Anim Cogn (2009) 12 (Suppl 1):S115–S125
DOI 10.1007/s10071-009-0278-0

ORIGINAL PAPER

Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): acquisition patterns and handedness

Cláudia Sousa · Dora Biro · Tetsuro Matsuzawa

Received: 28 April 2009 / Revised: 6 August 2009 / Accepted: 8 August 2009 / Published online: 21 August 2009

Abstract Chimpanzees (*Pan troglodytes*) are known to make and use a variety of tools, activities which require them to employ their hands in a skilful manner. The learning process underlying the acquisition of tool-using skills, and the degree of laterality evident in both immature and mature performers are investigated here focusing on the use of leaves for drinking water by members of the Bossou chimpanzee community in Guinea, West Africa. In addition, comparisons are drawn between the present findings and our previous data on the cracking of oil-palm nuts (*Elaeis guineensis*) using stone tools by members of the same community. The use of leaves for drinking water emerges approximately 2 years earlier than nut cracking, at around the age of 1.5 years, although the manufacture of leaf tools begins only at 3.5 years of age. In addition, in clear contrast with nut cracking, the majority of chimpanzees are ambidextrous in their use of leaves, with only certain individuals showing a bias for one hand. We discuss possible explanations for the earlier emergence and increased ambidextrousness that characterises leaf-tool use in comparison with other forms of tool use by wild chimpanzees. In summary, our results provide the first detailed description of the acquisition process underlying leaf-tool use along with the accompanying patterns of handedness, while also being the first to provide comparisons of the development of different forms of tool use within the same wild chimpanzee population.

Keywords Chimpanzees (*Pan troglodytes verus*) · Tool use · Drinking water with leaves · Learning · Laterality

This contribution is part of the Supplement Issue "The Chimpanzee Mind" (Matsuzawa 2009).

C. Sousa
CRIA, Centre for Research in Anthropology,
Lisbon, Portugal

C. Sousa (✉)
Department of Anthropology,
Faculty of Social and Humane Sciences,
New University of Lisbon, Avenida de Berna,
26-C, 1069-061 Lisbon, Portugal
e-mail: csousa@fcsh.unl.pt

D. Biro
Animal Behaviour Research Group,
Department of Zoology, University of Oxford,
Oxford, UK

T. Matsuzawa
Primate Research Institute, Kyoto University,
Kyoto, Japan

Introduction

Chimpanzees are known to make and use a variety of tools, in both subsistence and non-subsistence activities (McGrew 1992; Whiten et al. 1999). Such tool use activities are assumed to be transmitted culturally between communities and across generations (Matsuzawa and Yamakoshi 1996), that is, they are learned from others who are more proficient than the novice (McGrew 2004). Nevertheless, only a few studies have explored the acquisition process underlying tool use behaviours in wild chimpanzees. Those that exist have focused on nut cracking (Inoue-Nakamura and Matsuzawa 1997; Matsuzawa 1994, 1999, Biro et al. 2003, 2006), termite fishing (Lonsdorf et al. 2004, Lonsdorf 2005, 2006), ant dipping (Humle 2006), and the use of leaves for drinking water (Tonooka 2001; Biro et al. 2006).

As tool use is an activity that requires the use of hands in a skilful manner, manual dexterity, at least as reflected in increased frequency and proficiency in the use of the tool, is likely to progressively improve during the process of learning. Related to the refinement of manual actions is the question of "handedness": is an increasing degree of lateralisation part of the acquisition process? The few studies that have investigated laterality in tool use show that the majority of individuals are lateralised to one side or the other (Boesch 1991; Humle and Matsuzawa 2009; Lonsdorf and Hopkins 2005; Matsuzawa et al. 2001, McGrew and Marchant 1996; McGrew et al. 1999; see Marchant and McGrew 2007 for a recent summary). However, ant fishing at Mahale, Tanzania, appears to be a non-lateralised activity (Marchant and McGrew 2007), although potentially small sample sizes in the case of some individuals may leave these data inconclusive.

The scarcity of such studies may be due to the difficulties involved in conducting systematic direct observations on chimpanzees performing tool-use activities in the wild. Not all tool-use behaviours are frequent enough to allow researchers to accumulate sufficient data for in-depth analyses, and many may be seasonal or difficult to observe due to the nature of the chimpanzees' habitat. For these reasons, an "outdoor laboratory" was established in the home range of the chimpanzee community at Bossou, Guinea, which increased individual group members' opportunity to perform the behaviours, as well as researchers' chances of observing them (Matsuzawa 1994, 2009). As a result, we now have extensive annual records on various tool-using activities from every member of the Bossou community, spanning many years. The majority of these data focus on leaf tool use and nut cracking.

Wild chimpanzees are known to use leaves for drinking rain water from tree holes (Boesch and Boesch 1990; Ghiglieri 1984; Goodall 1968; McGrew 1977, 1992; Nishida 1990; Quiatt and Kiwede 1994; Sugiyama 1993, 1995; Tonooka et al. 1994; Wrangham 1992). Although this behavioural pattern has been observed at all long-term chimpanzee research sites, the precise technique used varies considerably across populations. Chimpanzees have been observed to drink water using 'sponges' made of leaves (Goodall 1968; McGrew 1977, 1992), 'leaf spoons' (Goodall 1968; McGrew 1977; Sugiyama 1995), and more recently, using a technique referred to as 'leaf folding' (Tonooka et al. 1994). The latter has been described in detail only for the chimpanzees of Bossou, Guinea, who use this technique more than any other form of the behaviour, preferring the leaves of *Hybophrynum braunianum* as the raw material for the tool (Tonooka 2001). Tools are manufactured prior to use by collecting a clump of fresh leaves and folding them inside the mouth, roughly in the shape of an accordion. The finished tool is then dipped into a tree hole, retrieved, and put inside the mouth, such that the water it carries can be drunk. The sequence is then repeated, reusing the same tool several times.

