

# In search of the last common ancestor: new findings on wild chimpanzees

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Modelling the behaviour of extinct hominins is essential in order to devise useful hypotheses of our species' evolutionary origins for testing in the palaeontological and archaeological records. One approach is to model the last common ancestor (LCA) of living apes and humans, based on current ethological and ecological knowledge of our closest living relations. Such referential modelling is based on rigorous, ongoing field studies of the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*). This paper reviews recent findings from nature, focusing on those with direct implications for hominin evolution, e.g. apes, using elementary technology to access basic resources such as food and water, or sheltering in caves or bathing as thermoregulatory adaptations. I give preference to studies that directly address key issues, such as whether stone artefacts are detectable before the Oldowian, based on the percussive technology of hammer and anvil use by living apes. Detailed comparative studies of chimpanzees living in varied habitats, from rainforest to savannah, reveal that some behavioural patterns are universal (e.g. shelter construction), while others show marked (e.g. extractive foraging) or nuanced (e.g. courtship) cross-populational variation. These findings allow us to distinguish between retained, primitive traits of the LCA versus derived ones in the human lineage.

**Keywords:** tool use; shelter; diet; ranging; last common ancestor; chimpanzee

## 1. INTRODUCTION

This paper aims to synthesize and to update recent (from 2005 onwards) findings from studies of the ethology and ecology of wild chimpanzees (*Pan troglodytes*) that are relevant to modelling human origins. Given space constraints, this exercise will be limited to field studies, and therefore mostly to observational data on the spontaneous behaviour of apes *in situ*, cited selectively. It emphasizes primary reports, usually journal articles, on the assumption that older secondary reviews (e.g. Mitani *et al.* 2002; McGrew 2004) provide access to earlier material. It concentrates on the eight study sites with fully habituated subjects, here listed in the order of seniority: Gombe (Tanzania), Budongo (Uganda), Mahale (Tanzania), Kanyawara (Uganda), Bossou (Guinea), Taï (Ivory Coast), Ngogo (Uganda) and Fongoli (Senegal). However, given the geographical bias to eastern and western Africa, other sites with partly habituated subjects, especially in central Africa, such as Goualougo (Republic of Congo), are necessarily invoked too. Most importantly, it focuses on topics that are relevant to modelling the behaviour of the last common ancestor (LCA) of the divergent lines that led to living humans and living chimpanzees. These topics are presented in terms of their 'directness' in comparisons between what primatologists see now in living apes, and what palaeoanthropologists seek to infer about

the extinct LCA, based on indirect evidence. Thus, this synthesis covers technology, diet, shelter and ranging and foraging.

Attempts to use findings from ethological and ecological (as opposed to morphological) research on chimpanzees to model the behaviour of ancestral humans are relatively recent, dating from the rise of primatological field studies in the last 50 years. Although most early field workers were interested in apes in their own right, their mentors often had in mind the potential applicability of the exciting new findings to human issues (e.g. Goodall & Hamburg 1974). Many of the early attempts now look crude and simplistic (e.g. McGrew 1981). For example, most were content to talk about extinct hominids as a single unspecified class, but as the hominin evolutionary record became more and more diverse, with more and more taxa unearthed, this monolithic exercise was less and less satisfactory. Furthermore, as data began to emerge on wild bonobos, *Pan paniscus* (Kano 1992), who are as equally closely related as chimpanzees to hominins, and as cross-populational variation began to emerge in chimpanzees (McGrew 1992), easy generalizations grew harder to make. Ecological studies of chimpanzees in a variety of ecotypes, from rainforest to savannah, forced more precise modelling (Moore 1996). Finally, debate over the best way to model human origins and evolution, that is, via referential versus strategic models, or by homology versus analogy, muddied the waters (e.g. Tooby & DeVore 1987). Sayers & Lovejoy (2008) took the extreme position that chimpanzees may be no more useful as models than other, more ecologically,

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One contribution of 14 to a Discussion Meeting Issue 'The first four million years of human evolution'.

zoogeographically and phylogenetically distant taxa, such as capuchin monkeys (*Cebus* spp.). More recently, Lovejoy (2009) has asserted that extant African ape-based models are no longer appropriate (for a contrary view, see Whiten *et al.* 2010). However, for focused studies, such as of Oldowan lithic industries, apes may still be the model of choice (Toth & Schick 2009).

This paper takes the conservative line that lacking a fossil record for apes since the Miocene (cf. McBrearty & Jablonski 2005), and having only a shallow archaeological record for apes, all that we sensibly can hope to model is the LCA. In doing so, I make several simplifying assumptions, such as that anything that a chimpanzee can do today, the LCA could have done 6–7 Myr ago. Another pragmatic assumption is that although the LCA could have resembled the living chimpanzee, or bonobo, or neither, or some combination of the two, most of what we have to work with on grounds of homology comes from *P. troglodytes*. Therefore, until comparable breadth and depth of data are available for *P. paniscus*, the chimpanzee must carry the load.

#### (a) *Technology*

Most of what behavioural primatologists have to offer to palaeoanthropology relies on artefacts, as these objects are comparable to what is found in the archaeological record. However, artefacts are the products of behaviour, and sometimes archaeological data are a further step removed: butchery cutmarks on bones are the products of the ephemeral acts that produced them. Whatever the caveats, primatologists can offer something that no archaeologist will ever see, that is, BOTH the product AND the behaviour, directly recorded. When a glancing blow of a stone hammer being used to crack a nut hits instead the stone anvil, producing a conchoidally fractured flake, the observer can see whether this was an accident. An archaeologist given only that same single flake could draw no valid inference about the percussionist's intentions.

Studies of tool use by apes in nature have come a long way from piecemeal natural history notes collected opportunistically and descriptively, to comprehensive, systematic, hypothesis-driven empirical efforts, some of which are experimental. Comparative analyses of chimpanzee material culture are done at every level, of individuals, lineages, communities, populations, subspecies and species (McGrew 2004).

The chimpanzee ethnographic record now spans so many study sites across equatorial Africa that even chimpologists have trouble keeping them straight. Although only eight sites consistently allow all-day, close-up observation, there are five times as many other sites with varying degrees of habituation. In the 5 years, long-term sites studying the central (Hicks *et al.* 2005; Sanz & Morgan 2007) and Nigerian (Fowler & Sommer 2007) subspecies have joined the longer term studies in eastern and western Africa. Even sites that have yet to habituate their subjects have yielded new behavioural patterns, e.g. root-digging at Ugalla, Tanzania (Hernandez-Aguilar *et al.* 2007), fruit-cleaving at Nimba, Guinea (Koops *et al.* 2010), etc. The only comprehensive study of

innovation in wild chimpanzees, at Mahale, shows inventiveness to be common, but the chance that a novel behavioural pattern will be propagated and become established in a population is rare (Nishida *et al.* 2009).

