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## **The conditions for tool use in primates: implications for the evolution of material culture**

In order to identify the conditions that favored the flourishing of primate tool use into hominid technology, we examine inter- and intraspecific variation in manufacture and use of tools in extant nonhuman primates, and develop a model to account for their distribution. We focus on tools used in acquiring food, usually by extraction. Any model for the evolution of the use of feeding tools must explain why tool use is found in only a small subset of primate species, why many of these species use tools much more readily in captivity, why routine reliance on feeding tools is found in only two species of ape, and why there is strong geographic variation within these two species. Because ecological factors alone cannot explain the distribution of tool use in the wild, we develop a model that focuses on social and cognitive factors affecting the invention and transmission of tool-using skills. The model posits that tool use in the wild depends on suitable ecological niches (especially extractive foraging) and the manipulative skills that go with them, a measure of intelligence that enables rapid acquisition of complex skills (through both invention and, more importantly, observational learning), and social tolerance in a gregarious setting (which facilitates both invention and transmission). The manipulative skills component explains the distribution across species of the use of feeding tools, intelligence explains why in the wild only apes are known to make and use feeding tools routinely, and social tolerance explains variation across populations of chimpanzees and orang-utans. We conclude that strong mutual tolerance was a key factor in the explosive increase in technology among hominids, probably intricately tied to a lifestyle involving food sharing and tool-based processing or the acquisition of large, shareable food packages.

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### **Introduction**

Material culture is one of the hallmarks of the human species. The origins of our material culture are often sought in Plio-Pleistocene hominids who are known to have used stone tools and probably also a variety of nonstone tools. However, hominids were probably not the first primates to do so, as some extant primates also make and use tools. In this paper we develop a model to explain the variation in the manu-

facture and use of tools among and within nonhuman primate species. If the model survives further testing it should inform speculation on the causes of the flourishing of primate tool use into the elaborate material culture of hominids.

Nonhuman primates show at least six functionally different modes of tool use (*sensu* Beck, 1980). First, many arboreal species dislodge branches, and terrestrial species dislodge rocks from cliff faces, to intimidate predators or rivals. Kortlandt &

Kooij (1963) and Hall (1963) consider this the basic tool use from which all other forms have been derived. It involves no manufacture and only crude manipulation, and is virtually universal in primates large enough to dislodge objects (see Table 1). The second form, defensive tool use, involving aimed clubbing and hitting of potential predators, is an elaboration of intimidation displays. It is quite rare even though the context is not (chimpanzees: Kortlandt & Kooij, 1963; capuchin monkeys: Boinski, 1988). Third, tools are made and used as hunting weapons, but only by hominids (Klein, 1989). Fourth, wild chimpanzees incorporate tools into social displays meant to attract rather than intimidate conspecifics, e.g., the leaf clipping display (McGrew, 1992). Although this may contribute to fitness, the tool use is arbitrary and derives its meaning from the universal use within a population; signals not involving tool use are expected to be equally effective. Fifth, objects (often leaves) may be used to clean body parts. This use has been observed in most apes and two monkey species (Tomasello & Call, 1997), but again is rare. Sixth, wild chimpanzees and orangutans make and use tools to extract insects or insect products or to smash nuts (Goodall, 1986; McGrew, 1992; Boesch, 1996; van Schaik *et al.*, 1996; Fox *et al.*, 1998). Some nonhominoid primates also do this occasionally in the wild, and more often in captivity (Beck, 1980; Candland, 1987).

The search for conditions favoring the origins of hominid technology is probably best focused on feeding tools, for several reasons. First, unlike some other forms of tool use, the use of feeding tools can greatly contribute to fitness in extant pre-agricultural people (McGrew, 1992:131), as in great apes (see below). Second, again unlike some other forms, feeding tool use shows strong phylogenetic continuity: population-wide manufacture and use of feeding tools is found only in hominids and

great apes, i.e., the hominoid clade. Third, many of the tools found in hominid sites are thought to be involved in food processing (Klein, 1989). Finally, feeding tools are more likely to require modification than other kinds of tools used by nonhuman primates; most great ape tool users learn to make feeding tools through some form of social learning, comparable to those involved in human material culture. Hence, this paper focuses on feeding tools.

#### *The distribution of tool use and manufacture*

Explanation of the evolution of material culture requires an overview of the manufacture and use of tools among primates in the wild and in captivity. Table 1 (second column) shows the taxonomic distribution of documented feeding tool use in primates. Many older reports, especially of digging with tools recounted by Kortlandt & Kooij (1963) and Beck (1980), are not included in Table 1, for lack of sufficiently detailed description and confirmation in spite of extensive subsequent field studies. Nonetheless, cases of possibly anecdotal or idiosyncratic (cf. McGrew & Marchant, 1997) tool use have been included if reliable primary reports were available, because they do reflect the capacity of the species. For both wild and captive information we must address the problem of negative evidence. Published field data now exist for over 150 nonhuman primate species (Nunn & van Schaik, *in press*), and primates have been studied intensively in zoos and institutions around the world. Hence, we presume that tool use, if it is routinely present in a species, has been reported in the literature. We also presume, therefore, that the distributional information is reasonably complete.

In the wild, only a few species have been observed to use feeding tools. There are various reports for capuchin monkeys (*Cebus* spp.). An adult male *C. apella* was observed using a piece of oyster shell to pound on other oysters (Fernandes, 1991), a subadult

**Table 1** The distribution of tool use among non-human primate genera: object-throwing and use of feeding tools

Genus	Throwing objects	Feeding tools*
<i>Otolemur</i>		N
<i>Galago</i>		N
<i>Galagoides</i>		N
<i>Nycticebus</i>		N
<i>Loris</i>		N
<i>Perodicticus</i>		N
<i>Cheirogaleus</i>		N
<i>Mirza</i>		N
<i>Microcebus</i>		N
<i>Lemur</i>		N
<i>Eulemur</i>		N
<i>Hapalemur</i>		N
<i>Varecia</i>		N
<i>Propithecus</i>		N
<i>Indri</i>		N
<i>Daubentonia</i>		N
<i>Tarsius</i>		N
<i>Callithrix</i>		N
<i>Cebuella</i>		N
<i>Saguinus</i>		N
<i>Leontopithecus</i>		N
<i>Callimico</i>		N
<i>Saimiri</i>	Y	N
<i>Cebus</i>	Y	U, C
<i>Aotus</i>		N
<i>Cellicebus</i>		N
<i>Cacajao</i>		N
<i>Pithecia</i>	Y	N
<i>Chiropotes</i>		N
<i>Alouatta</i>	Y	N
<i>Ateles</i>	Y	N
<i>Brachyteles</i>		N
<i>Lagothrix</i>	Y	N
<i>Macaca</i>	Y	U, C
<i>Cercocebus</i>		C
<i>Papio</i>	Y	U, C
<i>Mandrillus</i>	Y	C
<i>Theropithecus</i>		N
<i>Cercopithecus</i>	Y	C
<i>Erythrocebus</i>	Y	C
<i>Colobus</i>	Y	N
<i>Presbytis</i>	Y	N
<i>Nasalis</i>	Y	N
<i>Hylobates</i>	Y	C
<i>Pongo</i>	Y	U, M, C
<i>Pan</i>	Y	U, M, C
<i>Gorilla</i>	Y	C

Based on Beck (1980), Candland (1987), and Tomasello & Call (1997), and various references mentioned in the text. Y=present; N=absent; \*U=use of tools in the wild; M=manufacture of tools in wild; C=tool use in captivity.

male *C. capucinus* was once seen to insert a stick into a treehole, pull it out and put it into his mouth (Chevalier-Skolnikoff, 1990), and a few young *C. albifrons* were seen to use leaves to scoop up water from tree holes (Philipps, 1998). There are several observations of long-tailed and lion-tailed macaques (*Macaca fascicularis*, *M. silenus*) rolling hairy caterpillars in leaves until the stinging hairs are removed (Chiang, 1967; Hohmann, 1988). A male baboon (*Papio anubis*) was once seen using a twig to extract small stone fragments from a sticky soil matrix (Oyen, 1979). Beck (1980) reports on several observations of baboons (especially *P. ursinus*) using stones to pound on scorpions, etc.

Two features stand out in the feeding-tool use of wild monkeys. First, none of this tool use is habitual or customary [in McGrew & Marchant's (1997) classification] in the populations concerned (i.e., shown by many different individuals, regularly or predictably). Second, none of it involves manufacture: animals use objects as they find them. Thus, only chimpanzees and orang-utans are known to manufacture and use feeding tools on a regular, population-wide basis, in at least some wild populations.

Table 1 shows that in captivity feeding-tool use is more widespread. The published reports show remarkable overlap and clustering into a few taxa, the non-folivorous catarrhines and capuchins, for both feeding tools and other tools (Beck, 1980; Candland, 1987; Tomasello & Call, 1997). The capacity for tool use (but not necessarily actual tool use in the wild) therefore probably evolved three times: in capuchins, cercopithecines, and apes.

For the two ape species with documented manufacture and use of feeding tools in the wild, there is appreciable geographic variation in the overall frequency of the use of feeding tools, in the size of the tool kit used by the animals, and in the specific tasks for which these tools are used (Sugiyama, 1993;

**Table 2** Functionally different food-related tools used (mostly habitually, *sensu* McGrew & Marchandt, 1997) in different chimpanzee populations with long-term studies of well-habituated animals

Tool types	Gombe	Mahale	Kibale	Tai	Bossou
Leaf sponge	×		×	×	×
Termite fish	×	×			
Ant dip	×			×	×
Honey dip	×			×	
Nut hammer				×	×
Ant fish		×			
Bee probe				×	
Marrow pick				×	
Pestle pound					×
Gum gouge					×
Algae scoop					×
Hook stick					×
No. of feeding-tool types	4	2	1	6	7

Based on McGrew (1994), Boesch & Tomasello (1998) and Sugiyama (1993, 1997).

