

Elizabeth V. Lonsdorf

What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)?

Received: 23 February 2005 / Revised: 4 May 2005 / Accepted: 17 May 2005 / Published online: 30 September 2005
© Springer-Verlag 2005

Abstract This paper explores the role of maternal influences on the acquisition of a tool-using task in wild chimpanzees (*Pan troglodytes schweinfurthii*) in order to build on and complement previous work done in captivity. Young chimpanzees show a long period of offspring dependency on mothers and it is during this period that offspring learn several important skills, especially how to and on what to forage. At Gombe National Park, one skill that is acquired during dependency is termite-fishing, a complex behavior that involves inserting a tool made from the surrounding vegetation into a termite mound and extracting the termites that attack and cling to the tool. All chimpanzees observed at Gombe have acquired the termite-fishing skill by the age of 5.5 years. Since the mother is the primary source of information throughout this time period, I investigated the influence of mothers' individual termite-fishing characteristics on their offsprings' speed of acquisition and proficiency at the skill once acquired. Mother's time spent alone or with maternal family members, which is highly correlated to time spent termite-fishing, was positively correlated to offspring's acquisition of critical elements of the skill. I also investigated the specific types of social interactions that occur between mothers and offspring at the termite mound and found that mothers are highly tolerant to offspring, even when the behavior of the offspring may disrupt the termite-fishing attempt. However, no active facilitation by mothers of offsprings' attempts were observed.

Electronic supplementary material Supplementary material is available for this article at <http://dx.doi.org/10.1007/s10071-005-0002-7> and accessible for authorised users.

E. V. Lonsdorf (✉)
Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA
e-mail: elonsdorf@lpzoo.org
Tel.: +1-312-742-7354
Fax: +1-312-742-7220

Present address:

E. V. Lonsdorf
Department of Conservation and Science Lincoln Park Zoo & Committee on Evolutionary Biology, University of Chicago, 2001 N Clark Street, Chicago, IL 60614, USA

Keywords Chimpanzee · Tool-use · Mother-infant interactions · Learning

Introduction

Chimpanzees are known to have one of the most complex social systems and show the most diverse behavioral repertoires of any non-human animal (McGrew 1992; Whiten et al. 1999). One important example is the variety of food items included in the omnivorous chimpanzee diet. At one site alone, the Gombe Stream Research Centre, researchers have identified up to 235 food items eaten by chimpanzees from the long-term data records (I. Gilby, personal communication). Consequently, a young chimpanzee has much to learn about how, where and when to eat the various food items in its environment. The demands of learning such a diverse diet have been theorized as a possible selection pressure leading to the bigger brains and more advanced cognitive abilities of the higher primates (Milton 1981).

Studies in a variety of species have demonstrated that young individuals learn much of what they know about foraging via social learning, from observing and sampling what their mother eats (elephants—Lee and Moss 1999; felids—Kitchener 1999). Similarly, in chimpanzees, the mother is the primary source of information, due to the long period of offspring dependency that results in youngsters traveling almost exclusively with their mothers until between 8 and 10 years of age (Goodall 1967; Pusey 1983, 1990). Especially in the case of foods that require using tools to process, chimpanzees closely observe their mother to learn how to perform the skill (Goodall 1968; Biro et al. 2003; Lonsdorf et al. 2004). In the course of studying the acquisition of nut-cracking behavior in West African chimpanzees, Matsuzawa et al. (2001) characterized how youngsters learn these skills as “education by master–apprenticeship.” They described the process as follows: No active teaching occurs between master and apprentice, i.e. there is no shaping or molding of apprentice behavior by the master. Instead, the apprentice acquires the skill through

repeated observations of the master, and the master, in turn, exhibits high levels of tolerance for the close proximity of the apprentice. In the case of nut-cracking, this tolerance translates to allowing young chimpanzees to observe very closely and allowing them to manipulate stones or nuts. In many decades of research at several study sites, only two episodes of active teaching have been observed, in which mothers of the Tai Forest, Ivory Coast either appeared to demonstrate nut-cracking behavior to their offspring, or to correct an offspring's incorrect behavior (Boesch 1991).

A recent study (Hirata and Celli 2003) described the role of mothers in the acquisition of a honey-fishing task in three captive mother–infant pairs. Infants acquired the skill between the ages of 20 and 22 months, which is earlier than previous reports of tool-use skill acquisition in the wild. The authors hypothesized that the captive environment may have accelerated the development of the skill by providing more opportunities for object manipulation and observation than in the wild. The authors also found that infants observed not only their respective mother's performances but also other adults. They concluded that detailed observations of tool-use development from the wild were necessary to evaluate the possible effects of the captive environment.

The chimpanzees of Gombe National Park, Tanzania display an extractive tool-assisted foraging behavior known as termite-fishing, which is similar to the honey-fishing task used by Hirata and Celli (2003). This behavior requires fashioning an appropriate tool out of the surrounding vegetation, inserting the tool into a mound built by termites, and extracting the termites that attack and cling to the tool. Lonsdorf et al. (2004) reported finding distinct sex differences in the development of termite-fishing in that female offspring developed the skill more quickly than males, were more proficient at the skill once it was acquired and resembled their mothers' techniques of termite-fishing, while males did not. Lonsdorf (in press) provides a detailed description of infant activities during termite-fishing skill development. This report further explores the role of the mother in termite-fishing development to complement and expand on the previous work of Hirata and Celli (2003). Specifically, I investigated whether individual differences in sociality, skill and rate of termite-fishing among mothers at Gombe National Park affected the speed of acquisition and eventual proficiency of their offspring. In addition, I describe the types of social interactions that occur at the termite mound between mothers and infants.

