category by its central value (Lonsdorf et al. 2004). The categories 'none', 'less than 3', '3 to 5', '6 to 10' and 'more than 10' termites were chosen after initial inspection of the video suggesting that distinguishing between these categories could be done reliably. If the number of termites captured was not discernible, the dip was scored as 'can't tell' and not used in the analyses. For example, if for an hour-long session an individual was scored as having three unsuccessful dips (none), five dips in the 'less than 3' category, 10 dips in the '3 to 5' category, five dips in the '6 to 10' category, and none in the 'more than 10' category, the weighted average of termites captured was $((3 \times 0) + (5 \times 1.5) + (10 \times 4) + (5 \times 8) + (0 \times 10)) = 87.5$, giving a proficiency of $87.5/23 = 3.8$ termites per dip.

To measure technique, I scored the insertion length of tools used from the video footage. Insertion length of tool instead of overall length of the tool was used for two reasons. Although collecting and measuring tools in the field after they had been used was possible, tools were progressively modified and shortened during a termite-fishing session and multiple individuals would often use the same tool. In addition, a tool could have had an extremely long overall length, such as a 1-m-long blade of grass or piece of vine, but if the individual only inserted the first few centimetres of it, overall tool length was not as relevant a measure as functional tool length. Therefore, when a focal subject withdrew a tool completely from the

Table 1. Abbreviated list of target behaviours scored by using the Observer software

Behaviour code	Type	Definition
Termite-fishing behaviours		
Fish	State	Termite-fishing: composed of several dips
Dip	Event	One sequence of insert/withdraw when termite fishing
Watch	State	Watch another: face oriented to demonstrator for > 3 s
Mound-iv	State	Investigate mound by touching, sniffing, visually inspecting mound surface, and/or looking into holes on the mound
Mound-sw	Event	Sweep at the mound, usually removing vegetation
Mound-pr	Event	Probe a hole on the mound with finger
Mound-sn	Event	Sniff at hole on the mound
Mound-lk	Event	Look into a hole on the mound
Tool-mak	State	Make new tool, select and modify vegetation for use as a probe
Tool-mod	State	Modify a previously used tool
Tool-man	State	Manipulate a previously used tool with hands
Tool-mth	State	Investigate a previously used tool with the mouth
Both	State	Contact the mound with a tool
Both-s-m	Event	Swipe at the mound with a tool
Both-s-h	Event	Swipe a hole with a tool
Both-p-m	Event	Press the tool to the mound
Both-p-h	Event	Press the tool to a hole on the mound
Both-ins	Event	Insert tool into hole
Both-w	Event	Withdraw tool from a hole
Non-termite-fishing behaviours		
Can't see	State	Focal behaviour is out of view of observer
Other	State	Focal performing behaviour other than listed behaviours
Play	State	Play either alone or with another; with or without non-termite-fishing objects (tools, termites); may also include active swinging, dangling, leaping, somersaults, running, gamboling, pirouetting and bouncing; never accompanied by piloerection or agonism; may be accompanied by play-face and/or laughing.
Nurse	State	Focal attached at mother's breast via the mouth
Rest	State	Sitting or lying down with eyes open, not engaged in another activity
Sleep	State	Sitting or lying with eyes closed

Behaviours are listed as either state (duration) variables or event (frequency) variables. Event behaviours are listed as subtypes of state behaviours.

mound with his/her hand, I used a relative measure of functional tool length based on the size of the focal subject's fist. The following categories were scored: less than 3 fists long (short tool), 3–5 fists long (moderate tool), and more than 5 fists long (long tool). I then calculated the percentage of dips that fell in each category for each individual.

Statistical Analyses

I used the Observer to compute the percentage of the total duration of videotaped observation time spent in each of the target behaviours for each individual in each year. I then used general linear models (GLMs) (McCulloch & Searle 2000) to assess the effects of age and sex on particular behaviours. For models in which repeated measures on the same individual were used (e.g. percentage of time termite fishing) and models in which multiple offspring from the same mother were used (e.g. offspring proficiency), I used general linear mixed models (GLMMs)

to account for the potential correlation among observations. The GLMMs were not significantly different from the GLMs when tested with likelihood ratio tests, so only the results of the GLMs are presented here. SAS version 8.0 (SAS Institute, Inc., Cary, North Carolina, U.S.A.) was used for fitting GLMs, GLMMs, logistic growth models and for all nonparametric statistics. For small subgroup comparisons, Monte Carlo simulations were used to calculate exact Kruskal–Wallis test statistics. Due to the small size of the data set, this method is preferred over using asymptotic estimates. To investigate the effects of age and sex on the behaviours that displayed no obvious functional relationship with age, I used generalized additive models (GAMs) (Hastie & Tibshirani 1990). S-plus 2000 professional (Insightful, Inc., Seattle, Washington, U.S.A.) was used to fit GAMs for these behaviours.