McGrew, 1994; Boesch & Tomasello, 1998). Table 2 furnishes a preliminary summary of geographic variation in chimpanzee feeding-tool use. Although systematic and quantitative comparisons are still to be undertaken and researchers have differentially emphasized the documentation of different tool types, the comparison is limited to only the best-studied sites with well-habituated populations and contains predominantly tool types that are used habitually or customarily. Among orang-utans, feeding tools are so far known only from a limited region in South Aceh, Sumatra, despite extensive studies elsewhere (van Schaik *et al.*, 1996).

Any successful model for the evolution of the use of feeding tools should explain these four patterns: (1) why tool use beyond object-throwing can be observed in only a few primate clades; (2) why routine reliance on feeding tools and manufacture of tools in the wild is found in only two species of ape; (3) why there is strong geographic variation within the two species regularly using feeding tools; and (4) why tools are more readily used in captivity. The aim of this paper is to develop a model that can account for these

patterns and thus can form the basis for an extrapolation toward the conditions that gave rise to the extraordinary elaboration of tool use in the hominid lineage.

*A model for the evolution of feeding-tool use*  
*Suitable environmental conditions are necessary but not sufficient.* Parker & Gibson (1977) proposed that flexible (“intelligent”) tool use was expected in species “with extractive foraging on seasonally limited embedded foods and an omnivorous diet.” Although this hypothesis may seem plausible, extractive foraging alone cannot account for the whole pattern of tool use: many extractive foragers that are quite capable of tool use and even some tool manufacture in captivity, for example, capuchins (Westergaard & Frigaszy, 1987), show virtually no sustained tool use in the wild.

More subtle effects of ecological conditions can likewise be discounted as a general explanation for the distribution of tool use. While some of the intraspecific variation in the incidence of feeding tool use in chimpanzees (Table 2) and orang-utans can be ascribed to variation in environmental conditions (e.g., McGrew *et al.*, 1979), much of

it cannot. For chimpanzees, Boesch *et al.* (1994) and McGrew *et al.* (1997) compared different sites with and without nut-cracking. They could not find any obvious ecological differences among the sites in terms of abundance of nut trees or suitable hammers and anvils. The nuts are so nutritious that optimal foraging explanations invoking the presence of more profitable alternative foods are implausible. Hence, only geographic barriers explained the distribution, and both studies therefore concluded that the variation was cultural.

Orang-utan data similarly contradict a purely ecological hypothesis. *Neesia* seeds are embedded in irritant hairs that pierce the skin after the fruits have cracked open. At Suaq Balimbing on Sumatra, adult males eat the seeds before the fruit ripens and dehisces by using brute force to open the fruits and thus obtain the seeds. After the fruits open, all age–sex classes use tools to extract the seeds, and thus circumvent the hairs, although adult males occasionally continue to break the woody valves off the fruit. In contrast, in Gunung Palung on the island of Borneo, adult males are the predominant *Neesia* eaters, most of their feeding is on undehisced fruits that are opened with force, and all feeding is without tools. This strong contrast could be ascribed to the fact that other food species in Gunung Palung are more profitable to the local orang-utans. However, these seeds are very nutritious (46% lipids by dry weight) and may provide up to 4.5 Kcals per day to adult males before they dehisce (C. Knott, personal communication). At Suaq Balimbing, *Neesia* is the predominant fruit species for adult females and subadult males during several months. An unusual sequence of closely spaced *Neesia* crops is probably responsible for a birth peak in the population (van Schaik, unpublished data). Hence, it is implausible to argue that the ability to extract *Neesia* seeds is not energetically important for the

Gunung Palung orang-utans (Knott & van Schaik, in prep.).

Both the chimpanzee and orang-utan data indicate that the absence of tool use in a given population reflects the absence of knowledge within that population, rather than the absence of suitable ecological opportunities. Thus, we must also focus on the process through which the tool-using skill is acquired. Ecological explanations implicitly assume that these skills develop through maturation (cf. instinct) or are invented independently through some form of learning. However, acquisition through simple maturation is unlikely because at least some of the skills are highly complex (Boesch, 1993) and the contexts are varied. Acquisition through independent discovery of tool-using skills is unlikely for the same reasons and because of the uniformity within populations relative to the variability between populations (Boesch, 1996). The patterns therefore suggest that social learning is the predominant mode of skill acquisition in most individual apes in the wild.

*A socioecological model for tool use.* A complete model of the evolution of tool-using skills in primates should therefore contain the following elements: (1) ecological opportunities for feeding tool use; (2) sufficiently precise motor control for effective handling of objects; (3) the appropriate mental capabilities to invent or rapidly acquire, through social learning, appropriate tool-handling skills; and (4) social conditions that are appropriate for the social transmission of skills. We hypothesize that an increasing number of these essential elements is represented in ever narrowing subsets of species (Figure 1). Thus, we expect that a subset of extractive foragers will have the manipulative abilities needed to develop tool use, and that a subset of those dexterous species will have the required cognitive abilities and experience the right social conditions to

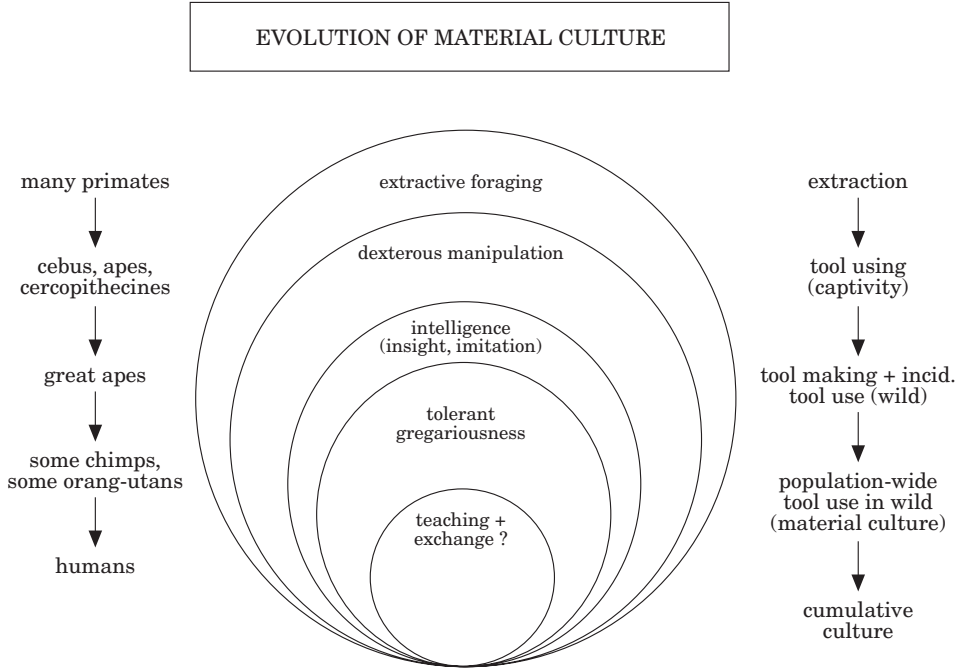


Figure 1. The nested set of conditions hypothesized to favor feeding-tool use, from ecological opportunities and manipulative abilities as preconditions to cognitive factors and social conditions favoring the invention and transmission of tool-using skills in captive or wild populations. On the left side, a summary is given of the taxa meeting the ever-narrowing requirements, on the right side the phenomena shown by the taxa mentioned on the left.

actually invent or learn tool use and tool making in the wild.

The general precondition for all use of feeding tools is a foraging niche that involves extraction (Parker & Gibson, 1977). Most foods eaten by primates are freely accessible, and can be picked with the hands or taken directly with the mouth. However, some food is encased in a matrix from which it needs to be extracted, e.g., insects in tree holes, nutmeat from a hard shell or corms from underground. There are three reasons to expect a strong interspecific association between extractive foraging, complex manipulative abilities, and feeding-tool use. First, almost all feeding tools in primates are used in an extractive foraging context. Second, almost inevitably, extractive foraging requires some level of manipulative skill. Where animals engage in a variety of distinct

extractive tasks, flexible behavior is needed rather than specialized anatomical structures. Hence, flexible extractive foragers are most likely to be capable of manipulations that require fine neuromotor control. Third, more dexterous species are more likely than less dexterous ones to discover tool use as a fortuitous effect of their greater diversity and effectiveness of manipulations, especially if the manipulations involve actions placing an object in relation to a substrate (Menzel, 1966; Fragaszy & Adams-Curtis, 1991). The fact that the invention of tool use by individuals is often accompanied by exploratory or playful actions (Fragaszy & Visalberghi, 1989) supports this idea.

