

Chimpanzee Cultures and Chimpanzees of the Mahale Mountains

Chimpanzee Cultures is an edited volume based on the work of many well known researchers including de Waal, Goodall, McGrew, and Wrangham who have all spent decades studying chimpanzees. The work summarizes material presented at two conferences allowing material from wild and captive studies to be integrated and assessed. As the title of the book suggests this work is focussed on those aspects of chimpanzee life which can be considered cultural. How much learning is involved in acquiring the ability to perform various behaviours? Do chimpanzees really 'teach' their young? How does learning occur? How much variability is there between populations in terms of diet, social signals and the intricacies of tool use? In order to deal with these types of questions the writers must also deal with the definitional uncertainty of what actually constitutes culture. Is culture a uniquely human characteristic? Most chimpanzee researchers argue that social learning is such an important part of becoming a functioning chimpanzee (as determined by the disastrous results of captive deprivation experiments) that the behavioural differences between groups can be classified as cultural. The potential for such differences to be due to habitat variability is taken into consideration as well as age and sex differences in behaviour, but the level of variability observed argues for population based learned solutions to problems.

Another aspect of understanding chimpanzees is the impact of their long lifespans and generation times. Unlike humans who are weaned at a much earlier age, chimpanzees can afford to take years to learn their basic subsistence techniques. They can also take their time to work their way into new groups because of their long lifespan and slow reproductive rate. Thus they are not under the same pressure to maximize the input of learning by imitation or emulation in learning how to deal with their environment. This may impact how they use these two learning strategies and may be a large part of why there are such major differences in learning patterns and outcomes when they are compared with human children. Also details of social interaction among kin are extremely important in developing group social relations and these have a long time to mature in chimpanzees. The differences between common chimpanzees and bonobos in terms of developing intra-group social relations is particularly interesting in this regard and the influence of differing patterns of aggression and affiliation between males and females in bonobos and common chimpanzees is addressed in this book.

Differences between various populations of chimpanzees become particularly evident in another book which is covered in this lecture. This work is a long term study of wild chimpanzees Chimpanzees of the Mahale Mountains edited by the famous Japanese researcher Toshisada Nishida. Here Nishida correlates research done over a 25 year period on a research population of wild chimpanzees who live 200 miles south of Gombe at a Japanese operated field site. The detailed comparison of the two populations (Gombe and Mahale Mountains) of the same sub-species in parallel habitats clarifies the level of similarity and difference in behaviours under ecologically similar conditions. Taken in conjunction with the preceding work on cultural variability between chimpanzee populations this book allows the reader to closely examine social and life history parameters which may impact behavioural differences between the two groups. In addition to this the book provides information which was only previously available in Japanese publications and not very accessible to western researchers.

Aping Culture

Chimpanzee Cultures. 1994. Edited by Richard W. Wrangham, W.C. McGrew, Frans B.M. de Waal and P.C. Heltane. Harvard University Press, Cambridge Mass. and London, England. xxiii + 424 pp. ISBN 0-674-11662-3

This comparative compilation of information about Chimpanzees and Bonobos grew out of two conferences sponsored by the Chicago Academy of Sciences. The first in 1986, called "Understanding Chimpanzees" brought together a wide range of researchers from field and captive study sites, and outlined both what we knew and large areas of knowledge that were lacking in our understanding of our closest relations. Efforts undertaken at this conference resulted in chimpanzees being classified as an endangered species which put into motion a number of regulations governing their importation, use and care in the United States. Five years later (1991) a second conference on chimpanzees focused on behaviour and diversity, with this book, *Chimpanzee Cultures*, being the published outcome. The book is founded on one explicit and two implicit questions, -- only one of which receives a clear answer. These questions are (1) What are chimpanzees? (2) What is culture? and (3) What (if any) aspects of chimpanzee behaviours could be regarded as cultural?