Although nut-cracking behaviour has also been observed in one other non-human primate species (e.g. bearded capuchin monkeys, Visalberghi et al. 2007), in chimpanzees it is restricted to West African communities (*P. t. verus*: Anderson et al. 1983; Biro et al. 2003, 2006; Boesch and Boesch 1983; Boesch et al. 1994; Carvalho et al. 2007; Matsuzawa 1994; McGrew et al. 1997, Sugiyama and Koman 1979; *P. t. vellerosus*: Morgan and Abwe 2006), even though there are nuts and stones available in the habitats of Central and East African populations. The behaviour, as performed at Bossou, involves the use of a pair of moveable stones as hammer and anvil, to extract the nutritious kernel of hard-shelled oil-palm nuts.

Our aim in the present paper is to draw together our recent data on the use of leaves for drinking water, focusing in particular on two aspects of the behaviours: the learning process underlying the acquisition of the skill, and the degree of laterality evident in both immature and mature performers. We also draw comparisons with the cracking of oil-palm nuts, within individual wherever possible, and offer hypotheses on the underlying causes of the differences observed with regard to developmental aspects and patterns of lateralisation.

Methods

Subjects and study site

Behavioural observations involved members of the chimpanzee community at Bossou (7°39′N, 8°30′W), situated in Guinea, West Africa, about 6-km north-west of the foot of the Nimba Mountains, near the country's border with Côte d'Ivoire and Liberia. This community has been studied since 1976 (Sugiyama and Koman 1979), and was habituated towards human observers without being provisioned with food. Since the start of the field project the size of the community has varied between 12 and 23 individuals. The core area of the community's range encompasses 5–6 km^2 composed of primary and secondary forest surrounded on all sides by dry savannah which the chimpanzees have never been seen to traverse.

Table 1 shows the group composition in each season of the present study. Individuals' ages ranged from 14 months to 53 (estimated) years, and they were divided into four age classes: adults (more than 11 years old), adolescents (between 8 and 10 years), juveniles (between 4 and 8 years), and infants (<4 years) (Table 1). All group members were recognised individually.

Data collection

Observations were carried out in a small clearing in the forest ("outdoor laboratory"; Matsuzawa 1994) located on the

Table 1 Composition of the wild chimpanzee community at Bossou in each field season of the present study

Name	Sex	Birth	Jan 2000		Jan 2003		Jan 2005		Jan 2006	
			Age (y:m)	Age class	Age (y:m)	Age class	Age (y:m)	Age class	Age (y:m)	Age class
Fana	♀	~1956	43	1	46	1	48	1	49	1
Fanle	♀	1997 Oct	2:3	4	5:3	3	7	3	8	2
Foaf	♂	1980 late	19	1	22	1	24	1	25	1
Fokaiye[a]	♂	2001 July	–	–	1:6	4	–	–	–	–
Fotayu[a]	♀	1991 mid	8	2	11	1	–	–	–	–
Jeje	♂	1997 Dec	2:1	4	5:1	3	7:1	3	8	2
Jimatou[b]	♂	2002 Oct	–	–	0:3	4	–	–	–	–
Jire	♀	~1958	41	1	44	1	46	1	47	1
Joya	♀	2004 Sep	–	–	–	–	0:4	4	1:4	4
Juru[c]	♀	1993Nov	6:2	3	–	–	–	–	–	–
Kai[b]	♀	~1950	49	1	52	1	–	–	–	–
Nina[b]	♀	~1954	46	1	49	1	–	–	–	–
Nto[c]	♀	1993 early	7	3	–	–	–	–	–	–
Pama	♀	~1967	32	1	35	1	37	1	38	1
Peley	♂	1998 Apr	1:9	4	4:9	3	6:9	3	7:8	3
Pili[c]	♀	1987 early	12	1	–	–	–	–	–	–
Pokru[c]	♂	1996 Aug	3:5	4	–	–	–	–	–	–
Poni[b]	♂	1993 Feb	6:11	3	9:11	2	–	–	–	–
Tua	♂	~1957	45	1	48	1	50	1	51	1
Velu	♀	~1959	40	1	43	1	45	1	46	1
Veve[b]	♀	2001May	–	–	1:8	4	–	–	–	–
Vuavua[a]	♀	1991 mid	8	2	11	1	–	–	–	–
Yo	♀	~1961	38	1	41	1	43	1	44	1
Yoro	♂	1991 mid	8	2	11	1	13	1	14	1

Age classes: *1* adult (11 years and above), *2* adolescent (8–10 years), *3* juvenile (4–7 years), *4* infant (<4 years); age presented in years and months (y:m)

[a] Individual disappeared in 2004

[b] Individual confirmed dead

[c] Individual disappeared by 2001

summit of Mont Gban, south of the village of Bossou (Fig. 1). The clearing was roughly rectangular, 7 × 20 m, with dense forest on three sides, and a wall on the fourth constructed from branches and leaves behind which the experimenters hid, out of view of the chimpanzees. Several paths used regularly by the chimpanzees to traverse Mont Gban converged in this clearing, such that parties of chimpanzees visited the outdoor laboratory regularly, on average once a day. A hole with two openings (front and side) was made in the trunk of a tree (*Richinodendron heudelotii*; located at the back of the outdoor laboratory, Fig. 1) and was refilled to the rim with water (approximately 17.5 l) after each visit by chimpanzees to provide fresh water and to monitor the quantity consumed by individuals. When cut in 1999, the front opening was 150-mm-wide and 220-mm-high, and the side opening was 130-mm-wide and 160-mm-high. Both openings shrank in subsequent years (the front opening, for example, down to 85 × 185 mm by 2002); when either became too small for the hands of adult chimpanzees to reach through easily, they were enlarged again. No leaves were provided by the experimenters, such that chimpanzees had to use the vegetation available in the surrounding environment, as under fully natural conditions.

Stones (a set of around 50) were permanently available at the outdoor laboratory during each period of study, and *Elaies guineensis* nuts (presented in several small piles; see Biro et al. 2003 for further methodological detail) were also replaced after each chimpanzee visit. When water, stones and nuts were made available by the experimenters, the chimpanzees passing through the outdoor laboratory stopped to drink and nut crack in the majority of cases.