In the case of a complex foraging behavior such as termite-fishing, an offspring's acquisition of the skill may be affected by several factors. One possibility is that individuals may become more or less skilled at the termite-fishing task due to differential opportunities for learning (van Schaik et al. 2003). For the purposes of this study, these opportunities can be expressed in two ways: mother's frequency of performing the skill and her level of sociality while performing the skill. van Schaik et al. (2003) have suggested that variation in the opportunity to watch several different models besides one's mother perform a tool-using task may increase tool-use skills. Therefore, if

individual mothers differ in their rate of tool-use or level of sociality during tool-use activities, we may expect to see those individual differences reflected in the speed of acquisition or skill level of their offspring. Another factor that may be important in offspring acquisition is the skill of the demonstrator (their mother). While previous social learning studies have focused on the gender (Benskin et al. 2002), age (Choleris et al. 1997), familiarity (Galef et al. 1998; Cadieu and Cadieu 2002), or dominance rank (Chalmeau and Gallo 1993; Nicol and Pope 1999) of the demonstrator, few have distinguished between different skill levels of demonstrators (Nicol and Pope 1999; Swaney et al. 2001).

Methods

Study site and field 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 Kasakela community, who have been studied for more than 40 years, were observed for this study. These chimpanzees are habituated to human observers, are easily recognized, and matrilineal kinship is known for as many as three generations. 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 at Gombe National Park, from October through December in 1998 (35 days), 1999 (41 days), 2000 (43 days) and 2001 (44 days) on a total of 5 mothers and 14 offspring (8 males, 6 females) over a 4-year period. 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, due to new births and aging past 11 years over the course of the study, not all offspring were observed in each year.

I performed all-day focal animal follows (Altmann 1974), over four consecutive termite-fishing seasons, on the mothers who had offspring under 11 years of age. Mothers were located as soon as possible each morning of data collection, usually at the sleeping nest where they had spent the previous evening. If the location of a focal mother's night sleeping nest was not known, I searched until one of the subjects was found and began the follow at that time. Due to the difficulty of finding particular chimpanzees on particular days, formal random sampling was not possible. Similarly, some females are much easier to follow than others due to their preferences for trails or easily accessible areas. Focal subjects that were difficult to track sometimes resulted in truncated follows when I lost the individual. In addition, torrential downpours often resulted in follow sessions being cut short. All of the aforementioned factors result in unequal observation time on the five focal mothers. Therefore, data are given as a percentage of total observation time on each mother.

In order to investigate maternal effects, I collected several types of data during the daily follows. To measure an offspring's opportunity for learning, I recorded the duration of all termite-fishing sessions for the mother from start to finish. The start of a mother's session was defined as approaching the termite mound to within 1 m and starting to manipulate the mound and/or a tool. The end was defined as when the mother left the vicinity of the mound or started to perform another behavior while still in the vicinity (sleeping or feeding on non-termite foods). In addition, I recorded when the focal mother's current social group changed in composition and the identity of the individuals in the group.

When a termite-fishing session occurred, I selected a focal target from a randomized order 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 random order. During the 15-min videotaped samples, I narrated information about various aspects of the task into the recorder, including data on (1) other individuals at the mound, (2) social interactions at mound, (3) apparent success/failure of the individual in acquiring termites, and (4) approximate number of termites acquired per dip. Following this methodology, I collected over 65 h of video footage from termite-fishing sessions.

Videotape analyses

I transferred all videotaped data to a digital format and copied it onto compact discs to facilitate analyses using the Observer Video-Pro™ by Noldus, a software package for behavioral analysis. After consulting the video footage and an unpublished glossary of termite-fishing behaviors (W. McGrew, personal communication), I created a list of over 50 target behaviors and used the Observer to score and calculate exact durations and frequencies of these behaviors. The target behaviors included termite-fishing behaviors such as inserting a tool into a termite tunnel, and watching another termite-fish, and non-termite-fishing behaviors such as nursing, sleeping, playing, etc. (see [Lonsdorf in press](#) for list of behaviors scored). For social interactions (see Table 1), the identity of the individual that the offspring was interacting with was recorded, as well as that individual's response to the offspring.

For mothers and older offspring that had already acquired the termite-fishing skill, the number of termites acquired per termite-fishing dip was measured from the video in the following categories: none, less than 3, 3–5, 6–10, and more than 10. Because chimpanzees pick termites off the fishing tool one by one with their lips, these categories were highly reliable measures of the number of termites captured.

Determining mothers' rate of fishing, sociality and skill

An offspring's opportunities for learning were determined in two different ways. A mother's relative amount of time

spent termite-fishing was calculated as the percentage of time she was recorded termite-fishing out of her total observation time: time spent fishing/total observation time. In order to test the effect of mother's sociality (opportunities to observe other models) on offspring acquisition and skill level, I calculated each mother's total observation time spent in different sized social groups in each individual year, and over the 4 years combined. Group size was divided into four different categories. "Alone" designated that a mother was only with her dependent offspring. "With family" denoted that a mother was with members of her maternal family. (This designation is important as adult daughters often spend large amounts of time with their mothers.) "Small group" indicated that a mother was with fewer than three other maternally unrelated adult individuals, and "large group" was assigned when a mother was with three or more other unrelated adults. To investigate the effect of group size at the actual termite mound, the same category divisions were made for each mother's termite-fishing sessions.

A mother's skill was measured as both "proficiency" and "efficiency." These were calculated following McGrew and Marchant (1999):

1. proficiency = # of termites / # of total withdrawals of the tool
2. efficiency = # of termites / total duration in minutes of termite-fishing

I used a weighted average to generate the number of termites captured by multiplying the number of dips scored in a particular category by its central value. If I was unable to categorize the number of termites captured, the dip was scored as "can't tell" and not used in the analyses. For example, if for an hour long session I scored an individual as having 3 unsuccessful dips (none), 5 dips in the less than 3 category, 10 dips in the 3–5 category, 5 in the 6–10 category, and none in the more than 10 category, her weighted average of termites captured was

Table 1 Social interactions scored by using the Observer software

Social interactions	
(1) Watch	Watch another termite-fish (face oriented to demonstrator for > 3 s)
(2) Reach	Reach to another's hand, mouth, or tool while the other is termite-fishing. Individual may touch the tool, but does not take possession of it
(3) Steal	Steal another's tool out of their hand. Individual takes possession of the tool
(4) Mound-inv-oth	Investigate mound where another is working, includes sniff, poking, "mopping," and looking directly into a hole on the mound
(5) Both-oth	Manipulate tool at same mound hole where another is fishing
(6) Term-int-oth	Interacting with another's termites by taking with either hands or mouth

$\{(3 \times 0) + (5 \times 1.5) + (10 \times 4) + (5 \times 8) + (0 \times 10)\} = 87.5$, giving a proficiency of $87.5/23 = 3.8$ termites per dip, and an efficiency of $87.5/60 = 1.46$ termites per minute. Since the “more than 10” category was scored only rarely and had no upper bound, 10 was used as the central value for that category. For mothers, proficiency and efficiency were measured across all the 4 years of the study. For offspring, only data from the last (oldest) year was used in calculations. For analyses, only measures of proficiency were used, as an individual’s efficiency was often confounded by interference from other individuals at the termite mound, especially when young individuals were present. Gender and age of all offspring and all maternal relationships were known.