Although the first question is easily answered, it is a more complex subject than many realize. There are three extant subspecies of common chimpanzees, *Pan troglodytes* which are spread across the equatorial belt of central Africa. These three subspecies may originally have been contiguous, but now they are localized in three areas. The western most are *Pan troglodytes verus*, in the western bulge of Africa from Senegal to the Ivory Coast. These are fairly large bodied chimps with cranial proportions more similar to *Pan troglodytes*, the 'middle' subspecies which is focused around Equatorial Guinea, Gabon, and into the Cameroons. These central chimps sometimes share their rainforest range with gorillas' and they seem to be the largest and most sexually dimorphic of the chimpanzee subspecies. The third subspecies, *Pan troglodytes schweinfurthii* is quite variable in body size with the easternmost Gombe population, studied by Goodall, about 25% to 35% smaller than members of the same subspecies at other locations in Tanzania and Zaire. This variability in body size is part of the reason why *Pan paniscus*, the other chimpanzee species found in Southern Zaire is now being called the 'bonobo' rather than the 'pygmy chimpanzee', because its average weight and body size are quite close to the Gombe common chimps. Bonobos also have smaller heads, longer legs and fingers better adapted for suspensory locomotion than common chimpanzees. Also, unlike common chimpanzees they show little sexual dimorphism in size, except for differences in their canine teeth, which parallel the other species.

Bonobos show some behavioral differences from chimpanzees which are interesting because these species diverged at about the same time that *Homo* and *Australopithecus* diverged (about 2.5 million years ago). Thus the level of genetic morphological and behavioral differences between the two closely related species gives us a model to examine developments in the human evolutionary sequence.

A third aspect of chimpanzee variability occurs between populations in captivity and those which are still free ranging. This book focuses on three groups of living captive populations; those at Arnhem in the Netherlands, Detroit Zoo, and the Yerkes Regional Primate Centre in Georgia, U.S.A. These captive populations have

provided opportunities for focused close examination of behaviours which are very difficult to study in the wild, such as female-female relations. However, it is clear from comparisons between wild and captive groups that researchers cannot assume that just because they are all chimpanzees, their behaviours are the same. Some of these investigations of diversity are studying the differing influences of resources and social stability on groups in various conditions.

The second question 'What is culture?' is approached in a rather fragmentary way by the authors of the various chapters. It is a major question for anthropologists who have been asking it for the last century without arriving at a definitive answer. Many definitions are species- centric in defining culture as a human trait with minimum requirements such as use of language, use of symbols, tool use, and a very long history. When the actual foundations of cultural behaviour are examined, the definition begins to broaden to behavioral methods of information transfer across generations, and McGrew's general statement that culture is an 'amorphous array of Contracts' (35) a set of conceptual abilities, actual or potential in members of a species. Some researchers go so far as to require learning by imitation, but given the break down of imitation - like behaviours (discussed below) this seems rather stringent. The important aspect of the question is whether culture can be part of an animal's life, or are behavioral traditions, and group variability founded on a different underpinning.

In order to examine this question we must ascertain what types of behaviour might be perceived as cultural and examine what factors could cause the variability seen within the species which seems to be one of the cornerstones of cultural definition. Among the behaviours discussed in the book are **population differences in party size and nest building behaviour, hunting behaviour, tool use, medicinal plant use, nonreproductive sexual behaviour, complex social interactions, deception, language like behaviour (use of symbols), imitation and other forms of social learning.** The method of investigation is a systematic comparison of animals in their natural state or in captivity, in conditions where usually only one variable is examined at a time. Comparisons are made between individuals, families, populations, subspecies, species, genera, and between the captive and wild state. Most of the research is quite recent and focuses on eleven free ranging study sites of the forty-five that are listed, and three captive populations.