To analyse the importance of particular behaviours that precede successful termite fishing, I used GLMs to determine the relationship between age of successful fishing and percentage of time spent in particular behaviours in the year preceding acquisition. I chose the behaviours 'watch', 'investigate mound', and 'contact the mound

with a tool' for these analyses as each accounted for large proportions of the total time spent at the termite mound.

Exploratory data analyses with age as either a continuous or categorical variable showed no differences between these approaches. Therefore, age was treated as a categorical variable (i.e. 'Age 0.5' for ages 0 to 1) in all models for ease of analysis and interpretation. Significance levels are reported at $P \leq 0.05$ but P values less than 0.10 are discussed as marginally significant due to the small sample size of individuals. Although results are based on a small number of chimpanzees, they are representative of the population, insofar as we observed all available offspring in the community over the four years of data collection. A few offspring were unavailable, due to the reclusive nature of their mothers.

RESULTS

Critical Elements

The critical elements that make up the adult form of the termite-fishing skill are as follows: identify hole on the mound, make tool, insert tool into hole, and extract termites. For young chimpanzees, an additional important behaviour is manipulating tools. Table 2 shows the age by which these behaviours had appeared in all the study subjects, and a range depicting the earliest and latest age that the behaviour appeared. I specify that, although the 'adult' form of the skill comprises the critical elements listed above, an individual does not have to make a tool in order to successfully extract termites. This is because chimpanzees regularly leave tools on top of and around the termite mound during fishing sessions that other individuals (including adults) may pick up and use. Nevertheless, all adult chimpanzees observed at Gombe made their own tools at some point during a fishing session, so tool making is a critical element of the adult form of the skill. For all chimpanzees observed, the order of acquisition for the behaviours is shown in Table 2. Despite the fact that young chimpanzees do not necessarily need to make a tool in order to fish, all showed tool-making ability either in the year before or in the same year that they showed the ability to insert a tool into the hole.

Table 2. Age by which the critical elements of termite fishing were acquired by all ($N = 8$) observed chimpanzees and range of earliest and latest appearance of the behaviour

Behaviour	Age by which all offspring had acquired the behaviour (years)	Range of earliest and latest appearance of the behaviour (years)
Identify hole	1.5	0.5–1.5
Manipulate tool	1.5	1.5
Make tool	3.5	1.5–3.5
Insert tool into hole	4.5	2.5–4.5
Extract termites	5.5	2.5–5.5

The critical elements for termite fishing were not acquired in the proper form by all chimpanzees until 5.5 years of age and the progression of the skill was as follows. From birth to 1 year of age, chimpanzee offspring typically slept or nursed while their mother was termite fishing. If they did contact the mound or tool material, it was the result of reaching out for any object passing through their visual field. By age 1.5 years, all chimpanzee youngsters had started investigating the mound on their own, typically by sweeping vegetation off the mound or visually inspecting the mound, and identifying holes on the mound by poking, sniffing or looking into holes. They also spent a large proportion of their time in the 1.5-year age category watching others termite-fish. By age 2.5 years, all began manipulating tools discarded by other chimpanzees. By age 3.5 years, all chimpanzee offspring studied had started to select and modify tool material into tools and had started contacting the mound with tool material. At this stage, they either pressed the tool to the mound or swiped at the mound with the tool, but they did not yet insert it into a hole. By age 4.5 years, all showed the correct sequence of choosing a hole, making a tool, and inserting it. However, for some, the technique of insertion was very haphazard and far too rapid; they typically did not insert the tool to any significant depth and did not catch termites. Finally, by age 5.5 years, all young chimpanzees had acquired the critical elements of the skill and began to catch termites.