Through the years, we recorded the use of leaves and nut-cracking ability (or lack thereof) in every member of the community along with the identity of the hand used to hold the tool while performing the behaviour. Data were collected in the dry season, December to February, over a total of 20–30 h of observation each year. Although nut cracking with stones has been studied continuously since 1988, the data on the use of leaves for drinking water reported here correspond to four field seasons: January 2000, 2003, 2005 and 2006. All chimpanzee visits to the outdoor laboratory were captured on videotape, using Sony DCR-TRV20 and Sony DCR-TRV9 digital cameras. Leaf tools were collected over one field season (December 2003), and systematic measurements (weight, size and quantity of water carried) were obtained, along with

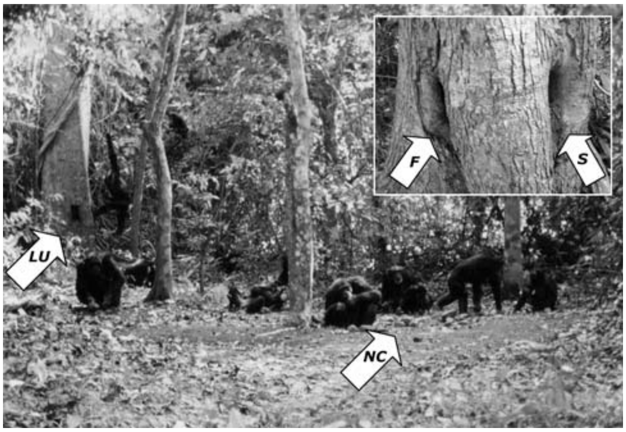

Fig. 1 The outdoor laboratory set-up at the top of Mont Gban, located within the Bossou chimpanzees' home range. The *arrow* labelled LU shows the location of the drinking tree, *Richinodendron heudelotii*, which contains a treehole filled with water. A chimpanzee can be seen drinking water from the hole with a tool made from leaves. Concurrently, several chimpanzees are cracking nuts (*arrow* labelled NC) with a pair of stones at another location within the outdoor laboratory. The *inset* in the *top right* shows a close up of the *Richinodendron heudelotii* tree used in the present study with the two openings of the treehole indicated by *F* (front opening) and *S* (side opening)

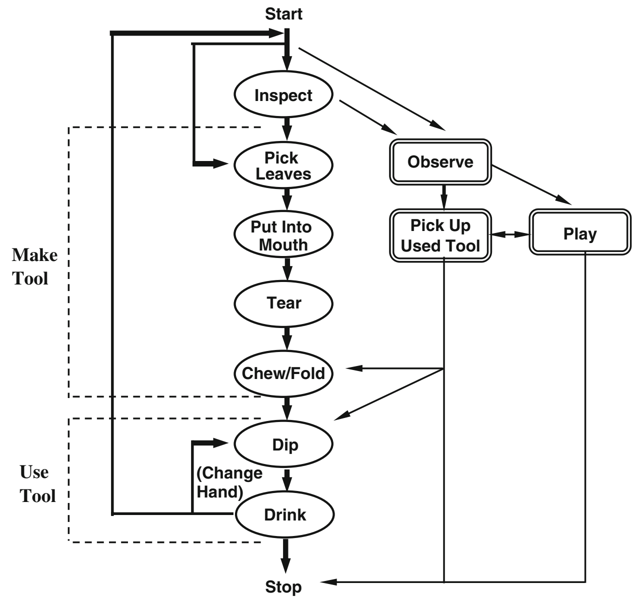

Fig. 2 Flow chart of the behaviours performed by chimpanzees during the making and use of leaf tools to drink water (*thick arrows*). Three other behavioural patterns that can occur during this tool-using context were also included (*right side* of the *flow chart*). See main text for details of each behavioural element

information about tool-user identity, whenever possible. Subsequent video analysis of the use of leaves for drinking water was conducted by CS to collect further detailed information concerning developmental changes and handedness.

On the basis of both video recordings and ad libitum observations, we gathered laterality data in hand use for the leaf-dipping action (see ethogram at the beginning of the "Results" section). Only independent bouts of the leaf-dipping behaviour were recorded, rather than every manual action. A bout of leaf-tool use for drinking water was defined as a period during which an individual was performing the tool-using behaviour (Humle and Matsuzawa 2009) with the following possible start and end points: a bout was said to have commenced when the subject started dipping a leaf tool in the water and ended when the subject moved away, changed hands during the dip action or moved from one opening in the tree to the other (in the latter two cases a new bout was said to have begun).

Results

To better understand the process of acquisition and development of leaf-tool use, we produced an ethogram of the behaviours involved, based on the data collected both from our video records and from in situ observations. Figure 2 presents a flow chart incorporating both major phases of this tool-use pattern (tool manufacture and tool use), allowing us to highlight which behaviours are characteristic of individuals in different age classes.

Ethogram

Inspect	the individual approaches the tree hole and looks inside
Pick leaves	the individual plucks fresh leaves from a tree or bush by hand
Put in mouth	the individual transfers the leaves into the mouth
Tear	the individual tears parts of the leaves out using a combination of teeth and hand
Chew/fold	the individual uses movements inside the mouth to fold or to rumple the leaves to produce the finished drinking tool
Dip	the individual inserts the drinking tool into the water, then retrieves it
Drink	the individual inserts the tool into the mouth and drinks the water it carries
Observe	the individual pays close attention to the actions of other individual(s) either during the process of making or using the drinking tool
Pick up used tool	the individual picks up from the ground or from inside the tree hole a tool previously used by another individual
Play	the individual plays alone or with other individuals in the immediate vicinity of the tree, or with the water contained within the tree

An adult chimpanzee performing the behaviour will start by inspecting the water inside the tree hole. She will then pick a number of leaves from a tree or bush with one hand, and put these inside her mouth. With her teeth and hand she will tear off parts of the leaves (often the petioles), and finally, with the help of jaw and tongue movements (resulting in either a chewed or a folded clump of leaves) produce the finished tool. This completes the first, tool-manufacturing phase.

In the second, tool-using phase, the chimpanzee will perform the action of leaf dipping: the tool is submerged into the water with one hand and then removed and taken to the mouth, thus allowing the individual to drink the water carried. During this phase, the individual may alternate the use of her hands to perform the dipping action. Besides this typical progression, three further behaviours are relevant. Chimpanzees can observe other individuals performing the behaviour, pick up leaf tools already used and abandoned by other individuals, or play in the immediate vicinity of the tree. Developmental differences are evident in the performance of these latter three behaviours, as described further below.