The book is divided into three main sections with a Foreword and Introduction and a Postscript. The three sections focus on major aspects which may underline diversity: **Ecological factors, Social Relations and Cognition.** Within these sections a number of behaviours are examined. The first section begins with an examination of genetics, morphology and demography as possible variables in explaining diversity in behaviour before going to ecological factors. In particular, this section discusses how behavioral variation could occur and be transmitted from population to population. Some behaviours could be quite adaptive, such as tool use to get the protein provided by insects, and thus there might be a strong selective pressure to preserve this function, even if the method varies from population to population (due to ecological factors). In other cases simple diffusion may spread behaviours or independent invention might occur. If populations were once contiguous, it is possible that behaviours were lost in intervening populations, as numbers decreased, so two now isolated populations have what was once a shared behaviour. Thus the history of a population is recognized as a very important variable and one which is already difficult to control for especially if comparing wild and captive data. This is even more emphasized because studies are not yet long enough to cover complete

lifespans of longlived individuals.

This section on ecology refers to basic variations in resources, such as height of the canopy and size of fruit tree patches, as underlying some aspects of diversity. Nesting behaviour seems to vary somewhat between species with chimps nesting at 5-30 meters with a mean of 10-11 meters, while bonobos nest at a range of 0-50 meters with a mean of 16 M. Thus the ranges overlapped, but bonobos tended to build in taller trees - in a taller forest, and usually had more nests in a group. Clearly nest height will vary with canopy height, but day nests for chimpanzees tended to be higher in trees than night sleeping nests, which suggests a different function (or need for stability). In forests shared with gorillas, chimps tended to nest in trees and gorillas at low height or on the ground, which suggests that nesting behaviour is not totally governed by tree availability. Another interesting factor is that neither chimps nor bonobos tended to nest in fruiting trees, although they would nest in the same species when they were not in fruit.

Size of fruit tree patches has been suggested as a variable influencing the average size of groups of chimpanzees and bonobos. Patch size can be defined in various ways, as can party size of groups but the general impression is that bonobos occur in larger groups than chimpanzees. However, if the fact that chimps tend to disperse into more available fruit trees, while bonobos tend to congregate is taken into account, comparable observations suggest that the range of party sizes is fairly equivalent. The variance of party size within a species is larger than the variance between species, with chimps ranging from 2.6 to 10.1 individuals and Bonobos 5.4 to 16.9. Rather than patch size or fruit density the year round availability of fruit may be a more important factor. Where chimps compete for food with gorillas (Ndoki Lowland Rain Forest) chimpanzees spend 95% of their time foraging in dry forest and gorillas 45% of their time in the swamp, whereas bonobos who are not competing with gorillas use swamp areas quite frequently and consume some of the same food plants. Thus external competition and minimal levels of food resource may constrain group size more than the average or abundant level of resources. On the other hand, group size may reflect social preferences of animals more than ecological constraints, and only succumb to ecological factors under stressful conditions. The wide range of variability in party size suggest a very adaptive flexible behaviour and little need for protection from predators.

Hunting interactions with adult red colobus monkeys also seemed to be related to canopy height. At Gombe with a low canopy of 10-15 meters and smaller chimpanzees, the adult red colobus monkeys would harass and mob chimpanzees even though chimps hunt and eat young red colobus. At Tai in the Ivory Coast chimpanzees often hunt in groups and will move towards red colobus if they hear them, and will not retreat from the monkeys. The taller trees at Tai (20-40 meters - emergents 40-60 M) give the colobus more time to react and they usually try to escape. The Tai chimps counteract this by using a collaborative group hunting strategy focusing on adult monkeys which is less frequently successful than the solitary hunting that mainly occurs at Gombe but nets a 9.6 kg prey (average) rather than a 1.6 kg average prey as at Gombe. Red colobus also chase chimpanzees at Mahale and Kibale even to the point of pursuing them on the ground, thus suggesting it is not only the small size of Gombe chimpanzees which makes them fearful. These chimpanzees often hunt alone or in a group but not collaboratively. The colobus seem to harass the Gombe animals whether or not they are hunting, with the result that the chimpanzees are quite wary of them. This means that when the low trees and vines of Gombe, are in fruit the colobus can eat in greater safety

because the chimpanzees usually hesitate before attacking a colobus group, and thus rarely completely surprise them. Colobus bites can injure a chimpanzee quite painfully with the result that subadult and female chimpanzees in particular are quite respectful of adult monkeys.