No longer is it enough just to list the types of tool found at a given site, as nominal (presence/absence) data. Now attention to relative frequency and competence of performance across age and sex classes is expected, along with data on context, variation in form and function of the tools' manufacture and use (e.g. Sanz *et al.* 2009a). Functional (e.g. extractive foraging), biomechanical (e.g. percussive) and cognitive (e.g. artefact complexity) aspects of technology are stressed. Anecdotal versus idiosyncratic versus habitual use of tools is differentiated. Distinction is drawn between a tool kit (i.e. the whole repertoire of a community's collective range of tools) and a tool set (i.e. the obligate sequence of two or more tools used to achieve a single goal). Composite tools (i.e. when two or more objects are used simultaneously and complementarily to achieve a goal), such as hammer and anvil (Carvalho *et al.* 2009), are distinguished from compound tools (i.e. when two or more elements of different types are combined into a single unit), such as a wedge used to level an anvil's working surface (Biro *et al.* in press). Typology is now part of chimpanzee technology.

Tool kits show both uniformity and variety across populations. Sanz & Morgan (2007) presented quantitative and qualitative findings from the Goualougo, Republic of Congo, chimpanzees, whose tool kit numbers 22 types, of which nine are used habitually (customary). In contrast, Watts (2008b) published comparable data from Ngogo, Uganda, where the total tool kit numbers only 10 types, with four of these being habitual. Such variation suggests the possibility of a normally distributed spectrum, but this is not the case. As with Goualougo, all habituated populations show about the same-sized tool kits: Gombe (22), Bossou (21), Taï (21) and Mahale (16). However, along with Ngogo, the other Ugandan sites show small tool kits: Budongo (8) and Kanyawara (10) (Sanz & Morgan 2007, table 3). Even more striking is the contrast between Goualougo and Ngogo with regard to the predominate types of tools: the top three at Goualougo are used in subsistence, that is, extractive foraging of termites, honey and water; the top three at Ngogo are used in hygiene, especially wiping the penis after copulation, and in courtship. (The reverse is equally true: Goualougo chimpanzees very rarely use napkins, and Ngogo chimpanzees rarely harvest insects.) However, some types of tool use are chimpanzee universals, being found in all long-studied populations across Africa, such as leaf sponge (drinking water), aimed throw (weapon), play start (toy), branch drag (display), etc.

Of particular importance is percussive technology, that is, the application of ballistic force via one object to another to achieve a goal (Ling *et al.* 2009). In chimpanzees, this most famously takes the form of hammer and anvil used to crack nuts, but it also occurs in smashing hard-shelled objects directly against anvils, in agonistic clubbing of adversaries or

in display, or in specialized extractive foraging such as pestle-pounding (Yamakoshi & Sugiyama 1995). In the latter case, the pestle is a detached palm frond, the mortar is the apical growth tip of an oil palm (*Elaeis guineensis*) and the result is a cavity full of mashed-up slurry, which is eaten. Anvil use without hammers occurs when a hand-held, hard-shelled fruit is bashed directly against a boulder or root, as with baobabs (*Adansonia digitata*). Marchant & McGrew (2004) hypothesized an evolutionary scenario that led from anvil use to stone-knapping.

Tool sets in apes were first recognized in honey extraction (Brewer & McGrew 1990). In seeking to harvest nature's most calorific food, the minimal tool set requires a tool to break into the bees' storage reservoir and another tool to extract the liquid. That is, some kind of percussive tool, such as hammer or chisel, plus some kind of dip-stick, are needed to secure the food item (for the most complete treatment of this resource's exploitation, see Sanz & Morgan 2009). Tool sets may be more complex: Boesch *et al.* (2009) recently described tool sets used by the chimpanzees of Loango, Gabon, in which up to five tools were needed, e.g. pounder, perforator, enlarger, collector and swab. Tool sets also are used to exploit other animal prey, e.g. termites (Deblauwe *et al.* 2006; Sanz & Morgan 2007), ants (Sanz *et al.* 2009b) and even when getting honey, the proteinaceous bonus of bee brood may be important too. The key point about a tool set is that it is sequential task: if an A-B-C-D is necessary, then A-C-B-D will not do; you cannot check the oil level in your car's engine via the dip-stick, until you have opened the car's bonnet. Although tool sets may suggest advanced cognitive abilities, many such mandatory sequences are shown by creatures with modest brains (Hansell 2004), especially in shelter construction (see below). What is impressive (and possibly unique) about chimpanzee tool sets is that alternative versions may be used flexibly by different apes to solve the same problem.

In human elementary technology, composite tools are well known: Mortar and pestle, bow and arrow, etc. Each element may stand alone, but is almost useless without its partner. (Tool composites differ from tool sets in that they are used simultaneously, rather than sequentially.) Tool composites are known for apes (see summary in Sugiyama 1997), and some are widespread, for example, in all populations where chimpanzees use long wands to dip for driver ants, they also use bent-over saplings as a perch while doing so, to avoid the painful bites of the ants swarming on the ground below (McGrew 1974). However, only recently have tool composites been systematically studied: Carvalho *et al.* (2009) showed that certain combinations of stone hammers and anvils were used over and over again by the chimpanzees of Bossou, even taking into account the apes' separate, independent preferences for hammer or anvil.

Compound tools are harder to find in living apes in nature, although their production is readily induced under contrived captive conditions. Combination of multiple items of the same type, e.g. leaves compressed together in leaf-sponging for water, is the simplest kind

of compound tool (Sousa *et al.* 2009), but it barely qualifies, being iterative. The most obvious example of compound technology (albeit not tool use) in non-human primates in nature is the sleeping platforms/nests/beds that are woven daily by great apes (see below). The best-known example in the extractive foraging of chimpanzees is the anvil-wedge, known only from the nut-cracking of the Bossou chimpanzees (Matsuzawa 2006). Bossou's stone anvils are movable, and so their positioning can be adjusted; anvils with near-horizontal working surfaces are the most efficient, as the yielded nut-meat is readily picked up. An angular anvil can be levelled by inserting a smaller stone as a wedge underneath, to make the working surface less tilted.