Sex Differences in Time Spent Termite Fishing

The time that young chimpanzees spent attempting to termite-fish, defined by a full sequence of tool insertion and withdrawal, increased with age (Fig. 1a). The increase in the percentage of time spent termite fishing with age closely resembled a logistic growth curve $(F_0K)/(F_0 + Ke^{-rt})$, where F_0 is an initial termite-fishing percentage, K is the final termite-fishing percentage, r is the per-age rate of increase and t is age ($P < 0.0001$ for model fit). The interpretation of this model for these data is that termite fishing did not occur before age 2.5 years (0%), but showed a sharp increase between ages 2.5 and 5.5 years from 10% to 75%, then a deceleration and flattening of the curve after age 5.5 years at 83.84%. The parameter estimates for rate (0.98) and K (final fishing percentage, 83.84%) were significant with 95% confidence intervals of 0.33–1.63 and 69.90–97.79, respectively. The 95% confidence interval for initial fishing percentage (F_0) was -2.29 to 5.74 , showing that F_0 was not significantly different from zero at age 0 years. Since the actual termite-fishing percentage in chimpanzees under the age of 2.5 years was zero, this result is logical. When the same data were analysed separately by sex, there was a distinct sex difference, with females spending more time termite fishing through the first six age classes (Fig. 1b). Therefore, I used GLMs to investigate the relationships between age and sex classes and percentage of time spent termite fishing in individuals under 6 years. The main effects of age and sex were significant, as was the age by sex interaction, with females termite fishing significantly

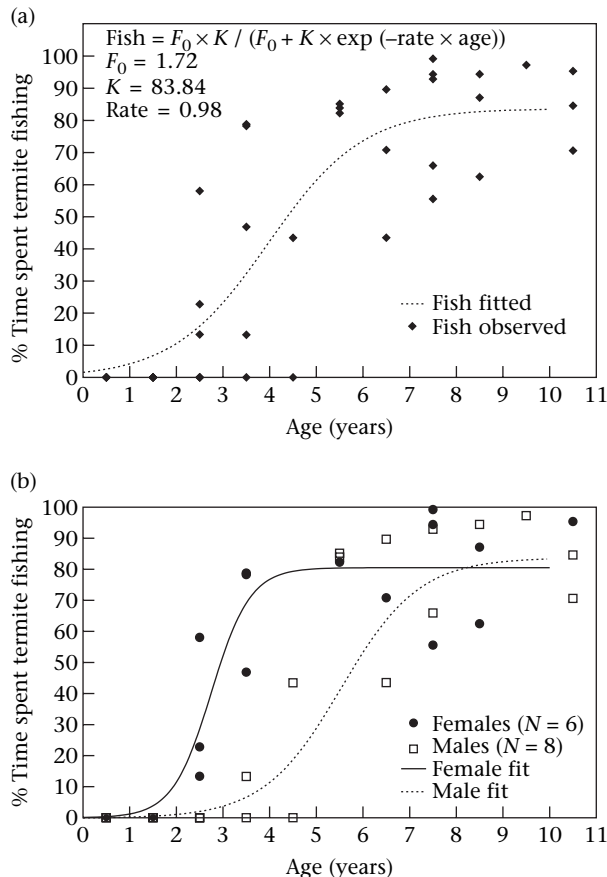


Figure 1. Scatterplots of the percentage of time young chimpanzees (age 0.5–10.5 years) spent termite fishing at termite mounds. (a) Single points are individual chimpanzees at a particular age. The fitted curve represents the logistic prediction of the percentage of time spent termite fishing by age. (b) Data are shown separately for males and females (reprinted from Lonsdorf et al. 2004). The fitted curves represent the logistic prediction of the percentage of time spent termite fishing by age for each sex.

more and earlier than males (GLM, adjusted $r^2 = 0.82$, $N = 25$: age: $F_{10,14} = 15.64$, $P < 0.0001$; sex: $F_{10,14} = 8.43$, $P = 0.0115$; age \times sex: $F_{10,14} = 4.29$, $P = 0.0179$). In fact, females were able to successfully termite-fish, defined by acquiring termites with a tool, an average of 27 months earlier ($N = 3$, mean \pm SD = 31 ± 4 months) than males ($N = 3$, 58 ± 6 months) (Lonsdorf et al. 2004).