Another aspect of behavioral diversity which may have ecological underpinnings is tool use. Various long thin objects are used as probes for ant and termite fishing. These include branches (stripped of leaves) vines, bark and grass stems. Some other chimpanzees catch termites by hand and still others ignore them totally. Different groups use different numbers of tools. The highest level is at Gombe with 11 habitual patterns whereas 12 groups show only 1 pattern each. Thus the tool use repertoire is far from species-typical, and shows some notable regional contrasts. Some are due to lack of prey species or a different type of tool source, (e.g. grass instead of vines). However nut cracking with a stone anvil and hammer only occurs in western chimpanzees even though plenty of nuts and stones occur in the ranges of Central and East African animals. The lack of anvil and hammer use for nut cracking at Lope in Gabon occurs in spite of 6 nut species being available. Since nuts are an available protein and fat source McGrew argues that ignorance of their food value is the probable reason they are not eaten. In Matsuzawa's study of chimpanzees at Bossou Guinea, he put a different kind of nut (Coula) out near the anvils and only 1 old female cracked and ate them initially. The only animals who followed her lead were two juveniles who were learning the nut cracking technique, and applied it to this new (and very hard shelled) form. Matsuzawa hypothesized that the old female might have migrated from a coula nut using troop about 10kms away, before the population at Bossou became so isolated.

McGrew argues that nut cracking is an example of a culturally transmitted behaviour, even if all criteria of imitation as the form of social learning are not present. The young spend about 4 years going through 4 states of increasingly complex behaviour to achieve nut cracking and another 4 to 6 years to perfect it. This along the lines of the time span Teleki (1981) suggested was necessary to effectively learn termite fishing techniques. Matsuzawa also tested local children and found that until 3 years of age they were using Stage 1 to 3 behaviour and not effectively cracking nuts, but after age 3 they succeeded, reaching a refined level of skill around age 10 years. This pattern of learning a sequence of objects, relationships and actions has been investigated as the foundation of a lot of learning patterns in humans involved in developing what eventually becomes complex sequences of behaviour. John Gatewood studied the acquisition of skills required to work on a commercial trawler experientially and found that it involved learning to do job No.1, then job No.2, then job No.3 with no explanation of how they fit together. It is only after the sequence is learned that some understanding of the hierarchical structure of the whole is evident. Many human tasks are learned this way especially in some cultures, and activities, such as learning music or learning the motor movements involved in many sports (Wynn 1993). In some cases tool making occurs this way in humans and the evidence assembled by McGrew and Matsuzawa in his book argues that the same pattern of learning occurs in mastering tool use by chimpanzees. This supports McGrew's argument that true imitation is not really necessary as long as the functional aspects of the task are learned, in order for a behaviorally transmitted tradition to be considered cultural.

This same argument could be considered to apply to the use of different types of medicinal plants by various populations of chimpanzees. It is both the type of material ingested and the manner and timing of consumption which differentiate this

intake from ordinary eating behaviour. Most of these plants are eaten first thing in the morning. Leaves of certain species, which are often tough or bristly, are rolled up in the mouth and held there, rather than being chewed. These are often recovered whole from fecal samples. Some of these plants have high levels of quite toxic compounds in them. Some plants are eaten seasonally; associated with high risk periods of infection or worm infestation. In other cases, the individuals appear ill - lethargic or with symptoms of a cold, and seem better a few days after consuming these plants. In most cases there is a very low frequency of intake of these plants on a regular basis, but concentrated consumption at certain period. One commonly used leaf at Gombe and Mahale is that of *Aspilia mossambicensis* which contains thiarubrine. A an antibiotic, and has antiparasitic properties. When eaten in the morning it is rolled around in the mouth and not chewed, but when eaten in the afternoon it is chewed like other food.