Determining offspring acquisition and proficiency

I measured speed of acquisition in two ways. The age at which a focal chimpanzee offspring was seen to extract at least one termite with a tool three times during a termite-fishing session was deemed the age at which they had acquired the skill. Three instances were required so that an individual that accidentally dislodged a termite one time was not determined to have acquired this skill. In this study, the earliest age of acquisition was approximately 2.5 years and the latest was approximately 5.5 years. The yearly 3-month study period encompassed the majority (70%), but not all of the time that chimpanzees are known to termite-fish (Goodall 1986). As a result, age of acquisition can be considered the coarsest measure, since any particular offspring may have acquired the skill shortly after the field season ended and would not have been acknowledged as having the skill until 9 months later. Consequently, I also used the number of critical elements (CE) achieved by each age as a finer measure of speed of acquisition of termite-fishing. The critical elements of termite-fishing are: (1) identify hole on the mound, (2) make tool, (3) manipulate tool, (4) insert tool into hole, and (5) extract termites (Lonsdorf in press). Offspring proficiency was measured the same way as for mothers (see the previous section).

Statistical analyses

I used general linear models (GLMs) to assess the association of gender and mother’s termite-fishing characteristics with offspring speed of acquisition and proficiency. Mother’s characteristics were averaged over the 4 years in analyses for offspring proficiency and age of acquisition (the coarsest measure of speed) to approximate the average amount of learning opportunities provided by a particular mother. Mother’s characteristics in individual years were used in analyzing number of critical elements acquired for their offspring. For testing correlates of offspring proficiency, I used general linear mixed models (GLMMs) to account for the presence of multiple offspring from the same mother. The GLMMs were not significantly different from the GLMs when tested with likelihood ratio tests,

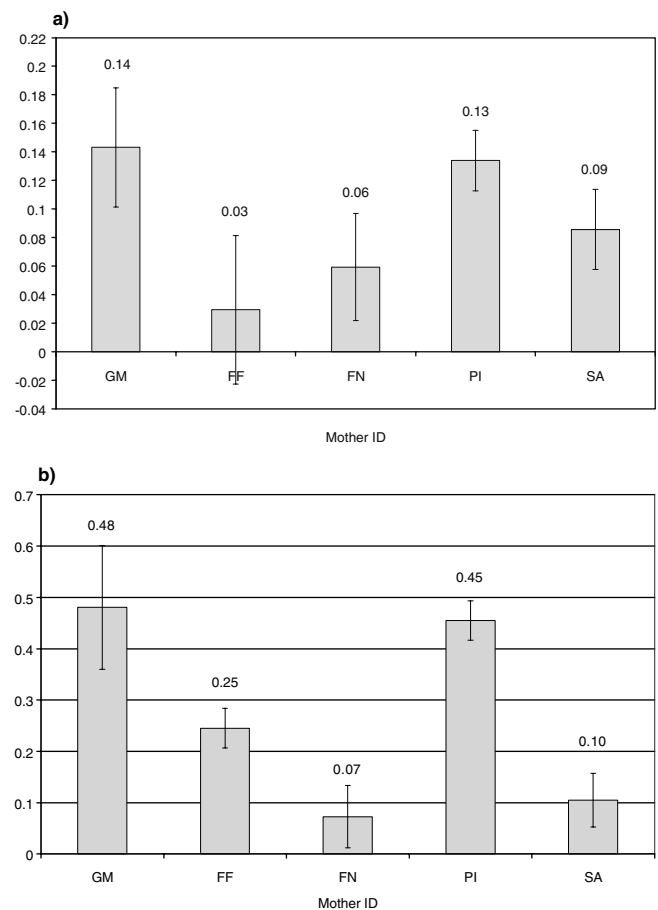


Fig. 1 (a) Mean percent of observation time spent termite-fishing for five mothers. Data are averaged across the 4 years of the study (1998–2001). (b) Mean percent of observation time spent alone for five mothers. Data are averaged across the 4 years of the study (1998–2001)

so only the results of the GLMs are presented here. In all models, I used age as a categorical variable instead of continuous for ease of analysis and interpretation. Exploratory data analyses with age as both a continuous and categorical variable showed no differences. SAS version 8.0 (SAS Institute Inc., Cary, NC) was used for fitting GLMs.

Results

Individual differences among mothers

Before testing the effects of the individual differences found in mothers on their offsprings’ learning of termite-fishing, it was necessary to show these differences exist. Figure 1a displays the percent of observation time spent termite-fishing, averaged over the 4 years for the five focal mothers. The data indicate that there were individual differences in the amount of time mothers spent termite-fishing, which served as a measure of learning opportunities for their offspring. Figure 1b shows that there were distinct

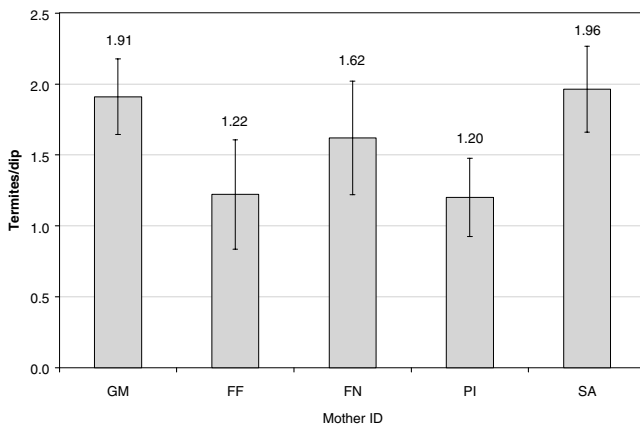


Fig. 2 Per dip proficiency (number of termites per dip) of five mothers averaged over 4 years (1998–2001)

and significant differences in the amount of time mothers spent alone versus in larger social groups, which translates into differential opportunities for their offspring to observe other models. Mothers also showed significant individual differences in their proficiency (termites per dip), as Fig. 2 shows that individuals GM and SA gather significantly more termites per dip than individuals FF, FN and PI.