To further investigate this sex difference, I performed nonparametric tests to investigate the specific ages at which the sex differences occurred. From ages 0.5 to 3.5 years, the percentage of time females spent termite fishing changed significantly from a mean of 0% at age 0.5 year to 67.97% at age 3.5 years (Kruskal–Wallis: $H_{11} = 9.01$, $P = 0.0035$), whereas for males, the percentage of time termite fishing increased from 0% at age 0.5 year to 6.64% at age 3.5 years ($H_9 = 3.5$, $P = 0.6675$). Across the first four age groups, there was a significant gender effect (Wilcoxon signed-ranks test: $T = 70$, $N = 20$, $P = 0.0162$) with females spending a greater percentage of time fishing. This difference disappeared thereafter (ages 4.5–10.5: $T = 93$, $N = 20$, $P = 0.5120$).

Sex Differences in Termite-fishing Behaviours

Because the onset of termite fishing showed a distinct sex difference, I investigated the possibility of a sex difference across all termite-fishing behaviours. I collapsed the percentages for all behaviours such as watch, investigate mound, manipulate tool, and so forth (see Table 1) to a single measure and investigated the effects of age and sex for ages 0.5–10.5 years. Note that no females in the age groups 4.5 and 9.5 years were observed during the course of the study. Using a general linear model, age and sex showed significant differences, with females spending significantly more time in all termite-fishing behaviours than males (GLM: age: $F_{11,28} = 15.87$, $N = 40$, $P < 0.0001$; sex: $F_{11,28} = 8.69$, $N = 40$, $P = 0.0064$, adjusted $r^2 = 0.80$; Fig. 2). Across the first four age groups combined, there was a significant gender effect (Wilcoxon signed-ranks test: ages 0.5–3.5: $T = 67$, $N = 20$, $P = 0.0201$), with females spending more time in termite-fishing activities, but this effect disappeared thereafter (ages 4.5–10.5: $T = 93$, $N = 20$, $P = 0.5198$).

Sex Differences in Specific Behaviours

I further analysed the sex differences for the first six age groups (0.5–5.5 years) in time spent investigating the mound, contacting the mound with a tool, and watching during a termite-fishing session.

Investigate mound

Because of the nonlinear trend across age, I fitted generalized additive models (GAMs) to test for the effects of age and sex on the percentage of time spent investigating the mound. Age was significant ($P = 0.0055$), as was the age by sex interaction ($P = 0.0082$). Time spent investigating the mound showed a steady increase until age 1.5 years for females and age 2.5 years for males, then decreased (Fig. 3).

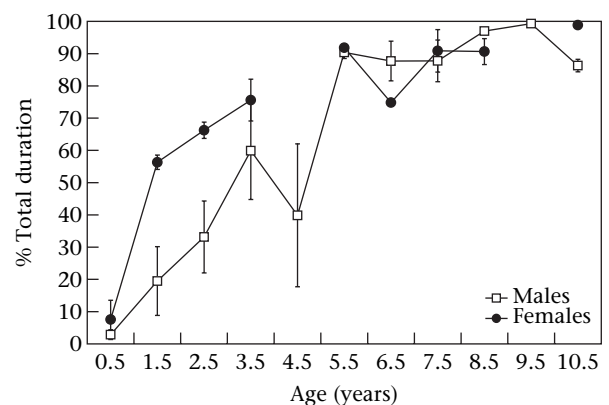


Figure 2. Average \pm SE percentage of time spent in all termite-fishing behaviours combined for each age group. Data points represent the mean across all individuals at a particular age. Data are shown separately for males and females.

Contacting the mound with a tool

I again fitted generalized additive models (GAMs) to test for the effects of age and sex on the percentage of time spent contacting the mound. Age was marginally significant ($P = 0.0872$), as was sex ($P = 0.0701$). The behaviour showed a steady increase until age 2.5 years for females and age 3.5 years for males, then decreased (Fig. 4).

Watch

When fitted with GAMs, the main effect for sex and the age by sex interaction on the percentage of time spent watching another individual termite-fish were both highly significant (both $P < 0.0001$). Watching increased until age 1.5 years in females and age 2.5 years in males before decreasing (Fig. 5).