Development of leaf-tool manufacture and use

The youngest individual observed to successfully drink water with the aid of leaves was 1.5 years old (Table 2). However, it is important to note that the leaf tools used by young infants are not their own—instead they use leaf tools previously made and discarded by older individuals. Only at the age of 3.5 years do young chimpanzees start to use leaf tools that they themselves manufactured, while also continuing to use those discarded by fellow group members for several more years (Table 3).

Table 2 Age (years:months) at which chimpanzees first performed two different tool-using behaviours: drinking water with the aid of leaves (LU) and nut cracking (NC)

Name	Sex	Leaf use (LU)	Nut cracking (NC)
Fanle	♀	1:3–2:3	2:4–4:4
Fokaiye	♂	1:5	No NC before disappearance (3:4)
Jeje	♂	2:1–4:1	6:1–7:1
Jimatou	♂	No LF before death (1:2)	No NC before death (1:2)
Joya	♀	1:5	No NC yet (3:3)
Peley	♂	1:9–3:9	1:9–3:9
Pokru	♂	1:5–2:5	No NC before disappearance (4:1)
Veve	♀	1:7	No NC before death (2:7)

Ranges are given in cases when the behaviour first appeared between two consecutive periods of observation, single figures when the behaviour appeared during a particular period of observation

The NC data are from Biro et al. 2003 and 2006

Table 3 Use of leaf tools (made and discarded by other individuals, or made by self) by chimpanzees in different age classes

Age class	Use	Use discarded tool	Make and use own tool
Adult			
11–	Yes	No	Yes
Adolescent			
8–10	Yes	No	Yes
Juvenile			
5–7	Yes	Yes	Yes
Infant			
3–4	Yes	Yes	Yes
2–3	Yes	Yes	No
1–2	Yes	Yes	No
0–1	No	No	No

Nevertheless, during this approximately 2-year period (1.5–3.5 years of age) infants do begin to manufacture their own leaf tools, albeit without succeeding to make usable tools. Failures are due mainly to using inappropriate raw material: sometimes infants gather very small leaves resulting in a tool that falls apart, while at other times they gather dry leaves from the ground that crumble into small pieces straight away. Despite these early attempts at tool manufacture, we did not observe infants younger than 3.5 years using the resulting tools for drinking water. Instead, they soon discarded them and returned to using tools made and abandoned by older individuals.

That young chimpanzees may benefit from using such discarded tools is also supported by our analysis of the efficiency of leaf tools made by individuals in different age groups. By collecting leaf tools immediately after the end of chimpanzee visits to the outdoor laboratory, we were able to measure both their weight and water-carrying capacity. The latter was assessed by experimenters dipping the tools in a bucket of water ten times consecutively, and then squeezing them over a measuring jug. Figure 3 shows that leaf tools manufactured by juveniles and adolescents tend to be smaller and tend to carry a smaller volume of water per dip than those of adults—suggesting that there is an advantage to be gained for younger chimpanzees in using leaf tools manufactured by adults.

Handedness and development

We calculated a handedness index (HI) score for each individual observed to use leaf tools at the outdoor laboratory, based on bouts of leaf-dipping action. The index was calculated by subtracting the number of left handed from the number of right-handed dipping bouts and dividing by the total number of bouts: HI = $(R - L)/(R + L)$. Thus, resulting

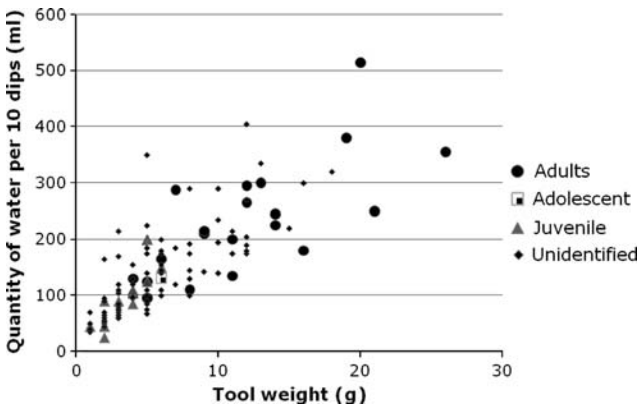

Fig. 3 Average quantity of water carried by particular leaf tools as function of their weight. Wherever possible, tools were assigned to the individual who manufactured them; these individuals were in turn categorised by age group. Data are from the 2003 field season

positive values reflect a right-hand bias, whereas negative HI scores indicate a left-handed bias. In addition, subjects were classified with regard to their handedness using a two-tailed binomial test based on bouts. The level of significance was set at $\alpha = 0.05$ (see Table 4 for more details).

Our records of leaf-tool use reveal little individual-level laterality. Figure 4 shows individual hand preference based on bouts of leaf dipping, combining data from all four field seasons. Of the 24 chimpanzees, two infants were never observed drinking water during the study period, and for one infant (Veve), we recorded only a single episode. Of the remaining 21 individuals, only three adults showed exclusive use of one hand, although these results are based on the extremely small sample sizes (Nina: 5, Kai: 2, and Fana: 6 episodes). The remaining 18 individuals were observed to use both the left and the right hand for the leaf-dipping action, with only four showing a clear preference for one of the hands (two-tailed binomial test, $P < 0.01$; Fig. 4).

Did the use of both hands for leaf dipping result from alternation between hands while drinking at the same tree hole or from changing hands when moving from one opening of the tree hole to the other? Juveniles were the ones most likely to change hands during or between leaf-dipping bouts, followed by adolescents (Fig. 5). Although adults also changed hands to dip, they did so much less frequently. Regarding the use of the two openings of the tree hole (front or side), juveniles were also the ones who alternated most frequently between the holes (Fig. 5). This behaviour is reminiscent of the elevated levels of hammer or anvil changes during bouts of nut cracking in younger performers (Carvalho et al. 2008)—adults are much more likely to continue to use the same hammer–anvil set throughout a bout.