To what extent is the technological repertoire of the chimpanzee now known? The steepness of the cumulative ethnographic curve may be less than in the last century, but it has not flattened out. New habitual patterns continue to be described: chimpanzees use spears to skewer small mammals (Pruetz & Bertolani 2007) and digging sticks to unearth roots (Hernandez-Aguilar *et al.* 2007). Furthermore, new modes of tool use continue to emerge, such as the chimpanzees of Nimba, Guinea, using cleavers to break apart large, fibrous *Treculia* fruits (Koops *et al.* 2010).

Much progress has also been made on how individual apes in nature learn to use elementary technology. Previous studies were descriptive or qualitative, whereas modern ones use sophisticated multivariate analyses (e.g. general linear mixed model) to tease out the influences of independent variables. Lonsdorf's (2006) study of termite fishing at Gombe showed that although all chimpanzees in the Kasakela community show this tool use by 5.5 years of age, daughters acquire the skills earlier, and this acquisition is a function of the mother's overall time spent in the activity. Humle *et al.* (2009) showed that chimpanzee infants at Bossou who had more opportunities to observe their mothers started ant-dipping sooner and were more proficient than their low-opportunity counterparts. However, in neither case were individual differences in mother's performance reflected in individual differences in their offspring, nor was there any direct teaching by mothers. Youngsters learned to fish or to dip by passive observational learning of tolerant models. Matsuzawa *et al.* (2001) have termed this dyadic conduit of information from one ape to another as 'education by master-apprenticeship'.

Some primatologists now apply archaeological methods to the study of chimpanzee technology in nature. Mercader *et al.* (2002, 2007) have shown that the past nut-cracking activities of the Taï chimpanzees leave behind a record of stone artefacts. These can be distinguished from human artefacts or naturally splintered rocks by 'blind' assessors, dated by standard radiometric techniques ( $C_{14}$ ), and yield organic residues (starch grains) that reveal their function. We can now speak of a chimpanzee 'stone age' with time depth. Carvalho *et al.* (2008) applied one of the core concepts of archaeology, the *chaîne opératoire*, to the nut-cracking of Bossou's chimpanzees, showing that from start to finish, this analytical technique is equally applicable to apes as to humans. Even retrospective

analyses of chimpanzee artefacts, in this case the brush-sticks used to fish for termites, as found in a museum, may explain how they were made (Heaton & Pickering 2006; cf. Sanz & Morgan 2007). The extent to which the archaeology of non-humans can be pushed back in time remains to be seen, but a new field is now underway (Haslam *et al.* 2009).

Finally, here is a sobering thought: of all the tools named so far, only some of the hammers and anvils, and some of the missiles thrown, will have a chance of persisting in the archaeological record, taphonomy willing, because they are made of stone. All of the others are made of organic raw materials, e.g. plant or animal matter, and so will perish over time. There are other lithic objects used, e.g. stones in self-tickle, pebbles in play start, boulders in splash display, etc., but it is unlikely that these will be archaeologically recognizable.

### (b) *Diet*

The chimpanzee is an omnivore, as all well-studied populations show a mix of herbivory and faunivory. The former is dominated by ripe fruit, but also includes leaves, pith, seeds, flowers, bark, gum, etc. The latter focuses on social insects (ants, bees, termites) and small- to medium-sized mammals, especially monkeys. Invertebrates usually are taken by tool-assisted extractive foraging, such as ant-dipping, ant-fishing, honey-dipping and termite-fishing, that is, by gathering. Until recently, vertebrate prey were known to be captured and dispatched only by hand, without technology. Pruetz & Bertolani (2007) showed that the chimpanzees of Fongoli, Senegal, use a weapon-assisted hunting technique to disable or kill bushbabies while they sleep during the day in tree holes. The weapon is a sharpened stick (spear), jammed into the prosimian's sleeping chamber. (Some sceptics have questioned whether the technique qualifies as hunting, or the instrument as a spear. When an Inuit waits beside a seal's air-hole in the ice, then thrusts a sharp-ended linear object into it, skewering the prey, we are happy to call it hunting, so why not for apes?).

Notably absent from the diets of most chimpanzee populations are the underground storage organs (USO) of plants, that is, bulbs, roots, tubers, corms, rhizomes, etc. This absence was thought to reflect the generalized, non-digging hands of primates, plus the apes' lack of the appropriate technology, that is, the digging stick. Hernandez-Aguilar *et al.* (2007) recently described how the chimpanzees of Ugalla, Tanzania, dig up roots, using sticks and pieces of bark that show the abraded wear patterns of repeatedly used digging tools. Spat-out wedges of fibrous roots show them to be chewed and sucked, then discarded. A similar processing technique is used by the chimpanzees of Tongo, Democratic Republic of Congo, to get drinking water from subterranean tubers, but these are dug up by hand from friable, volcanic soils (Lanjouw 2002).

Across the continent, from Tanzania to Ivory Coast, chimpanzee hunters take more monkeys as prey than all other types of vertebrates combined, especially favouring the red colobus (*Piliocolobus badius*) (e.g. Watts & Mitani 2002). Others also hunt ungulates,

but one of the keenest hunting populations, the chimpanzees of Tai, does not hunt the small forest antelopes (*Cephalophus* spp.) that are plentiful there. At the same time, several populations of bonobos avidly hunt antelope, but were said to show no interest in primate prey; this apparent species difference evaporated with Surbeck & Hohmann's (2008) report that the bonobos of Lui Kotale, Democratic Republic of Congo, also hunt guenons (*Cercopithecus* spp.). What differs between the two sibling species of chimpanzee and bonobo is the sexual politics of meat-sharing.

In bonobos, females control the carcass and distribute the meat, and their collective dominance over males sometimes leaves the males with none, even if individually a male can dominate a female (Hohmann & Fruth 2008). In chimpanzees, males often control carcasses, and there has been much debate about how the sharing of the meat functions in chimpanzee society. Now come solid data to test Stanford's (1999) hypothesis of meat-for-sex, that is, that males selectively give meat to females in exchange for sexual favours. Gomes & Boesch (2009) report that females copulate more often with males who share meat with them in the long term. Thus, the female need not be in oestrus at the time of the hunt, but rather forms a relationship that mutually enhances the lifetime reproductive success of male (insemination probability) and female (nutritional enhancement). However, meat-sharing in some chimpanzee populations, e.g. Gombe in Tanzania (Gilby 2006), appears to be driven by different mechanisms: intimidation, harassment, reciprocity, etc. Less likely is Tennie *et al.*'s (2009) 'meat-scrap' hypothesis that meat-sharing can be explained by the micro-nutrients found in even small amounts of meat. Meat-eating is only one kind of faunivory, and the same nutrients can be easily obtained from invertebrates, which chimpanzees eat daily.