The Importance of Behaviours that Precede Fishing

For those chimpanzees that began fishing successfully during the course of the study, I investigated the age of successful fishing of individual subjects regressed on the percentage of time he/she spent in particular behaviours (watch, investigate the mound, contact the mound with a tool) in the year before. The amount of time spent watching in the year before was the only factor that was significantly and negatively correlated with age of successful fishing (GLM: $F_{1,4} = 7.7$, $N = 6$, $r^2 = 0.66$, $P = 0.05$), however, the number of subjects used for this analysis was necessarily small. Note that females watched significantly more than males (see above), whereas males spent significantly more time at the termite mound playing (GAM: sex and age \times sex interaction, both $P < 0.0001$) (Lonsdorf et al. 2004).

Sex Differences in Proficiency and Learning Processes

In a preliminary description, Lonsdorf et al. (2004) reported that female offspring were more proficient at

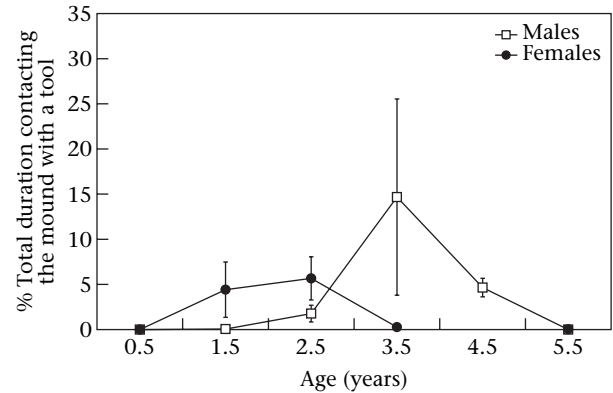


Figure 4. Average \pm SE percentage of time spent contacting the mound with a tool for each age group. Data points represent the mean across all individuals at a particular age. Data are shown separately for males and females.

termite fishing as measured by number of termites gathered per dip (GLM, adjusted $r^2 = 0.62$, $N = 12$: age: $F_{1,9} = 15.23$, $P = 0.004$; sex: $F_{1,9} = 10.94$, $P = 0.009$) after adjusting for age. Moreover, they reported a sex difference in the similarity of offspring termite-fishing technique to that of mothers. In every tool length category (short, moderate, long), each daughter's percentage of dips in that category correlated closely with her mother's percentage of dips in that category (Fig. 6a, reprinted from Lonsdorf et al. 2004). However, each son's percentage of dips in a particular category did not correlate with his mother's percentage of dips in the same category (Fig. 6b, reprinted from Lonsdorf et al. 2004). GLMs were used to directly test the significance of the interaction between the sex of offspring and the mother's tool category for each offspring tool category. For each tool insertion length, the interaction was highly significant and positive for females (for short insertion length: $P = 0.009$; for medium insertion length: $P = 0.01$; for long insertion length: $P = 0.02$). In contrast, mothers as a group varied more than sons, because sons generally used short tools, regardless of their mothers' pattern. Using short tools resulted in a higher failure rate (no

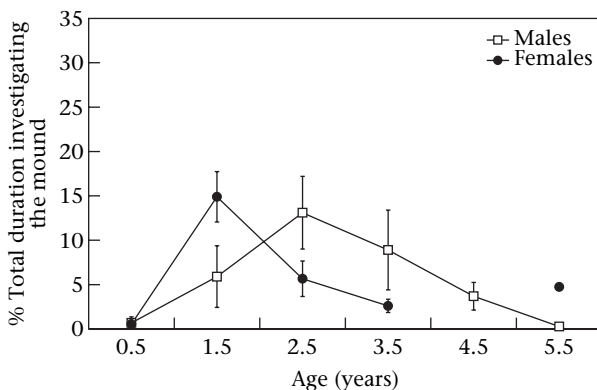


Figure 3. Average \pm SE percentage of time spent investigating the mound for each age group. Data points represent the mean across all individuals at a particular age. Data are shown separately for males and females.

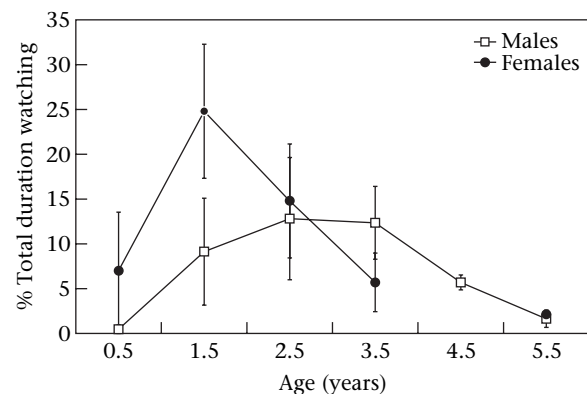


Figure 5. Average \pm SE percentage of time spent watching for each age group. Data points represent the mean across all individuals at a particular age. Data are shown separately for males and females.