Our model incorporates invention and transmission as factors limiting the incidence of feeding-tool use in gregarious primates that forage extractively. Specifically,



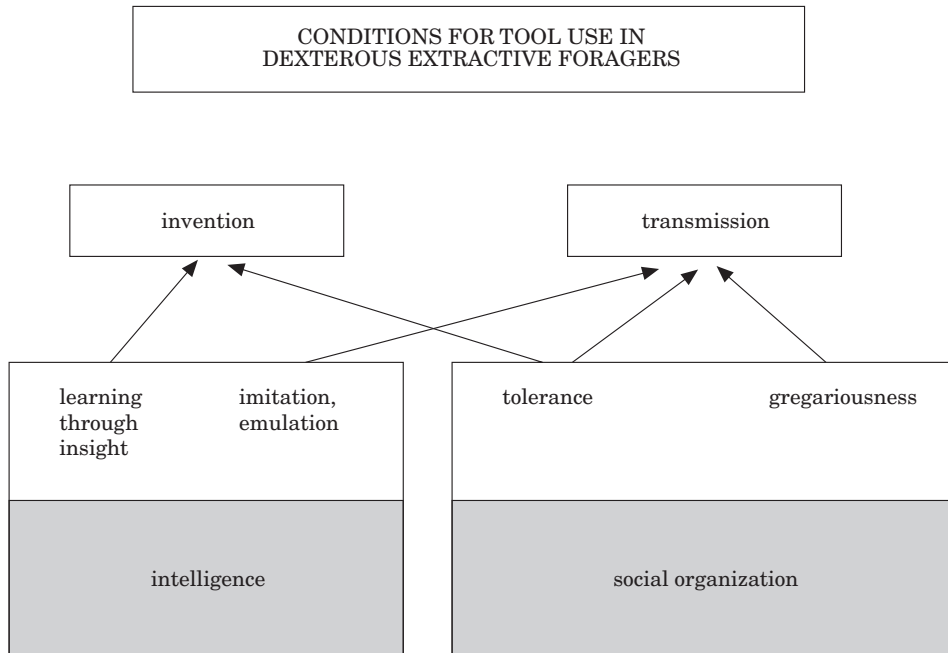


Figure 2. The social and cognitive factors hypothesized to favor the invention and social transmission of feeding-tool use in species physically capable of tool use.

we propose that at any given level of cognition, the probability that an individual invents a new behavior, is a function of the frequency with which the potential for expression occurs. Likewise, at any given level of cognition, the probability that a naive animal will acquire a skill through social transmission is a function of the frequency of opportunities for transmission. This in turn depends on how often the expression of the skill takes place in a context enabling transmission. Thus, two independent sets of factors are involved: the socioecological conditions in which invention or transmission are taking place, and the cognitive mechanisms underlying the invention or transmission process (Figure 2).

Consider invention first. Invention is rarely witnessed, so we know very little about the conditions favoring it (Kummer & Goodall, 1985), although one expects that in most cases, an operant behavior and a suitable target object or constellation of

objects must be present simultaneously. Socioecological context and cognition should also affect the rate of invention. With respect to socioecology, the subject's motivation to explore should not be hindered by social or ecological constraints. Factors enhancing the freedom to explore are reduced vulnerability to predation, and flexible spatial organization of individuals so that animals often feed alone, or, alternatively, high social tolerance. With respect to cognition, intelligent species could make the connection between an action upon an object and the desired outcome without stumbling upon the proper action through operant behavior alone, i.e., intelligent species can learn by insight (e.g., Byrne, 1995). Because the conditions favoring invention are a subset of those favoring social transmission of complex skills (see Figure 2), we focus on the more easily studied aspect of transmission, which is critical for maintenance of tool use in a population.

A new skill, once invented, is maintained in a population only if it spreads beyond the inventor. Obviously, most social transmission in primates is vertical, i.e., from mother to offspring. However, unless one is willing to assume that a new skill, say a form of tool use, becomes established in a population because the matriline of the inventor out-reproduces all other matrilines and eliminates them from the population, horizontal transmission is critical for the establishment of a population-wide technique. Thus, the conditions favoring horizontal transmission must be considered. The probability that a naive animal will socially acquire a skill should be a function of the frequency of opportunities to be present at close quarters when models show skilled tool use and of the efficiency with which this animal can learn from these exposures (cf. Westergaard & Frigaszy, 1987).

Social learning obviously requires a certain degree of gregariousness, which makes it unlikely in solitary or semi-solitary animals that meet infrequently (Figure 2). It also requires close proximity in a feeding context. This is not a trivial condition since most primates spread out during foraging for insects and other dispersed food, the context for most extractive tool use (e.g., van Schaik & van Noordwijk, 1986), and aggression toward subordinates is likely if they come too close to dominants. It has been shown experimentally that animals under risk of attack by conspecifics do not learn well (Fragaszy & Visalberghi, 1990; cf. Inoue-Nakamura & Matsuzawa, 1997). Hence, social tolerance in a potentially competitive foraging context is likely to strongly facilitate social learning (Coussi-Korbel & Fragaszy, 1995). It should do so in at least three ways: (1) it enhances behavioral coordination, and thus may bring animals in close proximity during foraging, making close-range observations possible; (2) it reduces anxiety levels, making it easier for animals to attend to the foraging tasks

(rather than to the risk of attack); and (3) it reduces the risk of losing food to scroungers (cf. Fragaszy & Visalberghi, 1990). Tolerance is expected in a society when its members, despite competing among themselves, are in some way mutually dependent, for example, because they must defend against a common enemy [predators, neighboring groups, or bullying males (van Schaik, 1989; Brereton, 1995)]. (This principle could be extended to the risk of predation, where animals may be able to attend to actions by others more often or for longer where the need for vigilance is reduced.)

Social learning could be accomplished after fewer exposures if the learners are intelligent (Figure 2). Intelligent animals often learn by emulation or imitation (Byrne, 1995), methods which require few exposures. Other animals learn less efficiently through stimulus or local enhancement, in which the naive animal is attracted to the situation in which stimulus and the tool co-occur and then acquires the skill by trial and error (Galef, 1990; Byrne, 1995).

An intelligent animal in a tolerant society would require the fewest exposures to learn a new skill. Natural selection should favor intelligence and social tolerance whenever the ability to use tools is adaptive. However, we do not know how much these two variables had to have changed from their original state before they produced fitness benefits through tool use. Hence, it is more parsimonious to argue that intelligence and social tolerance are more likely to act as preconditions in whose presence there is a highly increased probability that an extractive forager will learn to use feeding tools.

#### *Predictions*

We can now derive the following testable predictions from the model.

- (1) *Extractive foraging*: species showing dexterous manipulation should be a subset of extractive foraging species.



- (2) *Manual dexterity*: all species in which feeding-tool use has been observed, be it in the wild or in captivity, should show dexterous foraging skills in the wild (cf. Parker, 1974; Torigoe, 1985).
- (3) *Intelligence*: intelligent species, defined here as those which can learn through insight and emulation or imitation, require fewer exposures to acquire tool-using skills, be it through invention or through social learning. Hence, we predict that intelligent species (a) are the only ones to show population-wide tool use in the wild, and (b) to manufacture tools in the wild. We also predict that (c) only some captive settings will provide enough opportunities for invention or exposure to skilled users to allow the acquisition of tool use in species lacking insight or observational learning capabilities.
- (4) *Social tolerance*: social tolerance should be correlated with exploratory behavior, and thus invention and (when animals are gregarious) transmission of tool use. In particular, the intraspecific variation among great ape populations in the size of the tool kit should correlate with variation in social tolerance or in gregariousness.

Although some of the predictions under (3) were known to hold approximately before the study, they are examined in more detail here. All of them will either be tested by comparative methods or evaluated by reviewing existing studies.

## Methods

### Measures

*Extractive foraging*. In order to assess species for extractive foraging we examined numerous publications detailing primate feeding techniques (see below). Our preliminary work, however, showed that virtually every well-studied species engages at least occa-

sionally in extractive foraging (cf. King, 1986). In order to test our prediction, therefore, we needed more quantitative measures of extractive foraging, including the frequency, complexity and diversity of extractive foraging tasks. Unfortunately, such information cannot be gleaned from published foraging accounts, so we could not test the extractive foraging prediction.

*Manipulative abilities*. To test the predictions involving manipulative ability, we used three measures: manipulation pattern diversity, object-substrate combination, and bimanual asymmetric coordination (BAC).

Torigoe (1985) presented a knotted rope and wooden cube to 74 species of captive primates, and recorded for each species (1) the diversity of manipulation patterns (e.g., rubbing, rolling or rotating the rope), and (2) the diversity of object-substrate combinations (e.g., rubbing a rope toy on a wire mesh wall, pushing the toy into the wall). Torigoe called these primary and secondary manipulation patterns, respectively. Torigoe's study was a replication and extension of a smaller earlier study by Parker (1974), which is not used here. The two data sets are in general agreement (Parker's action types and Torigoe's primary manipulations are correlated with Pearson's  $r = +0.72$ ,  $n = 8$ ,  $P < 0.05$ , two-tailed).

We define bimanual asymmetric coordination (BAC) as using the hands to perform different but complementary actions on a detached object, e.g., grasping a fruit with one hand and peeling it with the other. BAC indicates manipulative skill because it involves the independent but complementary execution of motor programs (cf. Goldfield & Michel, 1986; Byrne & Byrne, 1993; Fagard & Pez , 1997). We collected data on BAC by reviewing published primate field studies which described foraging techniques because preliminary work suggested that BAC in non-foraging contexts is either extremely rare or is not mentioned in

the literature. We scored a species as engaging in BAC if an account clearly indicated that an individual used two hands simultaneously and asymmetrically in procuring a detached food. Ambiguous accounts were discarded, as were accounts of BAC during tool use (e.g., McGrew, 1974), in order to guarantee independence of the subsequent tests. Most commonly, BAC involved an animal holding a partially processed food with one hand, e.g., a handful of herbs still retaining thorns, and picking at it with the other. Actions such as bimanual digging and food rubbing were not counted unless it was clear that the two hands were used in different roles (see Table 3, first column). We attempted to be comprehensive in reviewing the published information on primate feeding techniques: (1) we systematically examined four primate journals (*Primates*, *Folia Primatologica*, *International Journal of Primatology*, and the *American Journal of Primatology*), carefully reading every English article which seemed even remotely likely to mention feeding techniques; (2) we reviewed several monographs and edited volumes which seemed likely to detail feeding techniques; (3) we examined additional resources as we became aware of their relevance; and (4) we included our personal observations where relevant. Negative evidence is problematic in the absence of reports explicitly stating that BAC does not occur. We therefore excluded taxa which have been poorly studied in the wild. This was quantified by searching the Biological Abstracts database between 1986 and 1997, entering the words "ecology" for each taxon. Only those taxa for which more than ten records were available were scored negatively.