The relationships among mothers' characteristics

During exploratory data analyses, I found a strong relationship between the two hypothesized predictors for learning opportunities: mother's time spent fishing and her time spent in certain sized social groups. Specifically, the overall amount of time a mother spent termite-fishing is highly correlated with the overall time she spent alone (linear regression: $F_{1,18}=12.2$, $N=20$, $p=0.003$, $r^2=0.40$). If the time spent alone is combined with time spent with maternal family, the relationship is stronger (linear regression: $F_{1,18}=17.4$, $N=20$, $p=0.0005$, $r^2=0.49$). Moreover, I found that during termite-fishing sessions, mothers were much more likely to be alone or with maternal family than in any other type of group (see Fig. 3). S-plus 2000 professional (Insightful Inc., Seattle, WA) was used to examine the equality of proportions between percent of time spent fishing in different sized groups. Binomial tests for the hypothesis that individual mothers were more likely to be either alone or with maternal family while termite-fishing, as compared to in small or in large groups, were all significant (binomial proportions χ^2 test: all $df=1$, all $p<0.001$). Therefore, all of the following characteristics were investigated as predictors of offspring speed of acquisition and proficiency:

- (1) mother's overall percent time spent fishing,
- (2) mother's overall percent time spent alone,
- (3) mother's overall percent time spent alone or with maternal family,
- (4) mother's percent time alone while fishing,

- (5) mother's percent time alone or with family while fishing,
- (6) mother's percent time with a small group while fishing,
- (7) mother's proficiency,
- (8) offspring gender.

Mother's time with a large group while fishing was excluded from the analyses, as all mothers spent less than 6% of their time fishing in a large group.

The relationships among mother's characteristics, offspring gender and offspring age of acquisition

General linear models were used to test correlations between the aforementioned predictors and offspring age of acquisition. For the coarsest measure, age of acquisition ($n=6$), none of the mother's characteristics (1–7, above) were significant in predicting age of acquisition. However, gender was significant (GLM: $F_{1,4}=7.2$, $n=6$, $p=0.05$, $r^2=0.68$) with female offspring acquiring termite-fishing at an earlier age.

For a finer analysis of speed of acquisition, I used the number of critical elements (CE) acquired by age class for each of the focal offspring. Table 2 shows the relevant study subjects, the number of critical elements acquired by each age for each individual, and the average and range for each age class. If the seven mother's characteristics are each averaged across the 4 years of data collection, none are significant predictors of number of critical elements acquired by age 1.5. However, mother's time spent alone and with family was significantly (GLM: $F_{1,4}=3.06$, $n=6$, $p=0.04$, $r^2=0.70$) and positively correlated to the number of critical elements acquired by age 2.5. Sex was not significant (GLM: $F_{1,4}=5$, $n=6$, $p=0.09$, $r^2=0.56$), but followed previous results with females acquiring more critical elements by age 2.5 than males. None of mother's characteristics nor gender were significant at ages 3.5 or 4.5.

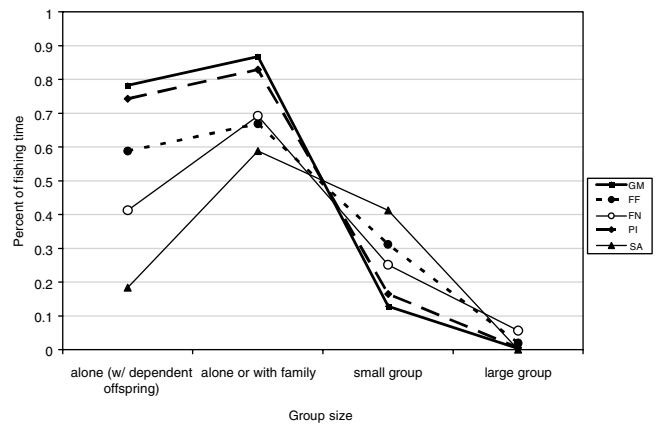


Fig. 3 Mother's percent of time spent termite-fishing in different sized groups. Lines represent five different mothers whose measures are summed over a 4-year period (1998–2001). Group sizes are: alone with dependent offspring, alone or with maternal family members, small group (<3 other unrelated adults), and large group (≥ 3 other unrelated adults)

Table 2 Study subjects for speed of acquisition

ID	Sex	Acquisition age	# CE age 1.5	# CE age 2.5	# CE age 3.5	# CE age 4.5
TZN	M	unknown	2	3	Unknown	Unknown
FU	M	3.5	3	3	5	5
SM	M	5.5	Unknown	2	3	4
TN	M	5.5	Unknown	Unknown	Unknown	4
GLT	F	2.5	2	5	5	5
GLD	F	2.5	3	5	5	5
FLR	F	3.5	2	3	5	5
Average (range)		3.8 (2.5–5.5)	2.4 (2–3)	3.5 (2–5)	4.6 (3–5)	4.67 (4–5)

Individuals are listed by their identification code (ID) and as either male (M) or female (F). The number of critical elements acquired by each age (# CE) is listed as well as the average and range at each age. “Unknown” denotes a year that was prior to the start of the study period (for SM and TN) or that did not occur before the end of the study (for TZN)

Averaging a mother’s time spent in different sized groups over the 4 years of the study may not be as accurate a gauge of her offspring’s learning opportunities as measuring her characteristics in a year that precedes or coincides with offspring performance. For that reason, I investigated mother’s time allocation characteristics (predictors 1–6, above) separately for each year prior to and during a year in which an offspring skill level was measured. For example, to predict number of critical elements (CE) acquired by age 2.5, I used combinations of mother’s characteristics at age offspring age 0.5, 1.5 and 2.5. The following is an example of a model used: # of CE by age 1.5=mother’s time alone at offspring age 0.5+mother’s time alone at offspring age 1.5.