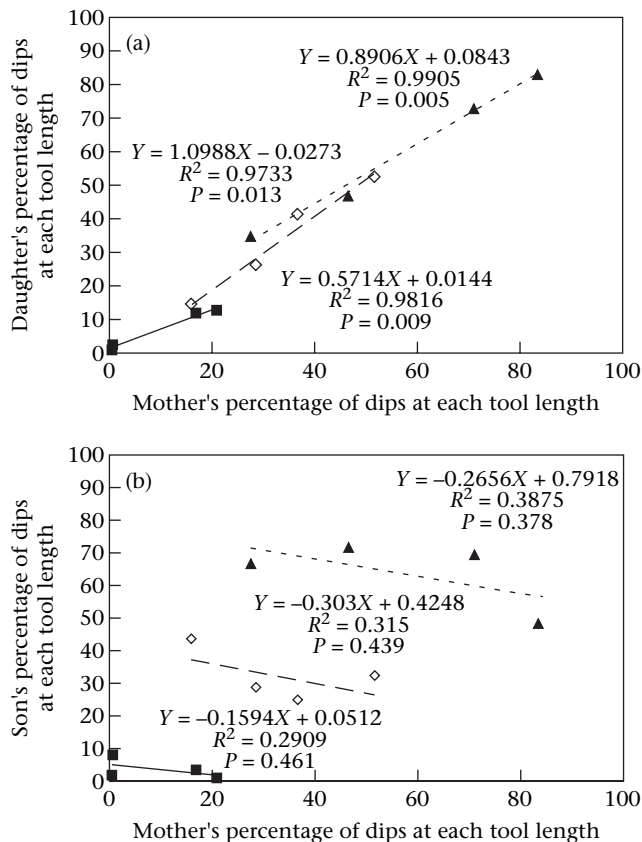


Figure 6. Offspring–parent regression of (a) daughters and (b) sons on mothers (reprinted from Lonsdorf et al. 2004). Individual points represent the offspring's percentage of dips at a particular tool insertion length plotted to the mother's percentage of dips at the same length. Three separate regression lines are shown, one for each of three tool lengths: short (less than 3 fists; ▲), moderate (3–5 fists; ◇) and long (more than 5 fists; ■).

termites caught on a given dip) than using moderate or long tools, so males were typically using a less successful technique than their mothers.

There were no significant differences between male and female offspring in frequency of social interactions with their mother, and mothers did not show differential tolerance for either sex (Lonsdorf, *in press*). Therefore, the sex differences described above were not the result of differing interactions between mothers and male offspring versus mothers and female offspring. Moreover, no cases of active teaching (e.g. actively offering a tool or a termite or shaping of offspring behaviour) by mothers or any other individuals were observed.

DISCUSSION

Sex Differences in Termite-fishing Behaviours

In studies of insect eating in adult chimpanzees, both McGrew (1979, at Gombe) and Uehara (1986, at Mahale) found that females were more insectivorous than males. The authors suggested that this sex difference represents a counterbalance of protein gained from insect eating (females) versus hunting (males). However, all adult chimpanzees at Gombe eventually learn to termite-fish

and spend large amounts of time doing so during the most productive season (October–December). Therefore, it is interesting that the age at which young males and females acquire the termite-fishing skill differs so dramatically as well as how much time they spend doing it in the first several years of life. At age 2.5 years, females in the present study spent 31.4% of their time at the mound termite fishing whereas males were not yet termite fishing at all (0%). By age 3.5 years, females spent a majority of their time (67.9%) termite fishing, whereas males only termite-fished 6.6% of the time and did not start spending a majority of their time at the mound termite fishing until age 5.5 years (84.53%). However, after age 5.5 years, when all males had acquired the skill, there was no significant difference in how much time males and females spent termite fishing during a session on the mound (Fig. 1b).