*Measures of social tolerance.* Two classes of measures of tolerance can be used. Direct measures are social: (1) relaxed proximity and grooming, accompanied by low mutual aggression and a high conciliatory tendency

(e.g., Aureli *et al.*, 1997); and (2) the degree to which aggressive actions within a dyad can go in both directions (Thierry, 1985). Other measures stress the nature of feeding competition: (1) frequency of food sharing; and (2) habitat productivity. Both will be used in the tests as needed and available.

#### *Analyses*

For many of the predictions it would be virtually impossible to conduct statistical tests at the species level since there is little overlap among the measures in terms of species availability. We overcame this problem by pooling information at the level of the genus. Torigoe (1985; Figures 1, 6) presents information for species groups, i.e., species of the same genus or of closely related genera. We incorporated this information by assigning to each genus represented in the species group the overall score of the species group, although in statistical analyses the original sample size was retained. Pooling information from lower order taxa is obviously not ideal; however, the possible heterogeneity among species within genera should make our tests more conservative.

Because of the low resolution of the data (BAC being discrete and Torigoe's data referring to species groups), we combined our three manipulation measures, which are highly intercorrelated (see Table 3), into an overall classification of high or low on manipulation abilities. A genus was scored as high if it was on or above the median for object-substrate combination or manipulation pattern diversity (the two measures produce identical classifications), or if it was scored as engaging in BAC (see Table 3). The only conflict between Torigoe's (1985) measures and BAC concerned *Cercopithecus*. Since the BAC evaluation is based upon a literature search rather than direct measurement, it is more likely to be in error. Hence, we classified *Cercopithecus* as being highly manipulative.

**Table 3 Bimanual asymmetric coordination (the number of literature references for ecology, number found providing BAC, and source), and manipulation repertoire (mean number of primary and secondary manipulations from Torigoe, 1985) for primate genera. See text for criteria to decide on high or low manipulation skills**

Genus	Refs	BAC	Primary	Secondary	Evaluation	Source
<i>Daubentonia</i>	10	1			High	1
<i>Haplemur</i>	3					
<i>Eulemur</i>	8		15.45	0.33	Low	
<i>Lemur</i>	7		15.45	0.33	Low	
<i>Indri</i>	1					
<i>Propithecus</i>	5					
<i>Varecia</i>	3		15.45	0.33	Low	
<i>Tarsius</i>	1					
<i>Cebuella</i>	2					
<i>Callimico</i>	1					
<i>Callithrix</i>	13	0	9.51	0	Low	
<i>Saguinus</i>	30	0	9.51	0	Low	
<i>Leontopithecus</i>	9					
<i>Callicebus</i>	7					
<i>Aotus</i>	6					
<i>Chiropotes</i>	2					
<i>Pithecia</i>	4					
<i>Saimiri</i>	11	0			Low	
<i>Cebus</i>	21	2	58.94	3.75	High	2
<i>Alouatta</i>	18	0			Low	
<i>Lagothrix</i>	2		6.7	0	Low	
<i>Brachyteles</i>	4					
<i>Ateles</i>	14	0	6.7	0	Low	
<i>Cercopithecus</i>	41	0	33.25	1.9	High?	
<i>Erythrocebus</i>	3	1			High	3
<i>Cercocebus</i>	6	1	33.33	2.16	High	4
<i>Mandrillus</i>	5		32.6	1	High	
<i>Theropithecus</i>	4		32.6	1	High	
<i>Papio</i>	39	2	32.6	1	High	5
<i>Macaca</i>	65	2	54.63	3.36	High	6
<i>Colobus</i>	26	0	15.12	0	Low	
<i>Presbytis/Trach.</i>	31	0	15.12	0	Low	
<i>Nasalis</i>	6		15.12	0	Low	
<i>Hylobates</i>	13	0	31.71	0	Low	
<i>Pongo</i>	10	1	68.54	7	High	7
<i>Pan</i>	211	2	68.54	7	High	8
<i>Gorilla</i>	32	3	68.54	7	High	9

1: Iwano & Iwakawa, 1988; 2: Izawa & Mizuno, 1977; Tomblin & Cranford, 1994; 3: Hall *et al.*, 1965; 4: Horn, 1987; 5: Rhine & Westlund, 1978; Hamilton & Tilson, 1985; 6: Kawai, 1965; Clark, 1979; 7: van Schaik, personal observation; 8: Bermejo *et al.*, 1994; Uehara, 1990; 9: Casimir, 1975; Goodall, 1977; Byrne & Byrne, 1993.

The patterns were analyzed using standard statistical tests. However, similarity in values among related genera may merely reflect common ancestry, and thus genera may not be statistically independent (Harvey & Pagel, 1991). For some of the analyses, we can couch the hypotheses in

terms of correlated trait evolution. We tested the evolutionary correlation between discrete traits using Maddison's (1990) concentrated changes test, which evaluates the probability that observed evolutionary gains and losses in tool use are concentrated on those branches of the phylogeny with high

manipulation skills, given the total number of reconstructed changes in tool use in the clade examined.

## Results

### *Dexterous manipulation and tool use*

Since extractive foraging in nature could not be quantified for this study, we could not test the first prediction. The second prediction suggests that all known tool users (Table 1) are also dexterous manipulators (Table 3); or more conservatively that the two are strongly associated. The association is indeed quite strong ( $X^2_{[1]}=11.69$ ,  $P<0.001$ ). While only 8% of the low-dexterity genera use tools in the wild or in captivity (exception: gibbons), 83% of the high-dexterity genera do (exceptions: geladas and aye-ayes) (see also Figure 3). Gibbons (*Hylobates* spp.) are not highly dexterous, scoring just under the median in Torigoe's tests; their tool use is very simple in captivity (see Beck, 1980) and absent in nature. Aye-ayes (*Daubentonia*) are highly dexterous but do not use tools; their highly specialized anatomical foraging adaptations may obviate the need to use tools. We can offer no explanation for the absence of tool use in geladas (*Theropithecus*). [Tool use is also predicted well by the three separate measures for dexterity. Separate Mann-Whitney *U*-tests show significantly larger repertoires of primary and secondary manipulations (Torigoe, 1985) for tool users than non-tool users, whereas there is also significant association between tool use and BAC.]

The association between dexterity and tool use is not simply due to phylogenetic inertia. Figure 3 shows the reconstructed evolution of high manipulation skills. It suggests four origins: in the aye-aye, in capuchins, in cercopithecines and in great apes. At the tips of the branches in Figure 3, we also map the distribution of tool use. The Maddison test shows that the probability of

the origins of tool use being independent of dexterous foraging skills is vanishingly small ( $P<0.001$ ). The association remains significant if we use slightly different assignments (changing the dexterity score for *Cercopithecus*; cf. Table 3), or slightly different reconstructions of the gains and losses in tool use. Thus, this analysis confirms the direct test of association conducted above.

### *Intelligence and tool use: great apes vs. monkeys*

So far, despite all attempts to prove otherwise, only great apes are known to show understanding of the physical relation between tools and other objects in the environment in their tool use (Limongelli *et al.*, 1995; Visalberghi *et al.*, 1995; cf. Fox *et al.*, 1999). There is also evidence that apes imitate (Russon, 1997; Whiten, 1998) and extensive evidence that they emulate (e.g., Tomasello & Call, 1997). Tomasello & Call's (1997) recent compilation of all studies of social learning in primates indicates that the cognitively more complex imitation or emulation mechanisms for social learning are almost exclusively shown by great apes: 46% of 35 experiments with the four great ape species yielded evidence for emulation or imitation, whereas only 3% of 29 studies showed these processes to operate in non-apes. The others demonstrated trial and error or stimulus enhancement.

Byrne (1995) and Russon & Bard (1996) suggested that the great apes have acquired general intelligence to deal with new and unexpected problems, as opposed to the domain-specific cognitive skills displayed by monkeys, expressed in a variety of unusual cognitive skills (e.g., self recognition, pretend play, comprehension and some production of language, insight, tactical deception, mental state attribution, etc.). Although Tomasello & Call (1997) did not accept this dichotomy, they did note