Male sharing of prized foodstuffs with females also occurs with plant foods, which otherwise is rare in apes, usually occurring only between mother and infant. However, Hockings *et al.* (2007) showed that when males at Bossou raided crops, especially papaya (*Carica papaya*), they almost always shared the proceeds with females of reproductive age, even when the latter were not in oestrus. These sharing patterns reflected patterns of later sexual consortship.

What about scavenging? Scattered, anecdotal reports of chimpanzee scavenging mammalian prey have appeared from time to time, but no systematic study was done until Watts (2008a) documented all known scavenging opportunities at Ngogo over 11 years of observations totalling over 10 000 h. In that period, he saw only four scavenging events, and opportunities were rare, occurring on average only every 100 h. This contrasts mightily with over 650 kills made in over 270 hunts in the same period (Watts & Mitani 2002). Similar pictures of rarity emerge from Gombe, Mahale and Tai. Chimpanzees are not scavengers, it seems.

### (c) *Shelter*

Shelter can be defined as the use of any material object to buffer the effects of the elements. A universal

behavioural pattern among great apes is their daily construction of arboreal sleeping platforms: every weaned individual builds an overnight nest and many also build day nests for napping. These compound artefacts are scattered over the landscape and may endure for months, leaving a record of points in space where chimpanzees spend most of their lives. (Chimpanzees typically retire at dusk and arise at dawn, and so spend half of each tropical circadian cycle in their beds.) Hernandez-Aguilar (2009) found 5354 nests over a 20 month period at Issa, an open-country, savannah area in western Tanzania. These shelters were highly clumped on woodland hill-sides, in particular sites that were re-used over and over again. The chimpanzees' ranging and consequent nest distribution varied predictably over wet and dry seasons, reflecting an annual cycle of movement that reflects availability of surface water and ripe fruit. However prominent a part these shelters play in their daily lives, these constructions later will be archaeologically invisible, being made entirely of woody vegetation.

At the same time, studies of individual nests and their making have yielded insights:

Koops *et al.* (2007) showed that at Nimba, surprisingly many nests were built on the ground. From the patterning and size of nests, they hypothesized that this reflected a pattern of male overnight mate-guarding, that is, when an oestrous female nested in a tree, a male seemed to nest on the ground at its base, to sequester her from the nocturnal attention of other males. Various functions for nests have been proposed: anti-predator, anti-parasite, anti-disease vector, thermoregulation, etc., but there has yet been no comprehensive study of these hypotheses. Meanwhile, Stewart *et al.* (2007) studied the proximal characteristics of nests, in terms of their architecture and materials. First-hand empirical data showed that chimpanzees prefer comfortable nests, presumably to gain restorative sleep for their big brains.

The species' name for the chimpanzee implies a cave dweller, yet until recently, there was no record of chimpanzees using caves as shelter. Pruettz (2007) reported that the Fongoli chimpanzees, who occupy one of the hottest and driest areas in the species' distribution, regularly use a cave during the hottest season of the year. They retreat to its cooler environment during the heat of the day for 'siestas' and picnics; overnight, they sleep in arboreal nests, just like other great ape populations.

Chimpanzees are notoriously hydrophobic, as they do not swim, which makes watercourses notable barriers to their geographical distribution. However, they enter surface water in certain circumstances: at Fongoli, they immerse themselves in temporary rain-filled pools at the beginning of the rainy season, when it is still hot and humid; there they rest, groom and play (Pruettz & Bertolani 2009). Thus, water becomes a thermoregulatory device, even when potentially risky.

#### (d) *Ranging*

Although some authors (e.g. Lovejoy 2009) stubbornly continue to characterize evergreen rainforest

as the typical ecotype for wild chimpanzees, and so contrast their ecological context with that of hominins who lived in more seasonal, mosaic habitats, this restrictive picture is less and less tenable. Most of the study sites at which chimpanzees have been studied, and at least (depending on definition) three (Fongoli, Gombe and Mahale) of the eight where the apes have been fully habituated to close-range observation, are not evergreen rainforest. More accurately, chimpanzees subsist in a range of ecotypes, from woodland savannah (not steppe) to rainforest, with mean annual rainfall that range from about 800 to more than 2000 mm per year. Many of these landscapes are vegetationally heterogenous, and chimpanzee use of this array of habitat types varies greatly.

At the other extreme, chimpanzees (unlike baboons, *Papio* spp.) do not survive in places that lack surface water for drinking or that lack the riverine forests that follow these watercourses, although only a tiny fraction of such gallery forest will suffice. Copeland's (2007, 2009) detailed comparison of several open and arid African habitats shows that landscapes with annual rainfall in the 500–750 mm range cannot support chimpanzees. Early hominins apparently relied on eating C<sub>4</sub> plants and USOs, both of which have yet to be shown to be important in the diets of chimpanzees, despite recent prominent findings (Hernandez-Aguilar *et al.* 2007). When drinking water runs short, that is, during the dry season when water table drops below the surface, chimpanzees turn to digging wells when riverbeds are sandy enough to allow this (Hunt & McGrew 2002). Although the wells are dug by hand, leaf sponges are used to extract water from the wells; it would not be surprising to find digging tools used to dig wells in other substrates, e.g. mud, gravel, etc.

On a day-to-day basis, chimpanzees must find ephemeral food. Frugivores in particular must find and monitor clumps of food that should be eaten at peak ripeness and which varies from year to year in availability. The same grove that yielded a bumper crop last year may not fruit at all this year. The biodiverse array of trees, shrubs and lianas, much less non-woody plants, may present a potential cornucopia of food, but the daily challenge is how to be in the right place at the right time. Various hypotheses have been put forward as to how chimpanzees achieve this, but the strategy turns out to be simple:

Normand *et al.* (2009) showed that chimpanzees in the Taï Forest memorize the locations of thousands of individual trees. Modelling of the apes' powerful spatial memory allows for their 'rules' of foraging to be inferred, e.g. travel longer distances to resources that allow longer feeding bouts, revisit more often sources where you last ate for long periods.

But how to acquire such information? Murray *et al.* (2008) showed at Gombe that even in adulthood and long after their mothers have died, males return to the core ranges used by their mothers, especially in lean times. Resource locations learned during dependent infancy are harvested lifelong.