In only 11 (16.2% of all cases of hand change by juveniles) of the 26 episodes in which the juveniles changed holes, this was also followed by the changing of hands. In adolescents this happened in 5 out of 12 episodes of changing holes (15.6% of all cases of hand change by adolescents), and 1 out of 2 episodes for adults (3.3% of all cases of hand change by adults). The only two episodes of hand change in infants also took place after changing holes, although they were also observed changing holes twice without changing hands.

Figure 6 shows the distribution of hand use as a function of which opening of the tree hole individuals were using. Adults exhibited a tendency to use the right hand when leaf dipping at the front opening of the tree hole, and to use the left hand when leaf dipping at the side opening. Four out of five adults for whom there was sufficient data used their right hand more often at the front hole than at the side hole (Chi-squared test: $\chi^2 = 13$, $df = 1$, $P < 0.001$; $\chi^2 = 9.56$, $df = 1$, $P = 0.002$; $\chi^2 = 20.251$, $df = 1$, $P < 0.001$; $\chi^2 = 6.321$, $df = 1$, $P = 0.012$). Only one of the two adolescents considered used the left hand when leaf dipping at the side opening of the tree hole ($\chi^2 = 6.718$, $df = 1$, $P = 0.009$). Likewise, juveniles did not seem to show a preference for using either hand when leaf dipping at the front opening, but showed a slight preference for the left hand when leaf dipping at the side opening. Two out of three juveniles used their left hand more often at the side hole ($\chi^2 = 11.26$, $df = 1$, $P < 0.001$; $\chi^2 = 26.077$, $df = 1$, $P < 0.001$). For infants, data are not sufficient to draw conclusions.

Discussion

The use of leaves for drinking water has been considered a less complex form of tool use than the use of a pair of stones as hammer and anvil to crack open nuts. Matsuzawa (1996) has proposed a way of classifying tool use according to its complexity; drinking with the aid of a leaf tool constitutes "level 1" tool use and nut cracking constitutes "level 2" tool use. Levels here are defined on the basis of the number of constituent elements that are combined during tool use: for leaf tools the number of objects is two (leaf tool and water) while in nut cracking three objects are related in succession (anvil, nut and hammer). This classification is in line with our findings that young chimpanzees begin to perform leaf drinking at the age of 1.5 years, while nut cracking only appears at the age of 3.5 years at the earliest (Inoue-Nakamura and Matsuzawa 1997; Biro et al. 2003)—more complex behavioural patterns are likely to appear later in development. In addition, laboratory results on the development of different types of object manipulation in infant chimpanzees may provide a clue to explaining disparities in timing during the development of various tool-use behaviours in the wild. Different forms of tool use require essentially different actions: for leaf-tool use, individuals must

Table 4 Handedness in the dipping action during the use of leaves for drinking water

Name	Sex	Jan 2000				Jan 2003				Jan 2005				Jan 2006			
		Left	Right	Hi	Handedness	Left	Right	Hi	Handedness	Left	Right	Hi	Handedness	Left	Right	Hi	Handedness
Fana	♀	0	4	1.00	Ar	0	0	–	X	0	2	1.00	*i*	0	0	–	X
Fanle	♀	1	2	0.33	A	28	19	−0.19	A	1	12	0.85	r	11	21	0.31	Ar
Foaf	♂	6	2	−0.50	A	3	0	−1.00	*i*	0	1	1.00	*i*	1	8	0.78	r
Fokaiye	♂	–	–	–	–	0	0	–	x	–	–	–	–	–	–	–	–
Fotayu	♀	10	19	0.31	Ar	5	27	0.69	r	–	–	–	–	–	–	–	–
Jeje	♂	0	0	–	x	44	24	−0.29	l	15	5	−0.50	l	35	22	−0.23	Al
Jimatou	♂	–	–	–	–	0	0	–	x	–	–	–	–	–	–	–	–
Jire	♀	5	10	0.33	A	4	16	0.60	r	5	1	−0.67	A	14	1	−0.87	l
Joya	♀	–	–	–	–	–	–	–	–	0	0	–	x	4	4	0.00	A
Juru	♀	5	27	0.69	r	–	–	–	–	–	–	–	–	–	–	–	–
Kai	♀	0	2	1.00	*i*	0	0	–	X	–	–	–	–	–	–	–	–
Nina	♀	0	1	1.00	*i*	0	4	1.00	r	–	–	–	–	–	–	–	–
Nto	♀	3	7	0.40	A	–	–	–	–	–	–	–	–	–	–	–	–
Pama	♀	0	0	–	X	2	3	0.20	A	2	0	−1.00	*i*	2	1	−0.33	A
Peley	♂	0	0	–	x	9	12	0.14	A	9	5	−0.29	A	18	22	0.10	A
Pili	♀	2	4	0.33	A	–	–	–	–	–	–	–	–	–	–	–	–
Pokru	♂	2	1	−0.33	A	–	–	–	–	–	–	–	–	–	–	–	–
Poni	♂	2	2	0.00	A	4	1	−0.60	A	–	–	–	–	–	–	–	–
Tua	♂	3	4	0.14	A	3	4	0.14	A	0	1	1.00	*i*	0	0	–	X
Velu	♀	0	0	–	X	1	1	0.00	A	0	0	–	X	0	1	1.00	*i*
Veve	♀	–	–	–	–	0	1	1.00	*i*	–	–	–	–	–	–	–	–
Vuavua	♀	3	1	−0.50	A	8	9	0.06	A	–	–	–	–	–	–	–	–
Yo	♀	3	1	−0.50	A	0	1	1.00	*i*	0	2	1.00	*i*	1	1	0.00	A
Yoro	♂	3	14	0.65	r	0	9	1.00	r	1	4	0.60	A	8	13	0.24	A

Handedness: *L* always uses left hand, *R* always uses right hand, *A* ambidextrous, *l* left biased ($P < 0.05$, statistically significant departures from equal use of both hands, two-tailed binomial test), *r* right biased ($P < 0.05$, statistically significant departures from equal use of both hands, two-tailed binomial test), *Al* ambidextrous with left-hand bias ($0.05 < P < 0.2$, statistically significant departures from equal use of both hands, two-tailed binomial test), *Ar* ambidextrous with right-hand bias ($0.05 < P < 0.2$, statistically significant departures from equal use of both hands, two-tailed binomial test), *X* no tool use observed during period of observation (although individual had previously performed the behaviour), *x* no tool use observed during period of observation or at any time previously, *i* inconclusive due to small number of observations