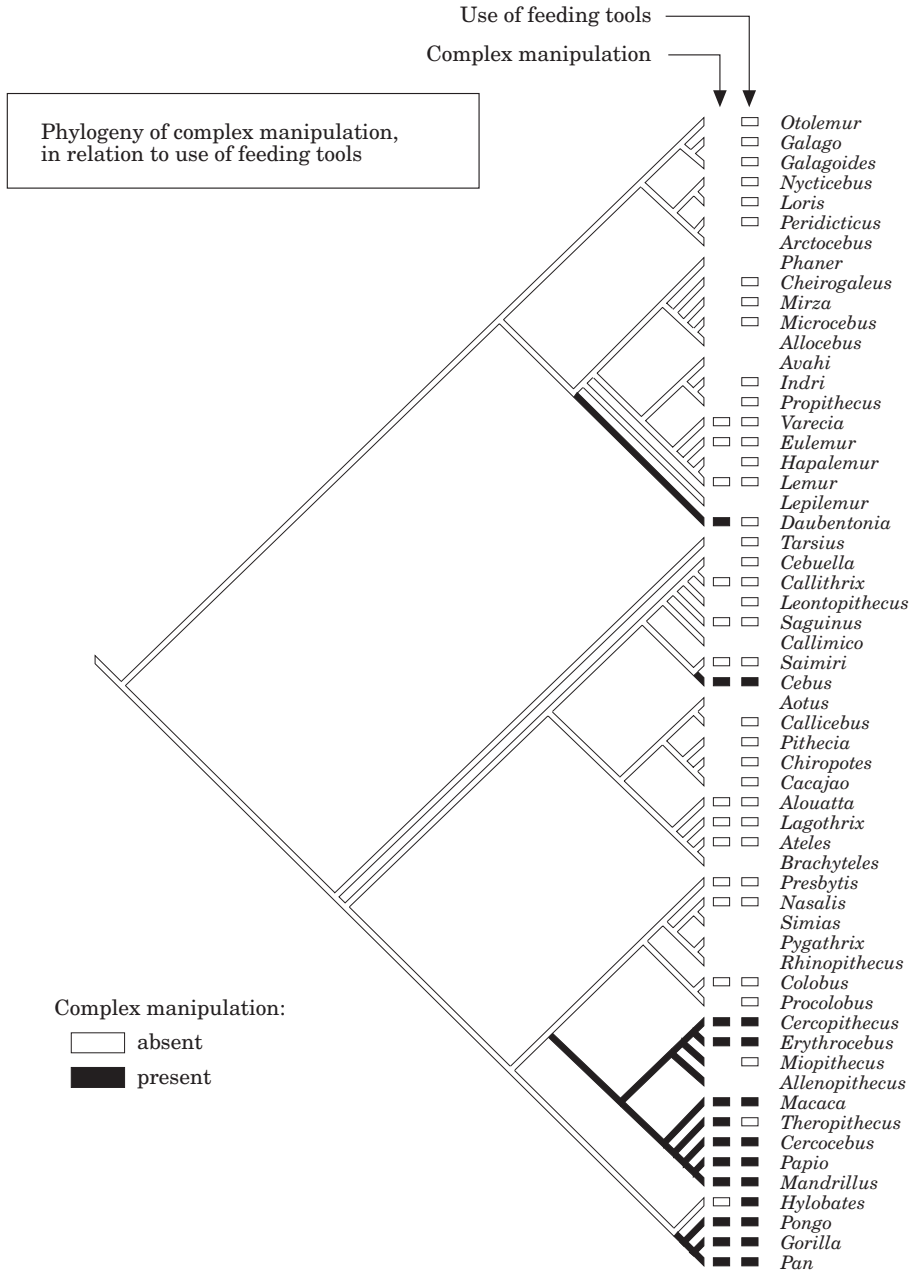


Figure 3. Reconstruction of the phylogenetic changes in complex manipulation, or dexterity, in primates (based on Table 3; phylogeny based on Purvis, 1995). Also mapped onto the tips of the phylogeny is the use of feeding tools (taken from Table 1).

(p. 376) that apes are quicker and more flexible learners. For our purposes, this amounts to a similar difference.

This major difference in learning abilities between apes and monkeys may explain various patterns in primate tool use. First,

extensive tool use in the wild is known only among great ape species. Social learning of tool use is more easily achieved when animals use imitation or emulation rather than local enhancement or stimulus enhancement, the processes known to be used by monkeys (Byrne, 1995; Russon, 1997). Tool use spreads remarkably slowly in groups of monkeys (Beck, 1980; Petit & Thierry, 1993; Zuberbühler *et al.*, 1996). Moreover, in none of the cases of feeding-tool use described for wild monkeys was there any evidence that the tool use had spread throughout the population (Oyen, 1979; Hohmann, 1988; Chevalier-Skolnikoff, 1990; Fernandes, 1991; Phillips, 1998; see also Sinha, 1997).

Second, tool making is expected to be more common in great apes than in monkeys because mental representation of the task should make tool manufacture far easier. Learning to use an existing object to acquire food may be relatively straightforward to achieve through positive reinforcement of some operant behavior. However, modifying an object to reach a certain goal may require hierarchical planning and a representation of the goal. All great apes make tools in captivity, and two species (chimpanzees and orang-utans) do so in the wild, whereas there is only limited evidence for monkeys making feeding tools in captivity (reviewed in Tomasello & Call, 1997) and one report of tool manufacture in the wild (Sinha, 1997). Thus, support for this prediction is rather weak.

Third, intelligence may indirectly explain the phenomenon that many species without (reported) sustained tool use in the wild can acquire these skills in suitable captive settings. The model suggests that species lacking great ape like intelligence need numerous exposures to learn the required skills through trial and error (cf. Box & Fragaszy, 1986). Most situations requiring tool use in the wild are uncommon and intermittent in time (e.g., seasonal), and

animals tend to be spread out most of the time during foraging. By contrast, the exposure to potential tool-use situations in captivity is continuous, as is (enforced) close proximity to any models that exist. Moreover, captive animals face neither foraging pressures nor predators, and should therefore be more predisposed toward play and exploration, facilitating invention and transmission. Accordingly, Menzel (1966) showed that captive Japanese monkeys were more inclined to manipulate offered objects than their wild counterparts. Likewise, Fragaszy & Adams-Curtis (1991) showed that captive capuchins had more diverse object handling techniques.

#### *Tolerance and tool use*

The hypothesis predicts that when afforded greater social tolerance, animals are better able to concentrate their attention on exploration without interference or aggression, and thus are more likely to invent or learn tool-using skills. There are three main sources of support for this hypothesis. First, tolerant species spend more time manipulating novel objects in captivity. Macaques vary widely in tolerance (Thierry, 1985; Preuschoft, 1995; Aureli *et al.*, 1997). Combining data from Thierry (1985) with Thierry *et al.* (1994), the three *Macaca* species in the sample show a perfect positive rank correlation between tolerance and time spent manipulating novel objects. In addition, the most manipulative macaque, *M. silenus*, is also socially highly tolerant (Preuschoft 1995).

Second, experiments to induce feeding tool manufacture in monkeys have succeeded primarily in tolerant species (see Tomasello & Call, 1997, Figure 3.5): *Cebus apella*, *Macaca tonkeana* and *M. silenus* (tolerance data from de Waal, 1997). One other case of experimentally induced tool manufacture is for a non-tolerant species (*M. fuscata*: Tokida *et al.*, 1994), but here the only tool maker was the daughter



of the alpha female, who would not be subject to harassment while concentrating on a task.

Third, differences in tolerance may lead to intraspecific differences in the invention of novel tool-use behaviors. Although capuchins are generally tolerant and readily share food (de Waal, 1997), Frigaszy & Visalberghi (1990) note that the high social vigilance in larger capuchin groups inhibits exploration of novel tool-use apparatuses and hinders the development of novel tool-use behaviors. In several species, the naive individuals who are first to learn tool-use or food-processing techniques usually have affiliative relationships with knowledgeable groupmates, so that relaxed proximity with a demonstrator is possible (Itani & Nishimura, 1973; Westergaard, 1988; Zuberbühler *et al.*, 1996).

#### *Intraspecific variation in tool use*

*Chimpanzees.* As noted above (see Table 2), there is appreciable variation in the kinds of tools used and the numbers of different feeding tools used across chimpanzee populations. Given an approximately equal rate of invention among sites and an approximately equal number of ecological opportunities for feeding-tool use, the hypothesis predicts that the size of the local tool kit reflects the frequency of opportunities for transmission, and hence gregariousness or social tolerance. Boesch (1996) has compared party sizes for most sites with long-term chimpanzee studies. Mean party size is not correlated with the size of the tool kit ( $r_s = -0.10$ ,  $n=5$ ,  $P=0.84$ ). Tolerance measures can not be directly compared across sites. We therefore compiled various tolerance indicators (Table 4). Their distribution over sites is consistent, allowing for a classification of the tolerance into three classes. The composite tolerance score and tool kit size show a strong correlation ( $r_s = +0.95$ ,  $n=5$ ,  $P=0.057$ ), consistent with the hypothesis that more tolerant popu-

lations of chimpanzees have more varied tool use.

*Orang-utans.* The use of feeding tools in orang-utans is limited to a few sites, all in south Aceh province in Sumatra. Because orang-utans are semi-solitary, both gregariousness and tolerance could vary. In addition, opportunities for tool use, i.e., the extent of extractive foraging, could vary. One population with tool use (Suaq Balimbing) has been studied in detail (van Schaik *et al.*, 1996; Fox *et al.*, 1999), as have several others without tool use.

Orang-utan densities in Sumatra are about twice that in Borneo in similar habitats (van Schaik *et al.*, 1995), suggesting that Sumatran forests are more productive than comparable Bornean ones. As a result, gregariousness and tolerance also vary. Adult orang-utan females seem to be far more gregarious at the Sumatran sites than at the Bornean ones (van Schaik, 1999). However, the importance of feeding aggregations in the mean party size is much greater in Ketambe, where large strangling figs are abundant, than in Suaq Balimbing, where virtually all parties are travel bands (*sensu* Sugardjito *et al.*, 1987) because large fruit trees with long patch residence time are rare. Although travel bands are more likely than aggregations to encounter opportunities for extractive foraging, the differences between Suaq Balimbing and Ketambe in gregariousness *per se* are not dramatic. With respect to tolerance, numerous cases of food sharing outside the mother–infant context have been observed at Suaq Balimbing (in ca 12,000 hours of focal observations: van Schaik, 1999), both in male–female and female–female associations, and including fruit, insect nests and meat. At Ketambe, food sharing is occasionally observed (S. Utami, personal communication, similar observation time). By contrast, no food sharing outside the mother–infant context is found in Tanjung Puting (Galdikas & Teleki,

**Table 4 Indicators of social tolerance in the chimpanzee populations listed in Table 2. Rankings are from low to high tolerance. Conclusion is based on mean relative ranks, which are highly consistent among indicators**

Site	Interbirth interval*	% lone individual†	Meat sharing‡	% hunts collaborative§	Female grooming	Medicinal plant use¶	Conclusion
Kibale	1	1				1	Low
Gombe	3	2	1	1	2	2.5	Medium
Mahale	2	3		2	1	2.5	Medium
Tai		5	2	3			High
Bossou	4	4			3		High

\*Interbirth interval is an index of habitat productivity, which is assumed to enhance tolerance. Shortest interbirth is ranked as highest tolerance. Data from Tutin (1994), with Kibale from Wrangham *et al.* (1996).