No single year predictors or combinations significantly predicted differences in CE acquired by age 1.5. However, the model that best predicts the number of CE’s acquired by age 2.5 was: # of CE by age 2.5=mother’s time spent fishing in a small group at offspring age 1.5+mother’s time spent fishing alone at offspring age 2.5.

Both predictors were positively correlated with number of critical elements (time fishing in a small group at age 1.5: GLM: $F_{2,2}=72.99$, $n=5$, $p=0.01$; time fishing in alone at age 2.5: GLM: $F_{2,2}=39.92$, $n=5$, $p=0.02$; adjusted $r^2=0.96$).

For offspring in age class 3.5, the model that best predicts number of CE acquired was: # of CE by age 3.5=mother’s time alone or with family at offspring age 2.5+mother’s time alone or with family at offspring age 3.5.

Both predictors were positively correlated with number of critical elements (time alone or with family at age 2.5: GLM: $F_{2,2}=21.41$, $n=5$, $p=0.04$; time alone or with family at age 3.5: GLM: $F_{2,2}=28.85$, $n=5$, $p=0.03$; adjusted $r^2=0.91$).

The relationships among mother’s characteristics, offspring gender and offspring proficiency

Table 3 lists the study subjects, ages, sexes, the number of dips scored, and the proficiency for each individual used

Table 3 Study subjects (mothers and offspring) for proficiency models

ID	Mother’s ID	Age when scored	Sex	No. of dips scored	Proficiency (termites per dip)
Mothers					
FF	–	40–44	Female	179	1.22
FN	–	17–21	Female	659	1.62
SA	–	24–28	Female	529	1.96
PI	–	37–41	Female	782	1.20
GM	–	27–31	Female	606	1.91
Offspring					
GLD	GM	3.5	Female	119	0.87
GLT	GM	3.5	Female	284	0.85
FLR	FF	3.5	Female	107	0.44
FU	FN	3.5	Male	35	0.47
SM	SA	5.5	Male	381	0.39
TN	PI	7.5	Male	238	0.86
GA	GM	8.5	Female	312	1.18
FE	FF	9.5	Male	46	1.10
SR	SA	10.5	Female	338	1.48
GD	GM	10.5	Male	279	0.92
FO	FF	10.5	Male	54	0.72

Age when the individual was scored, sex, and number of dips scored are noted. Mothers were scored over a 4-year period, while of offspring were scored in their oldest year of observation

in the analyses. I used the same seven maternal characteristics listed earlier as potential predictors of offspring termite-fishing proficiency post-acquisition. In addition, I investigated any effects of offspring age and gender on proficiency. For general linear models, only data from the offspring's last (oldest) year was used. The age range of offspring included in the analyses was from 3.5 to 10.5 years old. Mother's characteristics were averaged over the 4 years to approximate the average amount of learning opportunities provided by a particular mother.

No maternal characteristics were significantly correlated with their offspring's proficiency. However, in other analyses on this data set, Lonsdorf et al. (2004) found that offspring age and sex (female) were significant positive predictors of termites gathered per dip when incorporated into a general linear model.

Social interactions at the termite mound

Due to the distinct sex difference in age of acquisition and proficiency found earlier, I investigated whether mothers have differential tolerance for female and male offspring. I classified offspring actions towards other individuals at the termite mound as either "active" or "passive." The category "passive" contained only one behavior: "watch." The category "active," therefore, encompassed every other behavior in Table 1 listed under social learning behaviors. The behavior of the recipient of the action was then categorized as "neutral" or "negative." For example, neutral behaviors would include allowing the offspring to watch or manipulate a tool. Negative behaviors would include avoiding the offspring's behavior by changing body position, or shoving the offspring away (see Table 4, see also video clip S1 in the electronic supplementary material). No recipient responses were categorized as positive because I saw no active effort on the part of recipients to facilitate the behavior of an offspring.

Figure 4 shows the rate of social interactions (# of interactions/minutes of observation) that involved a focal offspring and his/her mother by age and separately by sex. I used the rate of interactions because I was unable to equalize observation time on particular individuals (see section "Methods"). The polynomial trendlines in Fig. 4 show that females tended to initiate interactions with their mother at a slightly higher rate in the younger years. I then analyzed mothers' responses to offsprings' actions and found that almost all offsprings' actions are followed

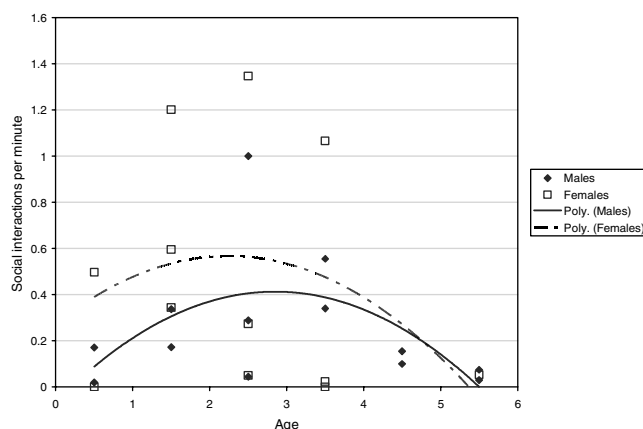


Fig. 4 Rate of social interactions with mother at the termite mound. Each data point represents an individual offspring's rate (interactions/minutes of observation at the mound) of interacting with his/her mother at a particular age. Data are shown separately for males and females. Polynomial trendlines corresponding to each sex are shown. (Supplementary 1. A youngster (left of screen) is seen interacting with her mother during a termite-fishing session. The youngster repeatedly attempts to steal termites from her mother's tool, which her mother tries to avoid (a negative response). Note that the mother makes no effort to facilitate the offspring's actions)

by the neutral reaction of "allow" by their mothers, and no sex difference exists. For male offspring, mothers respond neutrally to 85% of active actions and 99% of passive actions. For females, mothers respond neutrally to 86% of active actions and 99% of passive actions. Young chimpanzees also interacted with individuals other than their mothers at the termite mound. However, the vast majority of interactions (92%) occurred within the maternal family, with either mothers, siblings, or adult maternal relatives. Across all individuals at each age, offspring interacted with their mothers' for 67% percent of all social interactions.