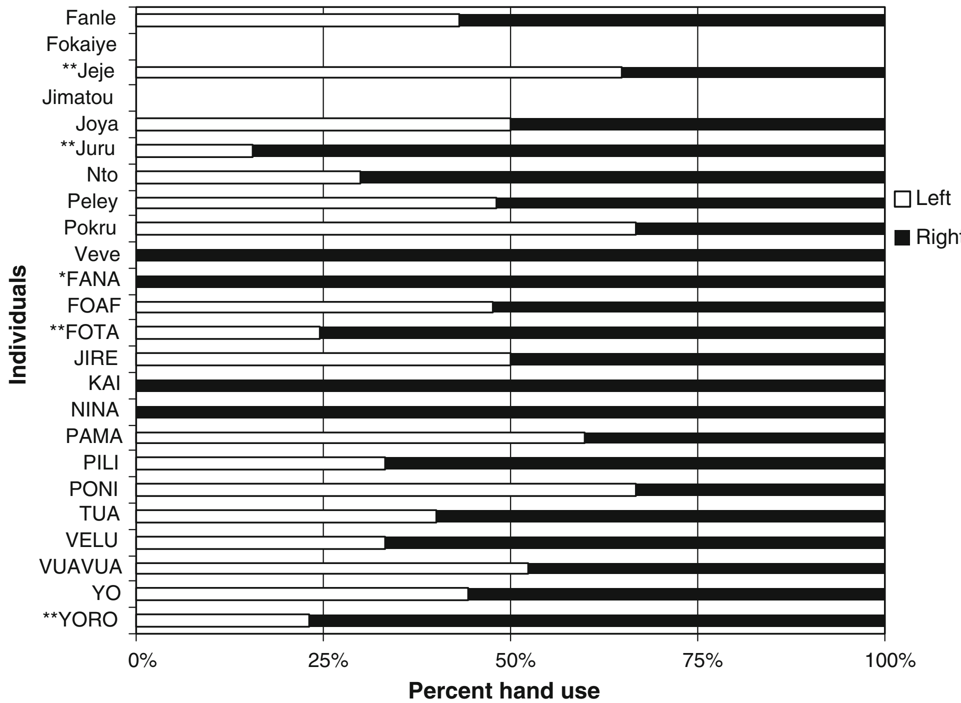

Fig. 4 Hand preference during the use of leaves for drinking water. The hand used for the dipping action was recorded for each bout. *Percentages* shown are calculated from the total number of bouts for each individual, across the four field seasons. Adults are in *capitals*, and non-adults in *lowercase* (statistically significant departures from equal use of both hands: $^*P < 0.05$, $^{**}P < 0.01$, two-tailed binomial test)

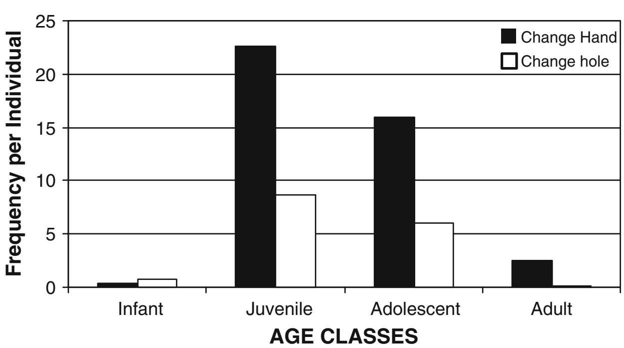

Fig. 5 Average number of times individuals in different age classes changed hands and changed hole openings during the use of leaves for drinking water at the outdoor laboratory

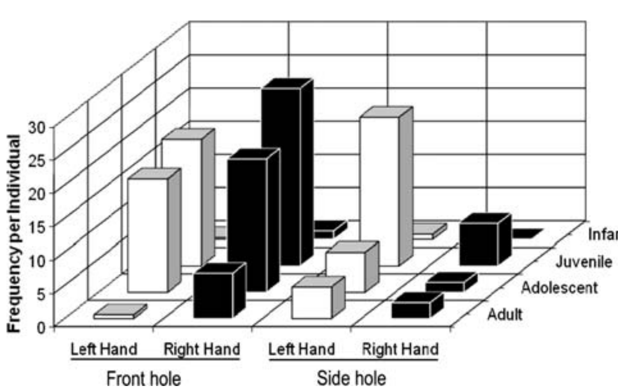

Fig. 6 Frequency of using the left and right hand at the two openings of the water hole by individuals in the four age classes

insert one object into another, while for nut cracking objects must be stacked stably on top of one another in a specific order. Hayashi and Matsuzawa (2003) have reported that in infant chimpanzees' free manipulation of objects, "inserting" actions, such as the insertion of a rod through a hole in a box, appear approximately a year earlier (at the age of around 1 year) than "stacking", such as the placement of one wooden block on top of another (which first appears around 2 years of age). This difference in naturally occurring propensities to perform specific manual manipulations may explain the precocious emergence of leaf-tool use in comparison with that of nut cracking.