†% of parties consisting of lone individuals, also an indicator of habitat productivity. Fewest lone individuals is ranked as highest tolerance. Data from Boesch (1996), with Bossou added from Sugiyama (1981). This measure is especially relevant for adult females; because they are the least gregarious age-sex class, variation among females in gregariousness should cause most of the variation among sites.

‡Meat sharing is a direct indicator of tolerance. Rates were compared by Boesch & Boesch (1989).  
 ¶In collaborative hunts, several hunters act together and adopt complementary roles (Boesch & Boesch, 1989), which is only expected when sharing is common and voluntary.

||Female-female grooming is an expression of female tolerance. Measure used is observed/expected ratios where >100 grooming bouts were recorded (Muroyama & Sugiyama, 1994).

¶¶Medicinal plant use is cultural behavior. Number of species used medicinally is a reflection of opportunities for close-range observation. Data from Huffman & Wrangham (1994).

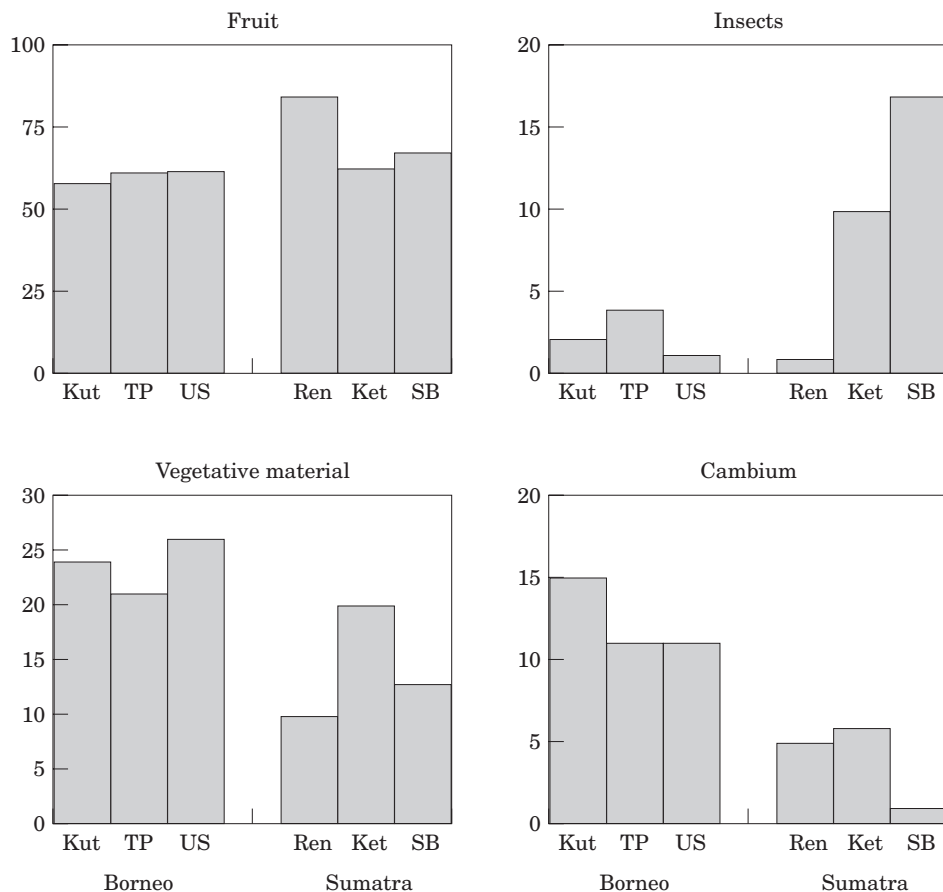


Figure 4. Variation in dietary composition, as estimated by percentage of total feeding time, among various wild orang-utan populations on Borneo and Sumatra. Kut=Kutai; TP=Tanjung Puting; US=Ulu Segama; Ren=Renun; Ket=Ketambe; SB=Suaq Balimbing. SB is the site with tool use. Data taken from Rodman (1988), supplemented by Suzuki (1989) for Kut, Sugardjito (1986) for Ket and van Schaik (unpublished) for SB.

1981), nor do any other reports on Bornean orang-utans mention it (also C. Knott, personal communication). Hence, the Sumatran sites, and especially Suaq Balimbing, have higher gregariousness and tolerance in foraging situations where tool use is likely, consistent with the hypothesis.

Opportunities for extractive tool use may also vary, however. Time spent foraging on insects is the best estimate for the frequency of opportunities for extractive foraging: much insectivory is extractive (tool use is relatively rare and thus unlikely to cause the

time spent foraging for insects). The published data on orang-utan time budgets show considerable variation in the distribution of feeding time (Figure 4), with the Sumatran populations spending more time on insect foraging and the Suaq Balimbing population spending by far the most. This higher tendency toward insectivory in Sumatra is shared by gibbons (Palombit, 1997) and long-tailed macaques [compare Wheatley (1980) with van Noordwijk & van Schaik (1987)], and reflects the productivity difference between the islands. Thus, the

site with tool use is also the site with the most frequent opportunities during routine foraging, which may provide an alternative explanation for the observed distribution of tool use. However, the absence of *Neesia* tool use in Borneo, despite abundant opportunities, is in favor of the hypothesis that tolerance during foraging is the key factor in the distribution of tool use in orang-utans.

## Discussion

### *Primate tool use*

Although extractive foraging and tool use are often thought to be linked (Parker & Gibson, 1977), we were unable to test this link directly. However, other evidence does not support Parker & Gibson's hypothesis. First, while all feeding-tool users in the wild or in captivity are dexterous extractive foragers, many species that show extractive foraging are not dexterous, and most of the dexterous extractive foragers do not use tools in the wild with any frequency. Second, there is doubt as to the theoretical basis for linking extractive activities to flexible tool use through the use of Piaget's sensori-motor stages (cf. Frigaszy & Adams-Curtis, 1991; Byrne, 1997; Tomasello & Call, 1997). Thus, extractive foraging is not directly linked to tool use.

The phylogenetic test showed a strong dependence of tool use (mainly in captivity) on the presence of manual dexterity. This is not unexpected if we view tool use as the byproduct of manipulative actions, especially those combining objects and substrates. Indeed, the tool use of many species in captivity shows many similarities to frequently shown operant behaviors. For instance, capuchin monkeys often pound objects, e.g., smashing nuts together or against branches (Struhsaker & Leland, 1977); where they use tools, they also tend to use these pounding actions (Fernandes, 1991; Frigaszy & Adams-Curtis, 1991).

Thus, extractive foraging has favored the evolution of dexterity in a subset of species and provides the tasks in which tools can profitably be used. However, as illustrated in Figure 1, ecological factors alone, while necessary, are not sufficient to explain the distribution patterns of primate tool use, and it is best to regard the required capacities as being present or expressed as skills in ever-narrowing subsets of species or populations.

Intelligence may account for the presence in some great apes of the use of feeding tools in the wild, the presence of tool kits and tool sets (Parker & Gibson, 1977; McGrew, 1992), and perhaps a greater ease of tool making (Figure 1). Unlike great apes, monkeys lack insight and efficient observational learning techniques, and therefore are not known to show population-wide tool use in the wild, although they can acquire tool-using skills if opportunities to do so are numerous and continuous. It is theoretically possible, therefore, that a socially tolerant monkey population will be found in which routine use of feeding tools occurs, especially if the skills used are close to naturally occurring operants, and if opportunities for would-be learners are abundant.

The causes of the cognitive divide between great apes and monkeys are not clear (Byrne, 1997). The cognitive factors favoring invention and transmission, though different (Figure 2), are evolutionarily linked because copying the behavior of others only provides a benefit if these individuals have developed skills that are worth copying (Boyd & Richerson, 1996). Thus, logically, insight historically preceded observational learning skills such as imitation and emulation. However, given the erratic distribution of tool use in living great apes, it is not likely that the intellectual capacity for tool use itself provided the selective force that produced more generalized cognitive skills in great apes.

Tolerance is a critical element of the model (cf. Figure 1). Although the social environment is often mentioned as a factor affecting learning latencies, tolerance has so far rarely been used to account for variation among species or populations within a species (Coussi-Korbel & Fragaszy, 1995). Yet there was support for a role of social tolerance. In monkeys social tolerance increases the time spent exploring objects and leads to more likely acquisition of tool-using skills. The geographic pattern among orang-utans is also consistent with a critical role for social tolerance in maintaining tool use at a site. The geographic variation in chimpanzee feeding-tool kit is correlated strongly with measures of social tolerance, and poorly with a gregariousness measure (mean party size). Although the robustness of these results needs to be evaluated using more systematic comparisons between sites, it remains strong in a preliminary analysis of a larger set of sites (van Schaik, in prep.). Finally, the well-known fact that immature animals engage in more exploration and invention than adults may be due in part to the greater tolerance afforded to juvenile primates. Nonetheless, while these various patterns are suggestive, they cannot as yet constitute a critical test. In particular, experimental tests of learning latency of tool skills in groups of varying tolerance are needed.