It is all very well to know *what* resources are in the home range, but how to know *where* they are, that is, how to navigate optimally between them? Again, various hypotheses have been proposed, e.g. spatial

orientation by means of landmarks. Normand & Boesch (2009) show from data on travel directions and distances that Tāi chimpanzees have sophisticated mental maps, that is, cognitive two-dimensional representations of the landscape that allow them to travel from resource to resource in straight lines.

## 2. DISCUSSION

What can now be said about the LCA, based on what has been learned over the past 5 years from field studies of wild chimpanzees?

Technology is the obvious starting point:

- Given the large and varied tool kits of the chimpanzee, we can expect that of the LCA to be similar. That is, tools were made and used not just for food acquisition and processing, but also in self-maintenance and shelter, as well as in social and sexual life (not covered here). However, just as the size of tool repertoire in chimpanzees is a function of research effort, so it will be in recovering the material culture of the LCA.
- Most of the presumed technology of the LCA is archaeologically unrecoverable, given its perishable, organic nature; thus the archaeological record is biased towards lithics. Short of a time machine, this problem is insoluble, but aspects of chimpanzee behaviour that are universal, such as bed-making or leaf-sponging, are hard to deny to the LCA.
- As with chimpanzees, the material culture of the LCA will show inter- and intra-regional differences (e.g. Schoening *et al.* 2008). Just as nut-cracking differs between East and West Africa (Morgan & Abwe 2006), despite the common presence of both prey and raw materials (McGrew *et al.* 1997), so it is for the LCA. Similarly, just as extractive foraging for social insects is central to Tanzanian populations of chimpanzees, but is largely absent in the neighbouring country of Uganda, so we should not be surprised to find such differences in e.g. Kenyan and Ethiopian populations of a species of hominin.
- Subsistence technology in chimpanzees involves reuse of artefacts, whether these are nut-cracking hammers or ant-dipping wands. Especially given that the extent of reuse seems to be a function of availability of raw materials (and some African forests afford no surface stones bigger than a walnut, e.g. Lui Kotale, W. C. McGrew & L. F. Marchant 2006, unpublished data), the same is expected of the LCA. Just as at Bossou, reuse of stone tools may increase the probability of predictable fracture or amplified use—wear that would leave archaeological signatures in the resulting artefacts. Lack of data on curation of tools by apes in nature may reflect lack of precise study, as evidence exists of such premeditated storage in captivity (Osvath 2009).
- Given tool sets in chimpanzees, we should expect the same in the LCA. But how to recognize sequential use from a static assemblage? This is further complicated by findings that anvils may

become hammers, as they are modified by use (Carvalho *et al.* 2009). That is, tools may change functional categories. (Studies of refitting may help to distinguish reduction products from tool sets; e.g. Delagnes & Roche 2005). Moreover, application of knowledge from ape tool sets may help make sense of patterned heterogeneity in archaeological assemblages, as revealed by multivariate statistical analyses.

- Composite tools probably were used by the LCA, but the challenge is to recognize such combinations in recovered lithic assemblages. It is not always clear what was the goal of reduction sequences in knapping, such as core or flake. The best candidate still may be pounding technology, as it seems likely that flaked stone did not spring *de novo* with the Oldowan, but more probably evolved from earlier lithic percussion for other reasons. Perhaps the analogues to chimpanzee hammers and anvils are there to be found in deposits older than 2.6 Ma? Primatologists should be able to help in seeking the pre-Oldowan (Haslam *et al.* 2009), based on reliably recognized modifications from chimpanzee hammers and anvils. This may help to clarify persisting confusion and controversy (e.g. Mora & de la Torre (2005) versus Diez-Martin *et al.* (2009)) among archaeologists.
- Apart from their nest-building, chimpanzees have few compound artefacts. In the evolution of human elementary technology, much is made of the first evidence of hafted weapons, that is, a compound tool of shaft, point and fixative. However, arguably, the earliest known compound technology was necklaces of snail shells, as found in Blombos Cave, South Africa (Henshilwood *et al.* 2004). Whether or not the LCA had compound tools is unclear, especially as not all components survive equally well, e.g. the spear's shaft versus its point, the necklace's string versus its shells.
- Studies of the acquisition and development of chimpanzee technology remind us that some proportion of what is found archaeologically is probably the immature version of the polished adult form of material culture. How much debitage reflects 'honest' mistakes by youthful learners versus clumsy or misguided efforts by adults? This problem probably applies as well to the LCA. Actualistic studies of children of various ages learning to knap stone might be useful.
- Finally, we must repeatedly remind ourselves that the LCA was almost certainly not a chimpanzee, and vice versa. Just as living apes continue to reveal new kinds of technology, so should we expect the same from the LCA. If chimpanzees turn out not to use tools to make other tools, or lack important but basic material cultural items like the container, or do not transport objects over long distances, we may have found important hominin watersheds (cf. Wynn & McGrew 1989).

Regarding diet:

- Chimpanzee opportunistic omnivory is clear, and so it is probably in the LCA. The same inference

derives from increasing evidence of dietary overlap (e.g. monkey-hunting) between chimpanzee and bonobo, although important differences remain between these taxa (e.g. extractive foraging for insects).

- Recent findings of chimpanzee use of USOs paradoxically show apes to be capable of harvesting these foodstuffs, yet in no known population are they a staple (cf. Hockings *et al.* 2009, for data on USOs as fallback foods). Experimental studies need to be done on the limits of chimpanzee-digging. Similarly, chimpanzees commonly consume the pith of C4 plants, yet not the seeds or corms, and so their stable isotope data are confusing (Sponheimer *et al.* 2006). (It seems likely that staple exploitation of cereals requires grinding technology, which seems to be absent in wild chimpanzees, but apparently has not been tested with apes in captivity.) Or, it may be that profitable use of USOs and cereals requires treatment by fire, that is, cooking, which came much later in human evolution (Carmody & Wrangham 2009). Here, studies of wild chimpanzees are not yet helpful in hypothesizing about the LCA.
- Chimpanzees are wide-ranging foragers, and their patterns of ranging map onto the distribution of their resources, as in any other organism. What we now are beginning to know is the extent of their *intelligent* foraging, and it exceeds our expectations, e.g. about spatial memory. This upgrades our estimation of the LCA, but inferring the timing and spacing of resources in the archaeological record is problematic.
- Recent findings on chimpanzee hunting confirm its seductiveness for evolutionary scenarios. (Conversely, scavenging's role seems less and less important, at least until after the LCA, in the hominin lineage.) However, estimations of the importance of hunting, based on chimpanzees, must be tempered: Most chimpanzee hunting is done arboreally, by 'four-handed' hunters who can leap about in the canopy, pursuing monkeys. This is not likely to be instructive about hunting by terrestrial bipeds, even if it applies to the LCA, who may have practised ambush hunting on the ground, as well as pursuit hunting in the treetops. More significantly, the function of carnivory is revealed to be much richer than expected: sharing meat may drive social and sexual life, almost as a currency (although many of the same arguments probably apply also to honey).