Discussion

Individual differences among mothers

In this study, I investigated the potential effects of maternal characteristics on offspring acquisition of a complex tool-assisted foraging behavior known as termite-fishing. I found significant individual differences among mothers in both the percent of time they spent termite-fishing (Fig. 1a) and the percent of time they spent alone with only their dependent offspring (Fig. 1b). I used these two characteristics as indicators of differential opportunities for learning. Mother's time spent fishing can be viewed as the primary learning opportunity for a young chimpanzee, as offspring stay with their mothers continually until at least the age of 8. Mother's sociality represents the opportunity that offspring has to observe and learn from other individuals, which is purported to be an indicator of tool-use specialization in other apes (van Schaik et al. 2003). In addition, I found significant differences among some mothers in their termite-fishing proficiency (termites per dip).

Table 4 Names and definitions of mothers' behaviors scored as responses to a young chimpanzee's behavior

Behavior name	Category	Definition
Allow	Neutral	Allow whatever the focal is doing
Shove	Negative	Push focal away
Move	Negative	Move self away from focal
Avoid	Negative	Avoid behavior of focal by changing body position

Termite-fishing as a solitary activity

My analyses showed that termite-fishing is a relatively solitary activity for female chimpanzees with dependent offspring. Figure 3 illustrates this relationship and shows that females are most likely to be with just their dependent offspring or with dependent offspring and other maternal family members while at the termite mound. The maternal family effect results from the tendency of Gombe females to spend much of their time with their adult daughters and grandchildren, which was especially true for members of this study (FF with her daughter, PI with her daughters, and SA with her mother). As most of the termite mounds at Gombe are too small to permit use by more than four or five individuals at a time, the risk of competition at a termite mound is high if a large group is present. Maternal family dynamics appear to mitigate some of this competition and family members, in general, have non-competitive termite-fishing sessions. However, this correlation results in offspring having very few opportunities to observe individuals other than maternal relatives termite-fish. In fact, 92% of social interactions initiated by offspring was directed to maternal family members and even when non-relatives were at the mound, youngsters interacted with maternal family members.

The relationships among mother's characteristics, offspring speed of acquisition and proficiency

No maternal characteristic (time spent fishing, time spent alone, etc.) proved to have a significant relationship with coarsest measure of acquisition: offspring age. However, gender was significantly related to age of acquisition with females acquiring the skill at an earlier age than males. For finer measures of acquisition, none of the mother's characteristics show significant relationships with the number of critical elements (CE) acquired by age 1.5 if those characteristics are averaged over the 4-year course of the study. This is not surprising in light of the data displayed in Table 2 demonstrating that there were not extreme differences in the number of elements acquired by this age group (either 2 or 3). However, by age 2.5, extreme differences in skill level did exist and these were positively related to how much time mothers spent alone or with maternal family. None of the maternal characteristics showed significant relationships with offspring acquisition level at age 3.5 or 4.5. From these results, there appears to be limited evidence for the importance of learning opportunities provided by the mother on the acquisition speed of termite-fishing.

Averaging mother's characteristics over the 4 years of the study may not accurately gauge her offspring's learning opportunities, as mother's time allocation in individual years may profoundly affect her offspring's rate of acquiring the skill. Therefore, I further investigated the effects of mother's characteristics separately for each year prior to and coinciding with the year in which her offspring were assessed for acquisition rate. Again, no maternal characteristics were found to be significant at age 1.5, most likely for the reasons discussed earlier. However, at age 2.5, maternal

characteristics proved to be very important. The strongest positive correlates of number of critical elements acquired were (1) mother's time spent fishing in a small group 1 year prior (age 1.5), and (2) mother's time spent fishing alone in the coinciding year (age 2.5). For age 3.5, the strongest correlates were (1) mother's overall time spent alone or with family 1 year prior (age 2.5), and (2) mother's overall time spent alone or with family in the coinciding year (age 3.5). By age 4.5, no maternal characteristics are important because as Table 2 shows there are not extreme differences in acquisition level by this age. It is interesting to note that mother's overall time spent fishing was not a significant correlate; however, this measure may be confounded by the varying effects of termite-fishing in different sized groups (see later).

These results thus far seem contradictory: in order to acquire the critical elements of the skill in the timely manner, is it better to have a mother who fishes in a small group, a mother who fishes alone or a mother who spends most of her time alone? Figure 3 shows that mothers were more likely to be alone or with family when actually fishing. Therefore, the significant correlates for number of CE acquired by age 2.5 seem inconsistent: Mother's time spent fishing *in a small group* at age 1.5 and mother's time spent fishing *alone* at age 2.5. One possible explanation is that age 1.5 was the age during which offspring did more watching than any other behavior. By age 2.5, this was not the case and most of the focal offspring spent more time performing active elements like investigating the mound and manipulating tools (see [Lonsdorf in press](#)). Perhaps having other individuals present to observe in the primary "watching" age is beneficial, but once offspring spend more time actually performing elements of the skill, the presence of other individuals creates competition and is detrimental. In order to quantitatively test this, data would be required on the number of holes and tools available at the mound as compared to the number of individuals. Unfortunately, as holes are continually being uncovered and tools are continually being made, re-used and modified, this data is impossible to collect in the wild. An additional explanation could be that allocation by youngsters of their time at the termite mound is more important than simply the amount of time their mother is at the mound. Lonsdorf et al. (2004) showed that females spend significantly more time watching others at the termite mound than males, while males spend more time playing. Swifter acquisition may therefore depend more on time allocation rather than the length of time the learning opportunity is presented.

I found no relationship between any maternal characteristic and offspring proficiency (termites per dip). However, age and gender were significant, with older offspring and female offspring showing higher proficiency. The age result is not surprising as older individuals have had more "practice" with the skill. Proficiency most likely continues to increase from acquisition (2.5–5.5 years) through at least the early teens before final adult proficiency is achieved. Analyses of the proficiency of adult offspring may therefore show a more tight correlation with their mothers' proficiency. In addition, the lack of correlation between mother

and offspring characteristics in this study may be due to sex differences, given that female offspring are known to resemble their mother's termite-fishing technique (Lonsdorf et al. 2004). A larger sample size of male and female offspring across older age groups is needed to further clarify these results.