At around the same time that infants start to use leaf tools, they also start to manufacture them. Nevertheless, they do not use the latter to drink water; rather, they discard them almost immediately and prefer to use tools previously abandoned by older individuals. One possible reason for this concerns the efficiency of tools that infants manufacture: they tend to be too small to function, or they carry much smaller quantities of water than those of adults. Younger individuals' leaf tools can thus be considered less efficient than those of adults, and it is possible that the use of abandoned tools—which may serve as large, "supernormal" stimuli that allow infants to obtain far more water than they could by themselves—also enhance acquisition of both the tool-making- and tool-using phases of the behaviour. Lower efficiency of tool use in younger individuals, when compared with the performance of adults, has also been reported for nut cracking, where younger individuals require larger numbers of hammer blows to break the shell and extract the kernel—this measure is around 1–2 blows in skilled performers at Bossou, but is generally considerably higher in the first few years of successful cracking (Biro et al. 2003). Nevertheless, lower efficiency of self-made tools may not be the main explanation behind their lack of use by infant tool makers: intriguingly, it is possible that in cognitive terms, infants are not yet able to relate the tool-making phase with the subsequent use of the same tool. This lack of ability to bridge the two phases of the process may stem from the fact that the process of tool making is essentially invisible—it takes place inside the mouth, and thus requires a mental representation of how the tool is shaped while out of view of the infant. Nevertheless, some aspects of tool manufacture acquisition may be beyond young infants' cognitive or motor capabilities, irrespective of limited opportunities to observe the process. A recent study by Bania et al. (2009), where chimpanzee subjects were required to modify a tool to retrieve a food reward, has shown that tool modification by infants—necessary for the tool-making phase—appeared to reflect a trial and error strategy. This suggests, as stated by the authors, that infants have yet to exhibit full understanding of the functional properties of tools for a specific task and/or may have potential difficulties with the motor requirements of the actions involved.

The question then arises whether we are right to consider as the starting age the first use of a leaf tool irrespective of the maker of the tool, and hence disregard the process of manufacture. If we take into account the manufacturing process (which must always precede the drinking action), then the full behaviour appears only at the age of 3.5 years, when individuals begin to make and use their own tools. Three and a half years is also the age at which "level 2" tool use appears in development. This would suggest that the combination of tool-making- and tool-using phases which together facilitate the use of leaves for drinking water considerably increase the cognitive demands of the task.

During leaf-tool use, chimpanzees exhibit a different pattern of handedness from that seen in nut cracking within the same population (Biro et al. 2006). Although nut cracking is a highly lateralised behaviour, with perfect handedness at the adult individual level, leaf-tool use is a non-lateralised activity, much like ant fishing (Marchant and McGrew 2007), or pestle-pounding (Humle and Matsuzawa 2009). The majority of chimpanzees are ambidextrous in their use of leaves, and only some show a bias for one hand. Similarly, these differences are evident when comparisons are drawn with the results obtained by Boesch (1991) for wedge-dipping to drink water from a puddle at the Taï forest, Cote d'Ivoire, and with those of Lonsdorf and Hopkins (2005) for termite fishing at Gombe, Tanzania, both of which are highly lateralised behaviours. In the case of ant fishing, where lateralisation is absent, Marchant and McGrew (2007) demonstrate a positive correlation between the frequency of hand changes and the incidence of major hand support, as ant fishing is an arboreal activity. Likewise, pestle-pounding, pounding the centre of the palm crown using a palm frond as pestle to extract the resulting softened palm heart, is also an arboreal tool-use task, which simultaneously requires strength and balance while standing bipedally on top of an oil-palm tree (Humle and Matsuzawa 2009). Although in our study leaf-tool use is not completely arboreal, it is also not fully terrestrial, as individuals were able to perform the behaviour either standing on the ground or hanging from lianas surrounding the tree containing water. In fact, in most cases, individuals were relying on their non-tool-using hand for postural support during bouts of leaf-tool use (although it should be noted that we have not carried out a systematic analysis of the precise conditions under which the alternate hand is freed from such duties, hence cannot conclude that leaf-tool use is typically accompanied by this constraint). Even when adult individuals do not change their hands frequently while leaf dipping for water, as in the case of ant fishing (Marchant and McGrew 2007), their ambidextrality might be explained by the necessity of adopting different postural positions depending on the location of the hole through which they extract water. That is, that they may choose to use one or the other hand in accordance with the demands of particular situations, which might reflect a degree of behavioural flexibility.

Our data also showed developmental changes related with handedness. Juveniles and adolescents frequently change hands when leaf dipping for water, in comparison with adults who do so much more rarely. A similar scenario is evident in nut cracking, where young chimpanzees are often ambidextrous in hammer use and frequently switch hands, before settling on one or the other hand later in development (Biro et al. 2006). In addition, while juveniles often change hammers and anvils during nut cracking (Carvalho et al. 2008), in leaf drinking they change from one opening of the tree hole to the other. Furthermore, juveniles also change hands more frequently when moving between the two openings of the tree hole. These developmental changes in handedness are in concordance with the suggestion by Lonsdorf and Hopkins (2005) that there is a relationship between different cognitive and motor demands and the tool use task-specific variation in hand preference.

Our data on laterality during leaf-tool use for drinking might suggest some adaptation in terms of handedness to postural position, as we found a tendency for individuals to prefer one hand over the other when leaf dipping at one of the two openings of the tree hole. Nevertheless, the switching of hands, as well as of openings of the tree hole during the performance of leaf-dipping actions also represent important steps towards the learning of the behaviour and suggest a trial and error process in acquisition by young individuals—analogous to the way in which the switching of tools during nut cracking may represent young chimpanzees' attempts to learn about the properties and efficiency of different tools (Biro et al. 2006).

Acknowledgments We thank the Direction National de la Recherche Scientifique et Technique, République de Guinée, for permission to conduct field work at Bossou. The research was supported by Grants in Aid for scientific research from the Ministry of Education, Science, Sports and Culture of Japan (grants 07102010, 12002009, 10CE2005 and the 21COE programme). DB was financially supported by the Royal Society. We would like to express our gratitude to the following people who have been involved in research at Bossou over the years and thus contributed to the data reported here: Gen Yamakoshi, Rikako Tonooka, Noriko Inoue-Nakamura, Tatyana Humle, Hiroyuki Takemoto, Satoshi Hirata, Gaku Ohashi, Makoto Shimada, Takao Fushimi, Osamu Sakura, Masako Myowa-Yamakoshi, Maura Celli, Tomomi Ochiai, Misato Hayashi and Susana Carvalho. We are also grateful to Yukimaru Sugiyama who began the study of wild chimpanzees at Bossou, to Guanou Goumy, Tino Camara, Paquile Cherif, and Pascal Goumy, Marcel Doré, Bonifas Zogbila, Jiles Doré and Henry Gbelegbe for assistance in the field. Three anonymous referees provided valuable comments on an earlier version of this manuscript.