The model presented here explains the distribution of feeding-tool use among primates, and should therefore bear on the material culture of early hominids. However, the absence of extensive tool use in wild bonobos and gorillas appears to be inconsistent with the model's main elements. This can mean three things. First, the model is wrong. Second, these two species may rely less on extractive foraging of the sort that invites tool use. Indeed, bonobos and gorillas rely more on herbs and monocotyledonous understory plants than do chimpanzees (Malenky & Wrangham, 1994). Accordingly, the object manipula-

tions of captive bonobos are less substrate-oriented than those of chimpanzees (Takeshita & Walraven, 1996). Note, too, that gorilla tool use, even in captivity, is less extensive than that of the other great apes (compiled in Tomasello & Call, 1997). Third, it is conceivable that more close-range observations of well-habituated individuals will yield new forms of extractive tool use in bonobos, and perhaps even in gorillas. In both orang-utans and chimpanzees between-site variation in tool use is extensive, and the number of sites with long-term observations of well-habituated bonobos and even gorillas is smaller than that for orang-utans and especially chimpanzees. At this stage, we cannot distinguish between these three possibilities.

#### *Hominid tool use*

The first manufactured stone tools appear in the archaeological record (Semaw *et al.*, 1997) about 2.5 m.y.a. We surmise that hominid tool use was probably not more advanced than that of extant chimpanzees before then. Among the main conditions of the model (extractive foraging tasks, dexterity, intelligence, gregariousness and social tolerance), the most likely elements differentiating the stone-tool-making hominids from great apes would be increased intelligence or a higher degree of tolerance accompanied by increased opportunities for strong reliance on tools.

Increased intelligence is likely to be expressed in increased relative brain size. It is still disputed whether the first Oldowan tool makers were *Australopithecus* (*Paranthropus*) or *Homo* (Wood, 1997), but since cranial material is lacking for both for this period, it is impossible to determine if the relative brain size of the earliest tool makers was already above the great ape range (Kappelman, 1996). However, experiments suggest that great apes cannot attain the level of sophistication reached by Oldowan tool makers (Wynn & McGrew, 1989; Toth

*et al.*, 1993). Hence, it is likely that these new skills do indeed reflect increased cognitive abilities. On the other hand, such abilities would not be maintained in the population unless accompanied by favorable social conditions for invention and transmission. The reduction in absolute canine size and canine size dimorphism in the genus *Homo* is consistent with the suggestion of enhanced social tolerance (Plavcan & van Schaik, 1997). Moreover, the Oldowan lifestyle involving communal processing of large food items, e.g., carcasses (Klein, 1989), is inevitably accompanied by extensive food sharing, or at least tolerated scrounging. Social tolerance is an essential condition for this lifestyle.

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### References

- Aureli, F., Das, M. & Veenema, H. C. (1997). Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis*, *M. fuscata*, and *M. sylvanus*). *J. Comp. Psych.* **111**, 91–99.
- Beck, B. B. (1980). *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. New York: Garland.
- Bermejo, M., Ilera, G. & Sabater Pi, J. (1994). Animals and mushrooms consumed by bonobos (*Pan paniscus*): new records from Lilunga (Ikela), Zaire. *Int. J. Primatol.* **15**, 879–898.
- Boesch, C. (1993). Aspects of transmission of tool-use in wild chimpanzees. In (K. Gibson & T. Ingold, Eds) *Tools, Language and Cognition in Human Evolution*, pp. 171–183. Cambridge: Cambridge University Press.
- Boesch, C. (1996). The emergence of cultures among wild chimpanzees. *Proc. Brit. Acad.* **88**, 251–268.
- Boesch, C. & Tomasello, M. (1998). Chimpanzee and human cultures. *Curr. Anthropol.* **39**, 591–614.
- Boesch, C., Marchesi, P., Marchesi, N., Fruth, B. & Joulain, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *J. hum. Evol.* **26**, 325–338.
- Boinski, S. (1988). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *Am. J. Primatol.* **14**, 177–179.
- Box, H. O. & Fragaszy, D. M. (1986). The development of social behaviour and cognitive abilities. In (J. G. Else & P. C. Lee, Eds) *Primate Ontogeny, Cognition and Social Behaviour*, pp. 119–128. Cambridge: Cambridge University Press.
- Boyd, R. & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proc. Brit. Acad.* **88**, 77–93.
- Brereton, A. R. (1995). Coercion–defence hypothesis: the evolution of primate sociality. *Folia primatol.* **64**, 207–214.
- Byrne, R. W. (1995). *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford: Oxford University Press.
- Byrne, R. W. (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In (A. Whiten & R. W. Byrne, Eds) *Machiavellian Intelligence II: Extension and Evaluations*, pp. 289–311. Cambridge: Cambridge University Press.
- Byrne, R. W. & Byrne, J. M. E. (1993). Complex leaf gathering skills of mountain gorillas (*Gorilla g. beringei*): variability and standardization. *Am. J. Primatol.* **31**, 241–261.
- Call, J. & Tomasello, M. (1994). The social learning of tool use by orang-utans (*Pongo pygmaeus*). *Hum. Evol.* **9**, 297–313.
- Candland, D. (1987). Tool use. In (G. Mitchell & J. Erwin, Eds) *Comparative Primate Biology; Vol. 2, Part B: Behavior, Cognition, and Motivation*, pp. 85–103. New York: Alan R. Liss.
- Casimir, M. J. (1975). Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region (République du Zaire). *Folia primatol.* **24**, 81–136.
- Chevalier-Skolnikoff, S. (1990). Tool use by wild cebus monkeys at Santa Rosa National Park, Costa Rica. *Primates* **31**, 375–383.
- Chiang, M. (1967). Use of tools by wild macaques in Singapore. *Nature* **214**, 1258–1259.



- Clark, T. W. (1979). Food adaptations of a transplanted Japanese macaque troop (Arashiyama West). *Primates* **20**, 399–410.
- Coussi-Korbel, S. & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Anim. Behav.* **50**, 1441–1453.
- Fagard, J. & Pezé, A. (1997). Age changes in interlimb coupling and the development of bimanual coordination. *J. Mot. Behav.* **29**, 199–208.
- Fernandes, M. E. B. (1991). Tool use and predation of oysters (*Crassostrea rhizophorae*) by the tufted capuchin, *Cebus apella apella*, in brackish water mangrove swamp. *Primates* **32**, 529–531.
- Fox, E. A., Sitompul, A. F. & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orang-utans. In (S. T. Parker, L. Miles & R. Mitchell, Eds) *The Mentality of Gorillas and Orangutans*, pp. 99–116. Cambridge: Cambridge University Press.
- Fragaszy, D. M. & Adams-Curtis, L. E. (1991). Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psych.* **105**, 387–397.
- Fragaszy, D. M. & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in capuchin monkeys (*Cebus apella*). *J. Comp. Psych.* **103**, 159–170.
- Fragaszy, D. M. & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviors in capuchin monkeys. *Folia primatol.* **54**, 155–165.
- Galdikas, B. M. F. & Teleki, G. (1981). Variations in subsistence activities of female and male pongids: new perspectives on the origins of hominid labor division. *Curr. Anthropol.* **22**, 241–256.
- Galef, B. G., Jr (1990). Tradition in animals: field observations and laboratory analysis. In (M. Bekoff & D. Jamieson, Eds) *Interpretations and Explanations in the Study of Behavior: Comparative Perspectives*, pp. 74–95. Boulder: Westview Press.
- Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In (J. G. Else & P. C. Lee, Eds) *Primate Ontogeny, Cognition, and Social Behaviour*, pp. 93–105. Cambridge: Cambridge University Press.
- Goldfield, E. C. & Michel, G. F. (1986). Spatio-temporal linkage in infant interlimb coordination. *Dev. Psychobiol.* **19**, 259–264.
- Goodall, A. G. (1977). Feeding and ranging behaviour of a mountain gorilla group (*Gorilla gorilla beringei*) in the Tshibinda-Kahuzi region (Zaire). In (T. H. Clutton-Brock, Ed.) *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, pp. 450–479. New York: Academic Press.
- Goodall, J. (1986). *The Chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.
- Hall, K. R. L. (1963). Tool-using performances as indicators of behavioral adaptability. *Curr. Anthropol.* **4**, 479–494.
- Hall, K. R., Boelkins, R. C. & Goswell, M. J. (1965). Behaviour of patas monkeys, *Erythrocebus patas*, in captivity, with notes on the natural habitat. *Folia primatol.* **3**, 22–49.
- Hamilton, W. J. & Tilson, R. L. (1985). Fishing baboons at desert waterholes. *Am. J. Primatol.* **8**, 255–257.
- Harvey, P. H. & Pagel, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hohmann, G. (1988). A case of simple tool use in wild liontailed macaques (*Macaca silenus*). *Primates* **29**, 565–567.
- Horn, A. D. (1987). The socioecology of the black mangabey (*Cercocebus aterrimus*) near Lake Tumba, Zaire. *Am. J. Primatol.* **12**, 165–180.
- Inoue-Nakamura, N. & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psych.* **111**, 159–173.
- Itani, J. & Nishimura, A. (1973). The study of infra-human culture in Japan. In (J. E. Menzel, Ed.) *Precultural Behavior*, pp. 26–50. Basel: Karger.
- Iwano, T. & Iwakawa, C. (1988). Feeding behaviour of the aye-aye (*Daubentonia madagascarensis*). *Folia primatol.* **50**, 136–142.
- Izawa, K. & Mizuno, A. (1977). Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates* **18**, 773–792.
- Kappelman, J. (1996). The evolution of body mass and relative brain size in fossil hominids. *J. hum. Evol.* **30**, 243–276.
- Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates* **6**, 1–30.
- King, B. J. (1986). Extractive foraging and the evolution of primate intelligence. *Hum. Evol.* **1**, 361–372.
- Klein, R. G. (1989). *The Human Career: Human Biological and Cultural Origins*. Chicago: University of Chicago Press.
- Kortlandt, A. & Kooij, M. (1963). Prohominid behaviour in primates. *Symp. zool. Soc. Lond.* **10**, 61–88.
- Kummer, H. & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Phil. Trans. R. Soc. Lond., Series B* **308**, 203–214.
- Limongelli, L., Boysen, S. T. & Visalberghi, E. (1995). Comprehension of cause-effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *J. Comp. Psych.* **109**, 18–26.
- Maddison, W. P. (1990). A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evol.* **44**, 539–557.
- Malenky, R. K. & Wrangham, R. (1994). A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako forest, Zaire, and *Pan troglodytes* in the Kibale forest, Uganda. *Am. J. Primatol.* **32**, 1–12.
- Matsuzawa, T. (1994). Field experiments on use of stone tools in the wild. In (R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, P. G. Heltne & L. A. Marquardt, Eds) *Chimpanzee Cultures*, pp. 351–370. Cambridge, MA: Harvard University Press.
- McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *J. hum. Evol.* **3**, 501–508.