Mother–offspring interactions at the termite mound

In this study, the single most significant predictor of offspring age of acquisition and proficiency was not due to any maternal characteristic, but rather to sex of the offspring. In an unpublished doctoral dissertation, Gardner-Roberts (1999) found that mothers at Gombe showed no difference in maternal maintenance behaviors, such as initiating contact or facilitating suckling, to sons versus daughters in the first 5 years after birth. This is consistent with results from this study on maternal behavior at the termite mound. While females tended to initiate interactions with their mothers at slightly higher rate during the younger years (Fig. 4), mothers were not differentially tolerant to male and female offspring. Indeed, mothers responded neutrally to the vast majority of their offsprings' attempts to interact, whether the attempt was a passive one, such as watching or active, such as reaching for a tool. Therefore, it is unlikely that differential tolerances by mothers at the termite mound resulted in a more favorable situation for females to learn.

As active teaching is one of the most important components of social learning in most human societies, I looked for evidence of active teaching by mothers at the termite mound. In no instance did I see a mother actively facilitate her offspring's learning in any way. Mothers were oriented completely to the task of termite-fishing and rarely even made eye contact with offspring. A mother never offered a termite to her offspring, never handed her offspring a tool and never molded the offspring's behavior while fishing. Chimpanzee offspring were simply allowed to observe and occasionally "steal" a tool or a termite, sometimes resulting in a negative reaction from their mothers (see S1). Female chimpanzees are known to actively respond to their offspring solicitations of other foods and share food with them (Silk 1978). However, no active food-sharing occurred with termite-fishing, perhaps because animal protein is limited in the chimpanzee diet and therefore represents a highly prized food source (McGrew 1979). Despite Boesch's (1991) description of active demonstration of nut-cracking by a mother in the Tai forest, other studies have found little evidence of active teaching in apes. In 960 min of maternal feeding time in wild chimpanzees, Corp and Byrne (2002) found only one instance of a mother actively giving a section of fruit to her offspring. Furthermore, Ueno and Matsuzawa (2005) tested chimpanzee infant responses to novel foods in the presence of their mother and found no active interference on the part of mothers when their offspring attempted to eat novel food items. In a study on captive gorillas, Maestriperi et al. (2002) found little or no active encouragement by mothers to offspring outside

of the motor contexts of walking or climbing. More data need to be gathered but at this point, it appears that active teaching in apes is restricted to those who have been taught, such as symbol-trained captive apes (Fouts et al. 1989, Miles 1994).

In this study, I provide results from an investigation of maternal influences on offspring acquisition of a complex skill in wild chimpanzees to complement the work done in the laboratory by Hirata and Celli (2003). Due to the differing methodologies required by the wild and captive environments, not all results of the two studies can be compared. However, some important conclusions can be drawn. The acquisition of honey-fishing skills in the captive chimpanzees studied by Hirata and Celli occurred before the age of 2 in all three individuals. The earliest age of acquisition found in this study was 2.5, slightly later than in the captive work. As the authors noted, the honey-fishing task was likely easier than termite-fishing in that honey is immobile and harmless, whereas termites are not. In addition, through the use of clear bottles, the entire honey-fishing task could be observed by youngsters. In termite-fishing, much of the task is invisible as termite mounds are opaque and the relationships between tools and termites inside of the mound cannot be observed. The authors also noted that the captive subjects may have had more prolonged exposure to the task than is the norm in the wild. Over the 16 months in which two individuals were observed in Hirata and Celli's study, the total duration of sessions in which a youngster had the opportunity to observe others perform the skill was 3,360 min, or 56 h. For comparison, a mother who spends an average amount of time termite-fishing (9% of observation time—see Fig. 1a) provides 64.8 h of opportunity for her offspring to observe over the course of a 2-month termite-fishing season ($0.09 \times 12 \text{ h a day awake} \times 60 \text{ days of termite-fishing season}$). While the amount of time that youngsters have the opportunity to learn in the wild is slightly longer, it is possible that the truncated termite-fishing season (2 months) as opposed to shorter bouts over a longer period (16 months) results in the swifter acquisition we see in captivity. This would particularly be expected when the 2-month termite-fishing season coincides with the time that the youngster is still quite young and spending a majority of his/her time nursing and sleeping. Therefore, it is likely that the timing difference, combined with the visibility of the captive task and harmlessness of honey explains the differences in acquisition we see between captivity and the wild.

Hirata and Celli (2003) provided 20 different objects as potential tools and found that offspring preferentially used the two items that their mothers most frequently used. In this study, providing different tool materials was not possible due to the strict observational policy that governs research at Gombe. However, Lonsdorf et al. (2004) did find that female offspring preferred to insert tools of similar length to the ones their mothers' used. Taken together, the tool choice results from these studies demonstrate the importance of observing others to develop the specifics of tool-use techniques.

Finally, this study complements the major conclusion of Hirata and Celli (2003) and provides additional evidence

from the wild for the “education by master–apprenticeship” model of skill learning in chimpanzees. Mothers and maternal family members showed high levels of tolerance for youngsters’ attempts to learn at the termite mound, even when this learning took the form of actively reaching for a tool or termite, as opposed to more passive watching. However, active instruction on the part of mothers or other individuals was not observed. Consistent with this is that in some traditional human societies, much learning of skills is done by passive observation (Hewlett and Cavalli-Sforza 1986; Greenfield et al. 2000) suggesting that the evolutionary history of learning in apes and humans shares important similarities. While studying the transmission mechanisms of learned behaviors in wild animal communities is difficult and interpretations are complicated by a lack of experimental controls, future experimental studies would benefit from manipulating learning situations to more closely mimic what is observed in the wild.