References

Anderson JR, Williamson EA, Cárter J (1983) Chimpanzees of Sapo Forest, Liberia: density, nests, tools and meat-eating. Primates 24:594–601

Bania AE, Harris S, Kinsley HR, Boysen ST (2009) Constructive and deconstructive tool modification by chimpanzees (*Pan troglodytes*). Anim Cogn 12:85–95. doi:10.1007/s10071-008-0173-0

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

Biro D, Sousa C, Matsuzawa T (2006) Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut cracking and leaf folding. In: Matsuzawa T, Tomonaga M, Tanaka M (eds) Cognitive development in chimpanzees. Springer, Tokyo, pp 476–508

Boesch C (1991) Handedness in wild chimpanzees. Int J Primatol 12:541–558

Boesch C, Boesch H (1983) Optimisation of nut-cracking with natural hammers by wild chimpanzees. Behaviour 83(3–4):265–286

Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. Folia Primatol 54:86–99

Boesch C, Marchesi P, Marchesi N, Fruth B, Joulian F (1994) Is nut cracking in wild chimpanzees a cultural behaviour? J Hum Evol 26(4):325–338

Carvalho S, Sousa C, Matsuzawa T (2007) New nut-cracking sites in Diecké Forest, Guinea: an overview of the surveys. Pan Africa News 14(1):11–13

Carvalho S, Cunha E, Sousa C, Matsuzawa T (2008) Chaînes Operatóires and resource exploitation strategies in chimpanzee nut-cracking (*Pan troglodytes*). J Hum Evol 55(1):148–163

Ghiglieri MP (1984) The chimpanzees of Kibale Forest. Columbia University Press, New York

Goodall J (1968) Behavior of free-living chimpanzees of the Gombe stream area. Anim Behav Monogr 1:163–311

Hayashi M, Matsuzawa T (2003) Cognitive development in object manipulation by infant chimpanzees. Anim Cogn 6:225–233

Humle T (2006) Ant dipping in chimpanzees: an example of how microecological variables, tool use, and culture reflect the cognitive abilities of chimpanzees. In: Matsuzawa T, Tomonaga M, Tanaka M (eds) Cognitive development in chimpanzees. Springer, Tokyo, pp 452–475

Humle T, Matsuzawa T (2009) Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea. West Afr Am J Primatol 71:40–48

Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). J Comp Psychol 111:159–173

Lonsdorf EV (2005) Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. Anim Behav 70:673–683

Lonsdorf EV (2006) What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Anim Cogn 9:36–46

Lonsdorf EV, Hopkins WD (2005) Wild chimpanzees show population-level handedness for tool use. Proc Natl Acad Sci USA 102(35):12634–12638

Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. Nature 428(6984):715–716

Marchant LF, McGrew WC (2007) Ant fishing by wild chimpanzees is not lateralised. Primates 48:22–26

Matsuzawa T (1994) Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge

Matsuzawa T (1996) Chimpanzee intelligence in nature and captivity: isomorphism of symbol use and tool use. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge, Cambridge University Press, pp 196–209

Matsuzawa T (1999) Communication and tool use in chimpanzees: cultural and social contexts. In: Hauser M, Konishi M (eds) Neural mechanisms of communication. MIT Press, Cambridge, pp 645–671

Matsuzawa T (2009) The chimpanzee mind: in search of the evolutionary roots of the human mind. Anim Cogn. doi 10.1007/s10071-009-0277-1

Matsuzawa T, Yamakoshi G (1996) Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: Russon A et al (eds) Reaching into thought. Cambridge University Press, Cambridge, pp 211–232

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, pp 557–574

McGrew WC (1977) Socialization and object manipulation of wild chimpanzees. In: Chevalier-Skolnikoff, Poirier (eds) Primate bio-social development. New York, Garland

McGrew WC (1992) Chimpanzee material culture. Cambridge University Press, Cambridge

McGrew WC (2004) Primatology: advanced ape technology. Curr Biol 14:R1046–R1047

McGrew WC, Marchant LF (1996) On which side of the apes? In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 255–272

McGrew WC, Ham RM, White LJT, Tutin CEG, Fernandez M (1997) Why don't chimpanzees in Gabon crack nuts? Int J Primatol 18:353–374

McGrew WC, Marchant LF, Wrangham RW, Klein H (1999) Manual laterality in anvil use: wild chimpanzees cracking *Strychnos* fruits. Laterality 4:79–87

Morgan BJ, Abwe EE (2006) Chimpanzees use stone hammers in Cameroon. Curr Biol 16:R632–R633
Nishida T (1990) A quarter century of research in the Mahale Mountains: an overview. In: Nishida T (ed) The chimpanzees of the Mahale Mountains: sexual and life history. University of Tokyo Press, Tokyo, pp 3–35
Quiatt D, Kiwede ZT (1994) Leaf sponge drinking by the Budongo forest chimpanzees. Am J Primatol 33:236
Sugiyama Y (1993) Local variation of tools and tool use among wild chimpanzee populations. In: Berthelet A, Chavaillon J (eds) The use of tools by human and non-human primates. Clarendon Press, Oxford, pp 175–187
Sugiyama Y (1995) Drinking tools of wild chimpanzees at Bossou. Am J Primatol 37:263–269
Sugiyama Y, Koman J (1979) Social structure and dynamics of wild chimpanzees at Bossou, Guinea. Primates 20:323–339
Tonooka R (2001) Leaf-folding behavior for drinking water by wild chimpanzees (*Pan troglodytes* verus) at Bossou, Guinea. Anim Cogn 4(3–4):325–334
Tonooka R, Inoue N, Matsuzawa T (1994) Leaf-folding behavior for drinking water by wild chimpanzees at Bossou, Guinea: a field experiment and leaf selectivity (in Japanese with English summary). Primate Res 10:307–313
Visalberghi E, Fragaszy D, Ottoni E, Izar P, Oliveira, MG de, Andrade FRD (2007) Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. Am J Phys Anthropol 132:426–444
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
Wrangham RW (1992) Living naturally: aspects of wild chimpanzee management. In: Erwin J, Landon JC (eds) Chimpanzee observation and public health. Rockville, Diagnon, pp 71–81