Hoffman and Wrangham note that 13 plant species from 10 genera and 8 families seem to be used for their medicinal value. These include leaves, bitter pith, bark, and cambium. Termite mound earth and saponin rich berries (which are used as antiworm medication by humans) are also eaten. Among the ailments treated by use of these plants by local human populations are headaches, malaria, stomach upset, parasitic infestations including worms, and diarrhea. Another possible function of non nutrient leaf use is as a fertility regulator. Some *Aspilia* species may serve as a fertility regulator, since they contain 2 acids with a uterostimulatory effect. There is some evidence that other primate species such as muraquis, vervets and howler monkeys use various plants to modify their fertility. In fact the active ingredient of kaurenoic acid has anti-bacterial and anti- hepatotoxic action which may improve the health of males and non-reproductive females who eat them. This pharmacological use of local plants seems common in neighbouring troops of chimpanzees, but different use patterns are seen in different groups, even for the same plants. Use of such plants has been seen by chimpanzees in the eastern study sites of Mahale, Gombe, Kibale and 5 other sites. The species who use them include *P.t. schweinfurthii*, *P.t. verus*, bonobo and Eastern lowland gorilla. How the use of these plants was developed and spread is not clear, but young animals watch their mothers eating them and may try them for themselves. The differences in plant use may reflect availability in some instances, but in many cases plants are available to several groups but used differentially suggesting that similarity in taste or effects may account for the spread of their use.

The second section of the book focuses on Social Relations and how chimpanzees appear to keep track of the strengths and weakness of their social companions, and use this information to compete for food and nesting sites. In order to examine what factors foster diversity, differences between individuals, populations, subspecies, and congeneric forms are investigated, as well as comparisons between captive and wild populations. Forcing chimpanzees to live together in captivity may influence their social behaviour by increasing the frequency, duration and intensity of interactions, especially among females, who in the wild tend to be fairly solitary. Boehm comments that the social effects of the inability to leave social companions in captive groups may find a parallel in the changes seen in human behaviour with the transition from hunter-gatherers to agriculturalists. When the impulse to stay outweighs the costs of leaving humans learned to cooperate at a basic level against outsiders, while competing for status in terms of access to resources within the group. Thus humans developed variable behaviour patterns depending on the social situation, which seem to be paralleled by differences in chimpanzee behaviour, particularly in terms of the level of social stability in the group.

The first chapter of this section deals with the non-copulatory sexual behaviour of bonobos which starts at a very early age. Adults have sexual contact with young animals mostly in a play context, although mothers use ventro-ventral genital contact with young males to reduce their own levels of emotional arousal. Youngsters have also been seen to present to adult males in agonistic contexts where mounting by the adult seemed to defuse the tension. Youngsters may become involved in the sexual behaviour of copulating adults, but not in a disruptive sense, unlike young chimpanzees and not with their own mothers. As the youngsters reach adolescence there is a sharp drop in the frequency of this behaviour as males move to the groups periphery and male adults become less tolerant of them. As these animals mature to adulthood quite different patterns of non copulatory sexual behaviour develop for males and females. Young adult immigrant females show frequent sexual contact with a wide range of individuals; both adolescent and mature males and females. Genital contact between adult females seems to occur in times of social excitement and agonism such as feeding or intergroup encounters. The females who rubbed genitals or rumps then often maintained close proximity and seemed to show reduced tension levels with each other, even in otherwise agonistic situations. Females show particularly high levels of sexual contacts with members of neighbouring groups if they meet, possibly developing relations with others which will benefit them if they emigrate. Males also used rump-rump contact or mounting to reduce tension with other males, but often followed this contact by moving further apart. In addition, males used kisses, touching, and embracing to reduce conflict and tension levels. All of these social aspects of sexual behaviour allow bonobos to develop and maintain social relations with a wide range of other individuals, and to reduce tension levels in 3 major potentially antagonistic situations; feeding aggregations, contact with immigrant females, and meeting other groups. Common chimpanzees frequently show quite high levels of displaying and aggression in these situations, and immigrant animals and strangers are sometimes hurt or killed. The affiliative benefits of using non copulatory sex to regulate tension seem to develop early in life among the bonobos, and persist in differing circumstances throughout development. Different patterns are used and the context and results vary by age and sex, but the overall function seems to be quite similar. The calming use of non copulatory sex may also be fostered by the longer estrus period of female bonobos over female chimpanzees, which means that even reproductive sex causes much less tension for them than for chimpanzees. The use of differing patterns of sexual contact as a variable behavioral phenomenon is quite interesting since reproduction is usually considered to be such an adaptively vital aspect of survival that it is very genetically and hormonally driven. However, bonobos appear to have relaxed some of these selective factors and modified the function of sex as a behaviour to serve social ends.