Acknowledgements I thank A. Pusey, L. Eberly, J. Goodall and E. Lonsdorf for invaluable assistance during this study. S. Hirata and S. Ross and three anonymous reviewers provided careful critiques of earlier versions of the text. I thank the Jane Goodall Institute (JGI), especially the JGI Center for Primate Studies, the Gombe Stream Research Centre, the Gombe National Park staff, the Government of Tanzania, Tanzania National Parks, Tanzania Commission for Science and Technology and Tanzania Wildlife Research Institute for valuable support with carrying out this research. Kadahaa John, Shadrack Kamenya and Anthony Collins provided essential assistance with field collection of data. This work was supported by the National Science Foundation, the L.S.B. Leakey Foundation, the Wenner-Gren Foundation, and the University of Minnesota Graduate School. All research performed for this study complied with the relevant laws of Tanzania and the United States of America

References

- Altmann J (1974) Observational study of behavior: sampling methods. *Behavior* 49:227–264
- Benskin CMH, Mann NI, Lachlan RF, Slater PBJ (2002) Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Anim Behav* 64:823–828
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T (2003) Cultural innovation and transmission of tool-use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6:213–223
- Boesch C (1991) Teaching among wild chimpanzees. *Anim Behav* 41:530–532
- Cadiou N, Cadiou J-C (2002) Is use of a novel food source by young canaries (*Serinus canaries*) influenced by the sex and familiarity of the adult demonstrator? *Behavior* 139:825–846
- Chalmeau R, Gallo A (1993) Social constraints determined what is learned in the chimpanzee. *Behav Proc* 28:173–180
- Choleris E, Guo C, Liu J, Mainardi M, Valsecchi P (1997) The effect of demonstrator age and number on duration of socially-induced food preferences in the house mouse (*Mus domesticus*). *Behav Proc* 41:69–77
- Corp N, Byrne RW (2002) The ontogeny of manual skill in wild chimpanzees: evidence from feeding of the fruit of *Saba florida*. *Behaviour* 139:137–168
- Fouts R, Fouts D, van Cantfort TE (1989) The infant Loulis learns signs from cross-fostered chimpanzees. In: Gardner RA, Gardner BT, van Cantfort TE (eds) Teaching sign language to chimpanzees. State University of New York Press, New York, pp 280–290
- Galef BG Jr, Rudolf B, Whiskin EE, Choleris E, Mainardi M, Valsecchi P (1998) Familiarity and relatedness: effects on social learning about foods by Norway rats and Mongolian gerbils. *Anim Learn Behav* 26:48–454
- Gardner-Roberts D (1999) The energetics and sociality of female chimpanzees: with special reference to mothers and infants. Doctoral dissertation, Cambridge University
- Goodall J (1967) Mother–offspring relationships in chimpanzees. In: Morris D (ed) Primate ethology. Weidenfeld and Nicolson, London, pp 287–346
- Goodall J (1968) The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Anim Behav Mono* 1:161–311
- Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge
- Greenfield PM, Maynard AE, Boehm C, Schmidtling EY (2000) Cultural apprenticeship and culture change: tool learning and imitation in chimpanzees and humans. In: Parker ST, Langer J, McKinney ML (eds) Biology, brains and behavior—the evolution of human development. School of American Research Press, Santa Fe, NM, pp 237–277
- Hewlett BS, Cavalli-Sforza LL (1986) Cultural transmission among Aka pygmies. *Am Anthropol* 88:922–934
- Hirata S, Celli ML (2003) Role of mothers in the acquisition of tool-use behaviors by captive infant chimpanzees. *Anim Cog* 6:235–244
- Kitchener AC (1999) Watch with mother: a review of social learning in the Felidae. In: Box HO, Gibson KR (eds) Mammalian social learning: comparative and ecological perspective. Cambridge University Press, Cambridge, pp 236–259
- Lee PC, Moss CJ (1999) The social context for learning and behavioural development among wild African elephants. In: Box HO, Gibson KR (eds) Mammalian social learning: comparative and ecological perspective. Cambridge University Press, Cambridge, pp 102–125
- Lonsdorf EV, Pusey AE, Eberly L (2004) Sex differences in learning in chimpanzees. *Nature* 428:715–716
- Lonsdorf EV (in press) Sex differences in the development of termite-fishing skills in wild chimpanzees (*Pan troglodytes schweinfurthii*) of Gombe National Park, Tanzania. *Anim Behav*
- Maestriperi D, Ross SK, Megna NL (2002) Mother–infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): spatial relationships, communication, and opportunities for social learning. *J Comp Psychol* 116:219–227
- Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G (2001) Emergence of culture in wild chimpanzees: education by master–apprenticeship. In: Matsuzawa T (ed) Primate origins of human cognition and behavior. Springer, Tokyo Berlin Heidelberg, pp 557–574
- McGrew WC (1979) Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg DA, McCown ER (eds) The Great Apes. Benjamin Cummings, London, pp 441–463
- McGrew WC (1992) Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge
- McGrew WC, Marchant LF (1999) Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates* 40:509–513
- Miles HL (1994) MECHANTEK: the development of self-awareness in a signing orangutan. In: Parker ST, Mitchell RW, Boccia ML (eds) Self-awareness in animals and humans: developmental perspectives. Cambridge University Press, New York, pp 254–272
- Milton K (1981) Distribution patterns of tropical plant foods as a stimulus to primate mental development. *Am Anthropol* 83:534–
- Nicol CJ, Pope SJ (1999) The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Anim Behav* 57:163–171
- Pusey AE (1983) Mother–offspring relationships in chimpanzees after weaning. *Anim Behav* 31:363–377
- Pusey AE (1990) Behavioural changes at adolescence in chimpanzees. *Behaviour* 115:203–246
- Silk J (1978) Patterns of food sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. *Fol Primatol* 31:191–141

- Swaney W, Kendal J, Capon H, Brown C, Laland K (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. *Anim Behav* 62:591–598
- Ueno A, Matsuzawa T (2005) Response to novel food in infant chimpanzees. Do infants refer to mothers before ingesting food on their own? *Behav Proc* 68:85–90
- van Schaik CP, Fox EA, Fechtman LT (2003) Individual variation in the rate of use of tree-hole tools among wild orangutans: implications for hominin evolution. *J Hum Evol* 44:11–23
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682–685