#### On shelter:

- Based on the near-uniformity of arboreal overnight sleeping off the ground in great apes, it seems likely that the LCA did the same. It may be that safe terrestrial sleeping came much later, with the domestication of fire (Pruetz & LaDuke 2010). But we now know that cave use, at least during the day, did not depend on fire, and that thermoregulation needs could have been for diurnal cooling, rather than nocturnal heat retention. However,

most chimpanzee field sites do not offer caves, although this has never been systematically studied.

- We now know that chimpanzee nests are more complex structures than hitherto realized, and this may imply that beyond a certain point of investment of time and effort, they began to be reused. This raises the possibility of home bases, already hinted at in the non-random distribution of chimpanzee nest sites on the landscape. But until we know the fitness-enhancing function of beds, it would be rash to infer the same for the LCA. Anti-predation is assumed, but equally attractive alternative hypotheses are there to be tested. The presence of ground nests is sometimes presumed to be based on local release from predation, but no correlative study of sympatric large carnivores and apes has been done.

#### On ranging and foraging:

- Chimpanzees are nomadic over areas that can be large, that is, tens or even hundreds of square kilometres. If the single most obvious influence on this ranging is food availability, the more crucial limiting factors may be drinking water and cover. Well-digging, especially with the technological assistance of digging tools and containers, appears to allow an expanded ecological niche. (Unlike temperature or humidity, which turn out not to be so important.) Similarly, no matter how dry and open the eco-type inhabited, every known population of great apes seems to require access to trees for shelter construction. Even savannah-dwelling chimpanzees need their ribbons of gallery forest. The same was probably true of the LCA.

In conclusion, even if one-tenth of what has been learned in the last five years about wild chimpanzees is applicable to the LCA of living apes and humans, then the case has been made for preserving them. Referential modelling requires living proxies upon which to base the models, and current expectations are that wild populations of great apes may be gone by the middle of the current century. Both primatologists and palaeoanthropologists should work together to save them.

Most of the author's data and ideas were supported by the US National Science Foundation, Researching Hominid Origins Initiative (Award no. BCS-0321893) grant awarded to Tim White and to the late Clark Howell. I am grateful to S. Carvalho, L. F. Marchant, P. Mellars and A. Walker for comments on the manuscript.

#### REFERENCES

- Biro, D., Carvalho, S. & Matsuzawa, T. In press. Tools, traditions, and technologies: interdisciplinary approaches to chimpanzee nut-cracking. In *The mind of the chimpanzee: ecological and experimental perspectives* (eds E. V. Lonsdorf, S. R. Ross & T. Matsuzawa). Chicago, IL: University of Chicago Press.
- Boesch, C., Head, J. & Robbins, M. M. 2009 Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *J. Hum. Evol.* **56**, 560–569. (doi:10.1016/j.jhevol.2009.04.001)