When time spent in all termite-fishing behaviours was combined, sex differences were evident that mirrored the data for termite fishing itself (Fig. 2). Females began dedicating the majority (56.3%) of their time at the termite mound to termite-fishing behaviours at age 1.5 years. At the same age, males only dedicated 19.5% of their time to termite-fishing behaviours, and spent the majority (52.2%) of their time playing. This difference continued until age 3.5 years, when males began to spend the majority of their time in termite-fishing behaviours. Similar patterns were seen in the percentage of time spent in specific behaviours such as investigating the mound, contacting the mound with a tool and watching others termite-fish (Figs 3–5). For each of these behaviours, females peaked in their amount of time dedicated to the activity a year earlier than males (1.5, 2.5, 1.5 years, respectively). By age 3.5 years females dedicated very little time to any of these behaviours because they were spending over 60% of their time termite fishing. Males did not show a similar decrease until age 5.5 years (Figs 3–5). The behaviour of investigating the mound showed a similar pattern for both sexes, with the males a year delayed. Different patterns emerged in watching and contacting the mound with a tool. Females watched quite a bit more at age 1.5 years (24.8%) than males did in any one of the first 4 years of their life (12.8% at age 2.5 years). Conversely, males spent more time contacting the mound with the tool at age 3.5 years (14.7%) than females did in any one of the first 4 years of their life (5.7% at age 2.5 years).

The results that females watched significantly more than males at young ages and began termite fishing earlier suggest that watching was especially important for acquiring the skill. Conversely, males did not watch as much at young ages and spent more time practising the mechanical aspects of the skill (contacting the mound with the tool) than did females, but they began termite fishing later than females (Figs 4, 5). Sumita et al. (1985) found similar results in a study of the ability of five captive chimpanzees to learn from a human demonstrator how to crack open nuts with stone tools. The single most important predictor of whether a chimpanzee successfully acquired the skill was showing interest in the nut-cracking behaviour itself. In contrast, showing interest only in the nuts was

recorded more frequently in the unsuccessful group. Similarly, Weeks et al. (1996) studied the ability of human children to learn handshapes of the American manual alphabet. Those children who were forced to delay imitation of the handshapes were more successful in later recall tests than those who practised concurrently with the demonstrator. Weeks et al. hypothesized that delaying reproduction of the handshapes required subjects to expend more cognitive effort to retain and produce the handshapes later; watching was more important than practising. The results presented here are compatible with this idea and suggest that, in chimpanzees, watching may be a more important behaviour for acquiring complex manual skills than actually practising the skill itself. However, in order to directly compare the importance of watching versus practising, larger sample sizes containing individuals of the same age and sex are needed.

Young female chimpanzees spent more time watching others termite-fish and acquired the termite-fishing skill more quickly than young males. Several studies have suggested that there are fundamental sex differences in inattentiveness and impulsivity in human children and adults, with males rating higher on all such scales (Ginsburg & Miller 1982; Burns & Owen 1990; Prior et al. 1993). The fact that young female chimpanzees are more proficient termite-fishers once they have acquired the skill is also consistent with human sex differences. Studies have shown that while human males perform better on gross motor and spatial tasks, human females perform better on fine motor tasks and those requiring attention and planning (Blote & Van Gool 1989; Blote & Van Haasteren 1989; Warrick & Naglieri 1993; Vederhus & Krekling 1996; Davis & Rose 2000). These results also complement findings that adult female chimpanzees are more skilled and more frequent tool users than males, and that males are primarily hunters (McGrew 1979). From an evolutionary perspective, the above findings suggest that there are fundamental sex differences in learning propensities that may date to the last common ancestor of chimpanzees and humans. Studies of sex differences in social learning in other primates and nonprimate animals would greatly increase our understanding of the evolutionary basis of this difference.

Sex Differences in Learning Processes

In an observational field study, it is extremely difficult to experimentally distinguish between types of learning. However, given that neither male nor female chimpanzees start spending the majority of their time away from their mothers until age 10 years, and that mothers are the primary subject of observation for offspring of both sexes (no significant paternal care occurs), the sex difference observed in this study allows inferences into the types of social learning that are occurring. Furthermore, ecological explanations do not account for the differences found between male and female offspring, because both sexes are present on the mound with their mother and therefore have access to the same mound characteristics and types of vegetation. Therefore, following a previous broad

categorization of social learning processes (Whiten & Ham 1992), I propose that the development of termite fishing includes social learning processes as well as individual trial-and-error learning as follows. Male and female offspring learn from their mother that the termite mound is the object to which attention should be directed (stimulus enhancement). Once the mother starts to termite-fish, male and female offspring learn that the goal of the behaviour is to capture termites (goal emulation). Male offspring then develop their own method of achieving this goal, while female offspring learn something about the form of the behaviour, namely how deep to insert the tool (imitation). For both sexes, individual trial-and-error learning follows, as the offspring learns how to withdraw the tool without dislodging the prey. This part of the behaviour must be learned individually, because it takes place inside the termite mound and cannot be seen.