- McGrew, W. C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C., Baldwin, J. P. & Tutin, C. E. G. (1979). Chimpanzees, tools, and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man* **14**, 185–214.
- 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.
- McGrew, W. C. & Marchant, L. F. (1997). Using the tools at hand: manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. *Int. J. Primatol.* **18**, 787–810.
- Menzel, E. W., Jr (1966). Responsiveness to objects in free-ranging Japanese monkeys. *Behav.* **26**, 130–150.
- Nunn, C. L. & van Schaik, C. P. (in press). Reconstructing the behavioral ecology of extinct primates: patterns among extant species. In (M. Plavcan, W. Jungers, R. Kay & C. van Schaik, Eds) *The Behavior of Extinct Primates*. New York: Plenum Press.
- Oyen, O. J. (1979). Tool-use in free-ranging baboons of Nairobi National Park. *Primates* **20**, 595–597.
- Palombit, R. A. (1997). Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia primatol.* **68**, 321–337.
- Parker, C. E. (1974). Behavioral density in ten species of nonhuman primates. *J. Comp. Phys. Psych.* **87**, 930–937.
- Parker, S. T. & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. *J. hum. Evol.* **6**, 623–641.
- Petit, O. & Thierry, B. (1993). Use of stone tools in a captive group of guinea baboons (*Papio papio*). *Folia primatol.* **61**, 160–164.
- Phillips, K. A. (1998). Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*). *Am. J. Primatol.* **46**, 259–261.
- Plavcan, J. M. & van Schaik, C. P. (1997). Interpreting hominid behavior on the basis of sexual dimorphism. *J. hum. Evol.* **32**, 345–374.
- Preuschoft, S. (1995). "Laughter" and "smiling" in macaques: an evolutionary perspective. Ph.D. Dissertation, University of Utrecht
- Purvis, A. (1995). A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Series B* **348**, 405–421.
- Rhine, R. J. & Westlund, B. J. (1978). The nature of a primary feeding habit in different age–sex classes of yellow baboons (*Papio cynocephalus*). *Folia primatol.* **30**, 64–79.
- Rodman, P. S. (1988). Diversity and consistency in ecology and behavior. In (J. H. Schwartz, Ed.) *Orang-utan Biology*, pp. 31–51. Oxford: Oxford University Press.
- Russon, A. E. (1997). Exploiting the expertise of others. In (A. Whiten & R. W. Byrne, Eds) *Machiavellian Intelligence II: Extensions and Evaluations*, pp. 174–206. Cambridge: Cambridge University Press.
- Russon, A. E. & Bard, K. A. (1996). Exploring the minds of great apes: issues and controversies. In (A. E. Russon, K. A. Bard & S. Parker, Eds) *Reaching into Thought: The Minds of the Great Apes*, pp. 1–20. Cambridge: Cambridge University Press.
- Russon, A. E., Mitchell, R. W., Lefebvre, L. & Abravanel, E. (in press). The comparative evolution of imitation. In (J. Langer & E. Killen, Eds) *Piaget, Evolution, and Development*, pp. 1–20. New York: Erlbaum.
- Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N. & Mowbray, K. (1997). 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* **385**, 333–336.
- Sinha, A. (1997). Complex tool manufacture by a wild bonnet macaque, *Macaca radiata*. *Folia primatol.* **68**, 23–25.
- Struhsaker, T. T. & Leland, L. (1977). Palm-nut smashing by *Cebus a. apella* in Colombia. *Biotrop.* **9**, 124–126.
- Sugardjito. (1986). Ecological constraints on the behaviour of Sumatran orang-utans (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. Ph.D. Dissertation, University of Utrecht
- Sugardjito, J., te Boekhorst, I. J. A. & van Hooff, J. A. R. A. M. (1987). Ecological constraints on the grouping of wild orang-utans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *Int. J. Primatol.* **8**, 17–41.
- Sugiyama, Y. (1993). Local variation of tools and tool use among wild chimpanzee populations. In (A. Berthelet & J. Chavaillon, Eds) *The Use of Tools by Human and Non-human Primates*, pp. 175–190. Oxford: Clarendon Press.
- Suzuki, A. (1989). Socio-ecological studies of orang-utans and primates in Kutai National Park, East Kalimantan in 1988–1989. *Kyoto Univ. Overseas Res. Rep. of Studies on Asian Non-human Primates* **7**, 1–42.
- Takeshita, H. & Walraven, V. (1996). A comparative study of the variety and complexity of object manipulation in captive chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). *Primates* **37**, 423–441.
- Thierry, B. (1985). Patterns of agonistic interaction in three species of macaque (*Macaca mulatta*, *M. fascicularis*, *M. tonkeana*). *Aggr. Behav.* **11**, 223–233.
- Thierry, B., Anderson, J. R., Demaria, C., Desportes, C. & Petit, O. (1994). Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In (J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschildt, Eds) *Current Primatology, Vol. II: Social Development, Learning and Behaviour*, pp. 103–117. Strasbourg: Université Louis Pasteur.
- Tokida, E., Tanaka, I., Takefushi, H. & Hagiwara, T. (1994). Tool-using in Japanese macaques: use of stone tools to obtain fruit from a pipe. *Anim. Behav.* **47**, 1023–1030.
- Tomasello, M. & Call, J. (1997). *Primate Cognition*. New York: Oxford University Press.

- Tomblin, D. C. & Cranford, J. A. (1994). Ecological niche differences between *Alouatta palliata* and *Cebus capucinus* comparing feeding modes, branch use, and diet. *Primates* **35**, 265–274.
- Torigoe, T. (1985). Comparison of object manipulation among 74 species of nonhuman primates. *Primates* **26**, 182–194.
- Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A. & Rumbaugh, D. (1993). *Pan* the tool-maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *J. Archaeol. Sci.* **20**, 81–91.
- Tutin, C. E. G. (1994). Reproductive success story: variability among chimpanzees and comparisons with gorillas. In (R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, P. G. Heltne and L. A. Marquardt, Eds) *Chimpanzee Cultures*, pp. 181–193. Cambridge: Harvard University Press.
- Uehara, S. (1990). A preliminary report on age differences in plant-feeding behaviors among adult and adolescent males. In (T. Nishida, Ed.) *The Chimpanzees of the Mahale Mountains*, pp. 223–236. Tokyo: University of Tokyo Press.
- van Noordwijk, M. A. & van Schaik, C. P. (1987). Competition among female long-tailed macaques, *Macaca fascicularis*. *Anim. Behav.* **35**, 577–589.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In (V. Standen & R. A. Foley, Eds) *Comparative Socioecology*, pp. 195–218. Oxford: Blackwell.
- van Schaik, C. P. (1999). Fission-fusion sociality in Sumatran orang-utans. *Primates* **40**, 73–90.
- van Schaik, C. P., Azwar & Priatna, D. (1995). Population estimates and habitat preferences of orang-utans based on line transects of nests. In (R. D. Nadler, B. F. M. Galdikas, L. K. Sheeran & N. Rosen, Eds) *The Neglected Ape*, pp. 129–147. New York: Plenum Press.
- van Schaik, C. P., Fox, E. A. & Sitompul, A. F. (1996). Manufacture and use of tools in wild Sumatran orang-utans. *Naturwiss.* **83**, 186–188.
- van Schaik, C. P. & van Noordwijk, M. A. (1986). The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour* **99**, 296–315.
- Visalberghi, E., Fragaszy, D. M. & Savage-Rumbaugh, S. (1995). Performance in a tool-using task by common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), an orang-utan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*). *J. Comp. Psych.* **109**, 52–60.
- Waal, F. B. M. de (1997). Food transfers through mesh in brown capuchins. *J. Comp. Psychol.* **111**, 370–378.
- Westergaard, G. C. (1988). Lion-tailed macaques (*Macaca silenus*) manufacture and use tools. *J. Comp. Psych.* **102**, 152–159.
- Westergaard, G. C. & Fragaszy, D. M. (1987). The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *J. Comp. Psych.* **101**, 159–168.
- Wheatley, B. P. (1980). Feeding and ranging of East Bornean *Macaca fascicularis*. In (D. G. Lindburg, Ed.) *The Macaques*, pp. 215–246. New York: Van Nostrand Reinhold Co.
- Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees. *J. Comp. Psych.* **112**, 270–281.
- Wood, B. (1997). The oldest whodunnit in the world. *Nature* **385**, 292–293.
- Wynn, T. & McGrew, W. C. (1989). An ape's view of the Oldowan. *Man* **24**, 383–398.
- Zuberbühler, K., Gyax, L., Harley, N. & Kummer, H. (1996). Stimulus enhancement and spread of a spontaneous tool use in a colony of long-tailed macaques. *Primates* **37**, 1–12.