- Brewer, S. M. & McGrew, W. C. 1990 Chimpanzee use of a tool-set to get honey. *Folia Primatol.* **54**, 100–104. (doi:10.1159/000156429)
- Carmody, R. & Wrangham, R. W. 2009 The energetic significance of cooking. *J. Hum. Evol.* **57**, 379–391. (doi:10.1016/j.jhevol.2009.02.011)
- Carvalho, S., Cunha, E., Sousa, C. & Matsuzawa, T. 2008 *Chaines operatoires* and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut-cracking. *J. Hum. Evol.* **55**, 148–163. (doi:10.1016/j.jhevol.2008.02.005)
- Carvalho, S., Biro, D., McGrew, W. C. & Matsuzawa, T. 2009 Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Anim. Cogn.* **12**(Suppl. 1), 103–114. (doi:10.1007/s10071-009-0271-7)
- Copeland, S. 2007 Vegetation and plant reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs. *J. Hum. Evol.* **53**, 146–175. (doi:10.1016/j.jhevol.2007.03.002)
- Copeland, S. 2009 Potential hominin plants foods in northern Tanzania: semi-arid savannas versus savanna chimpanzee sites. *J. Hum. Evol.* **57**, 365–378. (doi:10.1016/j.jhevol.2009.06.007)
- Deblauwe, I., Guislain, P., Dupain, J. & van Elsacker, L. 2006 Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *Am. J. Primatol.* **68**, 1191–1196. (doi:10.1002/ajp.20318)
- Delagnes, A. & Roche, H. 2005 Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya. *J. Hum. Evol.* **48**, 435–472. (doi:10.1016/j.jhevol.2004.12.005)
- Diez-Martin, F., Sanchez, P., Dominguez-Rodrigo, M., Mabulla, A. & Barba, R. 2009 Were Olduvai hominins making butchering tools or battering tools? Analysis of a recently excavated lithic assemblage from BK (Bed II, Olduvai Gorge, Tanzania). *J. Anthropol. Archaeol.* **28**, 274–289. (doi:10.1016/j.jaa.2009.03.001)
- Fowler, A. & Sommer, V. 2007 Subsistence technology of Nigerian chimpanzees. *Int. J. Primatol.* **28**, 997–1023. (doi:10.1007/s10764-007-9166-0)
- Gilby, I. C. 2006 Meat sharing among Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* **71**, 953–963. (doi:10.1016/j.anbehav.2005.09.009)
- Gomes, C. M. & Boesch, C. 2009 Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE* **4**, e5116. (doi:10.1371/journal.pone.0005116)
- Goodall, J. & Hamburg, D. A. 1974 Chimpanzee behavior as a model for the behavior of early man. New evidence on possible origins of human behavior. *Am. Handb. Psychiat.* **6**, 14–43.
- Hansell, M. H. 2004 *Animal architecture*. Oxford, UK: Oxford University Press.
- Haslam, M. *et al.* 2009 Primate archaeology. *Nature* **460**, 339–344. (doi:10.1038/nature08188)
- Heaton, J. L. & Pickering, T. R. 2006 Archaeological analysis does not support intentionality in the production of brushed ends on chimpanzee termiting tools. *Int. J. Primatol.* **27**, 1619–1633. (doi:10.1007/s10764-006-9091-7)
- Henshilwood, C. A., d'Errico, F., Vanhaeren, M., van Niekerk, K. & Jacobs, Z. 2004 Middle Stone Age shell beads from South Africa. *Science* **304**, 404. (doi:10.1126/science.1095905)
- Hernandez-Aguilar, A. 2009 Chimpanzee nest distribution and site re-use in a dry habitat: implications for early hominin ranging. *J. Hum. Evol.* **57**, 350–364. (doi:10.1016/j.jhevol.2009.03.007)
- Hernandez-Aguilar, A., Moore, J. & Pickering, T. R. 2007 Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proc. Natl Acad. Sci. USA* **104**, 19 210–19 213. (doi:10.1073/pnas.0707929104)
- Hicks, T. C., Fouts, R. S. & Fouts, D. H. 2005 Chimpanzee (*Pan troglodytes troglodytes*) tool use in the Ngotto Forest, Central African Republic. *Am. J. Primatol.* **65**, 221–237. (doi:10.1002/ajp.20111)
- Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G. & Matsuzawa, T. 2007 Chimpanzees share forbidden fruit. *PLoS ONE* **2**, e886. (doi:10.1371/journal.pone.0000886)
- Hockings, K. J., Anderson, J. R. & Matsuzawa, T. 2009 Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa. *J. Hum. Evol.* **58**, 227–233 (doi:10.1016/j.jhevol.2009.11.004)
- Hohmann, G. & Fruth, B. 2008 New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatol.* **79**, 103–110. (doi:10.1159/000110679)
- Humle, T., Snowdon, C. T. & Matsuzawa, T. 2009 Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim. Cogn.* **12**, 37–48. (doi:10.1007/s10071-009-0272-6)
- Hunt, K. D. & McGrew, W. C. 2002 Chimpanzees in the dry areas of Assirik, Senegal, and Semliki Wildlife Reserve, Uganda. In *Behavioural diversity in chimpanzees and bonobos* (eds C. Boesch, G. Hohmann & L. F. Marchant), pp. 35–51. Cambridge, UK: Cambridge University Press.
- Kano, T. 1992 *The last ape: pygmy chimpanzee behavior and ecology*. Stanford, CA: Stanford University Press.
- Koops, K., Humle, T., Sterck, E. H. M. & Matsuzawa, T. 2007 Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: Environmentally or socially determined? *Am. J. Primatol.* **69**, 407–419. (doi:10.1002/ajp.20358)
- Koops, K., McGrew, W. C. & Matsuzawa, T. 2010 Do chimpanzees (*Pan troglodytes*) use cleavers and anvils to fracture *Treculia africana* fruits? Preliminary data on a new form of percussive technology. *Primates* **51**, 175–178. (doi:10.1007/s.10329-009-0178-6)
- Lanjouw, A. 2002 Behavioural adaptations to water scarcity in Tongo chimpanzees. In *Behavioural diversity in chimpanzees and bonobos* (eds C. Boesch, G. Hohmann & L. F. Marchant), pp. 52–60. Cambridge, UK: Cambridge University Press.
- Ling, V., Hernandez-Aguilar, A., Haslam, M. & Carvalho, S. 2009 The origins of percussive technology; a smashing time at Cambridge. *Evol. Anthropol.* **18**, 48–49. (doi:10.1002/evan.20197)
- Lonsdorf, E. V. 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. (doi:10.1007/s10071-005-0002-7)
- Lovejoy, C. O. 2009 Reexamining human origins in light of *Ardipithecus ramidus*. *Science* **326**, 74e1–74e8. (doi:10.1126/science.1175834)
- Marchant, L. F. & McGrew, W. C. 2004 Percussive technology: chimpanzee baobab smashing and the evolutionary modeling of hominid knapping. In *Stone knapping: the necessary conditions for a uniquely hominin behaviour?* (eds V. Roux & B. Brill), pp. 341–350. Cambridge, UK: McDonald Institute for Archaeological Research.
- Matsuzawa, T. 2006 Sociocognitive development in chimpanzees: a synthesis of laboratory work and fieldwork. In *Cognitive development in chimpanzees* (eds T. Matsuzawa, M. Tomonaga & M. Tanaka), pp. 3–33. Tokyo, Japan: Springer.