The data presented here appear to differ from some results found by scientists studying social learning processes in captivity. Why is it that the chimpanzees studied by Tomasello et al. (1987) and Nagell et al. (1993) did not appear to imitate? I suggest that the time course of the studies is the likely explanation. All the chimpanzee offspring that were subjects for the technique portion of this study were over 5.5 years. To arrive at a conservative estimate of how much time a young chimpanzee would have had to observe its mother termite-fish over the first 5.5 years of their life, we can use study subject Fifi, the mother who was observed to termite-fish the least (3% of her observation time). If Fifi termite-fished for 3% of her waking hours over 2 months between October and December, her offspring would have had the opportunity to observe her termite-fish for 118.8 h over the first 5.5 years of life ($0.03 \times 12 \text{ h day awake} \times 60 \text{ days} \times 5.5 \text{ years}$). Moreover, a mother who spends an average amount of time termite fishing (9% of observation time) provides 356.4 h of potential observation for her offspring. In the Tomasello et al. (1987) study, chimpanzees were tested for imitation after two sessions consisting of 35 1-min trials that took place on subsequent days. In the Nagell study, each subject participated in a total of 50 1-min trials given over a 2- to 5-day period. Both of these time frames are far shorter than the time a chimpanzee would spend observing a complex behaviour in the wild. Granted, the human children in the above studies were able to imitate after a few trials. However, this may be because human children have been 'rewarded' for imitating throughout their evolutionary history (Miklosi 1999). It is well known that human imitation is bi-directional, with children imitating adults and adults reciprocating (Stern 1985). Such interactions reinforce and reward infant imitation, but do not typically occur in chimpanzees. In fact, the best-known cases of imitation in apes have been in apes that have been home-raised by humans (Hayes & Hayes 1952) or symbol-trained apes reared in captivity with daily, long-term interactions with the same researchers (Savage-Rumbaugh et al. 1986; Gardner et al. 1989; Miles 1990; Tomasello et al. 1993a). It has been suggested that the appearance of imitation in these 'enculturated' apes is a result of their unnatural rearing in close contact with humans and that wild apes, without

the same experiences, are unlikely to have the same abilities (Tomasello et al. 1993a). In commentaries on that work, both Boesch (1993) and Whiten (1993) suggested that the long-term, repeated interactions typical of human-reared chimpanzees have important similarities to the rearing of wild chimpanzees. My data concur and support the notion that long-term, repeated interaction with a well-known individual is the natural circumstance under which imitation appears in chimpanzees, whether mother-reared in the wild, or human-reared in captivity.

The results presented above suggest that there exist fundamental differences in how young female and male chimpanzees learn to termite-fish. Young female chimpanzees (1) started to termite-fish at a younger age than males, (2) were more successful than males once they had acquired the skill and (3) used techniques that were similar to their mothers', whereas males did not. Moreover, young females spent significantly more time watching other individuals perform the task. This is the first systematic evidence of sex differences in learning of a tool-use skill in wild chimpanzees. This is also the first evidence of imitation of tool-use technique in wild chimpanzees, and highlights the different learning processes used by male and female offspring to learn this task. However, I do not wish to suggest that young chimpanzee males do not have the ability to imitate, only that they do not imitate the details of the termite-fishing technique. Socioecological theory predicts that while female reproductive success is limited by access to resources, male reproductive success is limited by access to mates (Wrangham 1982). Applied to chimpanzees, adult females should primarily be interested in finding food and adult males in establishing themselves socially so that they have access to females, either through the dominance hierarchy or through alliances (Wrangham & Smuts 1980). Therefore, it is likely that young male offspring may learn by imitation those tasks that are more important for their reproductive success, such as dominance behaviours or hunting. Future research should focus on further exploring sex differences in socially learned behaviours.

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