- 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 *Primate origins of human cognition and behavior* (ed. T. Matsuzawa), pp. 557–574. Tokyo, Japan: Springer.
- McBrearty, S. & Jablonski, N. G. 2005 First fossil chimpanzee. *Nature* **437**, 105–108. (doi:10.1038/nature.04008)
- McGrew, W. C. 1974 Tool use by wild chimpanzees in feeding upon driver ants. *J. Hum. Evol.* **3**, 501–508. (doi:10.1016/0047-2484(74)90010-4)
- McGrew, W. C. 1981 The female chimpanzee as a human evolutionary prototype. In *Woman the gatherer* (ed. F. Dahlberg), pp. 35–73. New Haven, CT: Yale University Press.
- McGrew, W. C. 1992 *Chimpanzee material culture: implications for human evolution*. Cambridge, UK: Cambridge University Press.
- McGrew, W. C. 2004 *The cultured chimpanzee: reflections on cultural primatology*. Cambridge, UK: Cambridge University Press.
- McGrew, W. C., Ham, R. M., White, L. T. J., Tutin, C. E. G. & Fernandez, M. 1997 Why don't chimpanzees in Gabon crack nuts? *Int. J. Primatol.* **18**, 353–374. (doi:10.1023/A:1026382316131)
- Mercader, J., Panger, M. & Boesch, C. 2002 Excavation of a chimpanzee stone tool site in the African rainforest. *Science* **296**, 1452–1455. (doi:10.1126/science.1070268)
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R. & Boesch, C. 2007 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proc. Natl Acad. Sci. USA* **104**, 3043–3048. (doi:10.1073/pnas.0607909104)
- Mitani, J. C., Watts, D. P. & Muller, M. N. 2002 Recent developments in the study of wild chimpanzee behavior. *Evol. Anthropol.* **11**, 9–25. (doi:10.1002/evan.10008)
- Moore, J. J. 1996 Savanna chimpanzees, referential models and the last common ancestor. In *Great ape societies* (eds W. C. McGrew, L. F. Marchant & T. Nishida), pp. 275–292. Cambridge, UK: Cambridge University Press.
- Mora, R. & de la Torre, I. 2005 Percussion tools in Olduvai Beds I and II (Tanzania): implications for early human activities. *J. Anthropol. Archaeol.* **24**, 179–192. (doi:10.1016/j.jaa.2004.12.001)
- Morgan, B. J. & Abwe, E. E. 2006 Chimpanzees use stone hammers in Cameroon. *Curr. Biol.* **16**, R632–R633. (doi:10.1016/j.cub.2006.07.045)
- Murray, C. M., Gilby, I. C., Mane, S. V. & Pusey, A. E. 2008 Adult males inherit maternal ranging patterns. *Curr. Biol.* **18**, 20–24. (doi:10.1016/j.cub.2007.11.044)
- Nishida, T., Matsusaka, T. & McGrew, W. C. 2009 Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates* **50**, 23–36. (doi:10.1007/s10329-008-0109-y)
- Normand, E. & Boesch, C. 2009 Sophisticated Euclidean maps in forest chimpanzees. *Anim. Behav.* **77**, 1195–1201. (doi:10.1016/anbehav2009.01.025)
- Normand, E., Ban, S. D. & Boesch, C. 2009 Forest chimpanzees (*Pan troglodytes verus*) remember the location of numerous fruit trees. *Anim. Cogn.* **12**, 797–807. (doi:10.1007/s10071-009-0239-7)
- Osvath, M. 2009 Spontaneous planning for future stone throwing by a male chimpanzee. *Curr. Biol.* **19**, R190–R191. (doi:10.1016/j.cub.2009.01.010)
- Pruetz, J. D. 2007 Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. *Primates* **48**, 316–319. (doi:10.1007/s10329-007-0038-1)
- Pruetz, J. D. & Bertolani, P. 2007 Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr. Biol.* **17**, 412–417. (doi:10.1016/j.cub.2006.12.042)
- Pruetz, J. D. & Bertolani, P. 2009 Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: implications for hominin adaptations to open habitats. *Palaeoanthropology* **2009**, 252–262. (doi:10.4207/PA.2009.ART33)
- Pruetz, J. D. & LaDuke, T. C. 2010 Reaction to fire by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: conceptualization of 'fire behavior' and the case for a chimpanzee model. *Am. J. Phys. Anthropol.* **141**, 646–650. (doi:10.1002/ajpa.21245)
- Sanz, C. M. & Morgan, D. B. 2007 Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *J. Hum. Evol.* **52**, 420–433. (doi:10.1016/j.jhevol.2006.11.001)
- Sanz, C. M. & Morgan, D. B. 2009 Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *Int. J. Primatol.* **30**, 411–427. (doi:10.1007/s10764-009-9359-5)
- Sanz, C., Call, J. & Morgan, D. 2009a Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* **5**, 293–296. (doi:10.1098/rsbl.2008.0786)
- Sanz, C. M., Schoening, C. & Morgan, D. B. 2009b Chimpanzees prey on driver ants with specialized tool set. *Am. J. Primatol.* **71**, 1–8. (doi:10.1002/ajp.20744)
- Sayers, K. & Lovejoy, C. O. 2008 The chimpanzee has no clothes. A critical examination of *Pan troglodytes* in models of human evolution. *Curr. Anthropol.* **49**, 87–114. (doi:10.1086.523765)
- Schoening, C., Humle, T., Moebius, Y. & McGrew, W. C. 2008 The nature of culture: technological variation in chimpanzee predation on army ants revisited. *J. Hum. Evol.* **55**, 48–59. (doi:10.1016/j.jhevol.2007.12.002)
- Sousa, C., Biro, D. & Matsuzawa, T. 2009 Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): acquisition patterns and handedness. *Anim. Cogn.* **12**, S115–S125. (doi:10.1007/s.10071-009-0278-0)
- Sponheimer, M., Loudon, J. E., Codron, C., Howells, M. E., Pruetz, J. D., Codron, J., de Ruiter, D. J. & Lee-Thorp, J. A. 2006 Do 'savanna' chimpanzees consume C<sub>4</sub> resources? *J. Hum. Evol.* **51**, 128–133. (doi:10.1016/j.jhevol.2006.02.002)
- Stanford, C. B. 1999 *The hunting apes. Meat eating and the origins of human behavior*. Princeton, NJ: Princeton University Press.
- Stewart, F. A., Pruetz, J. D. & Hansell, M. H. 2007 Do chimpanzees build comfortable nests? *Am. J. Primatol.* **69**, 930–939. (doi:10.1002/ajp.20432)
- Sugiyama, Y. 1997 Social tradition and the use of tool-composites by wild chimpanzees. *Evol. Anthropol.* **6**, 23–27. (doi:10.1002/(SICI)1520-6505(1997)6:1<23::AID-EVAN7>3.0.CO;2-X)
- Surbeck, M. & Hohmann, G. 2008 Primate hunting by bonobos at LuiKotale, Salonga National Park. *Curr. Biol.* **18**, R906–R907. (doi:10.1016/j.cub.2008.08.040)
- Tennie, C., Gilby, I. C. & Mundry, R. 2009 The meat-scrap hypothesis: small quantities of meat may promote cooperative hunting in wild chimpanzees (*Pan troglodytes*). *Behav. Ecol. Sociobiol.* **63**, 421–431. (doi:10.1007/s00265-008-0676-3)
- Tooby, J. & DeVore, I. 1987 The reconstruction of hominid behavioral evolution through strategic modeling. In *The evolution of human behavior: primate models* (ed. W. G. Kinzey), pp. 183–237. Albany, NY: State University of New York Press.
- Toth, N. & Schick, K. 2009 The Oldowan: the tool making of early hominins chimpanzees compared.

- Ann. Rev. Anthropol.* **38**, 289–305. (doi:10.1146/annurev-anthro-091908-164521)
- Watts, D. P. 2008*a* Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioral ecology. *J. Hum. Evol.* **54**, 125–133. (doi:10.1016/j.jhevol.2007.07.008)
- Watts, D. P. 2008*b* Tool use by chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* **29**, 83–94. (doi:10.1007/s10764-007-9227-4)
- Watts, D. P. & Mitani, J. C. 2002 Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* **23**, 1–28. (doi:10.1023/A:1013270606320)
- Whiten, A. *et al.* 2010 Studying extant species to model our past. *Science* **327**, 410. (doi:10.1126/science.327.5964.410-a)
- Wynn, T. G. & McGrew, W. C. 1989 An ape's view of the Oldowan. *Man* **24**, 383–398. (doi:10.2307/2802697)
- Yamakoshi, G. & Sugiyama, Y. 1995 Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. *Primates* **36**, 489–500. (doi:10.1007/BF02382871)