Another very social behaviour which shows quite a lot of variability between bonobos and chimpanzees is social grooming. Among chimpanzees the frequency of male to male grooming is higher than either male to female or female to female. Chimpanzee males also groom more different males partners than they do females, or than females groom, suggesting that the maintenance of bonds among males is a higher priority than maintaining bonds with females. Male grooming serves to establish alliances, achieve dominance and aid access to estrus females. Males need to maintain cooperative alliances within the group in order to resist inter-group antagonisms. Bonobos, on the other hand have less need for conflict over estrus females, since the estrus period is longer, and they show less antagonism with outside groups. Thus bonobo males spend more time grooming with females than with other males. Female chimpanzees groom their kin at quite a high rate, but tend

to be fairly solitary otherwise and mainly groom non related males when consorting sexually with them. Bonobo females groom other females about as much as expected given the numbers of possible grooming dyads that exist. and do not seem to differentiate in frequency between kin and non kin. This differential pattern of grooming may have a number of causes, including differences in the level of strength in kin bonds between chimpanzees and bonobos. Another possible factor investigated when looking at female social interactions, is the possibility that differences in social stability and female range use patterns may affect how females may relate to each other.

The initial comparison for this study of female interactions occurred in captive settings because it occurs at such a low rate among wild chimpanzees that it is difficult to study. In the Detroit zoo a chimpanzee group was newly established, and the females were very active in aggressive, reconciliation and coalition behaviours. These are common types of behaviour in males, who use them in a complex social strategy to compete intensively for dominance status. Males will change alliance partners quite frequently in order to maintain a balance of power maximally advantageous to themselves. In free ranging groups females are seldom seen engaging in these behaviours, and even in long standing stable captive groups such as at Arnhem Zoo there was little aggression in 'dominance contexts'. The females there seemed to have a clear stable system of relations; perhaps what could be called a respect relationship or subordination hierarchy, as Burton (1971), and Rowell (1972) would respectively term this behaviour. Comparisons of rates of female-female aggression with female to male fights or females with juvenile animals revealed that there was not an increase in overall aggression, but particularly in aggression between females. Baker and Smutts suggest that the differences in female-female aggression levels between situations might be due to the females tendency to compete for position when establishing relations, but to cease such overt competition when interactions were stabilized. This pattern may rise from the wild situation in which incoming migrant females may have to compete strongly with already established females for a core range to support themselves when they move into an area, but once they acquire this range they can establish and maintain peaceable interactions with their neighbours. This proposal is supported by observations that established females fiercely attack migrant ones, and the migrants will fight with each other. Once a female has a range she will ally herself with her neighbours in order to defend the area from newly arriving migrants. This whole pattern of initial antagonism and then alliance behaviour is quite different from males who can afford friendly relations with other males because dominance has little effect on resource acquisition up till the point at which they are competing for the top few ranks. When a male is in the position to challenge for alpha rank, even one position higher on the ranking scale can be quite significant in terms of reproductive success. Thus competing males change allies opportunistically, play off one party in a dispute against the other, and engage in a lot of formal dominance rituals and display to consolidate their positions and remind everyone of their rank. The females have hierarchical relations but very seldom express them in display or formal dominance interactions. Females do not need to compete in captivity for reproductive success or for food, so they mainly intervene in fights to protect their friends and offspring or to promote social stability (control behaviour). At Arnhem Zoo female support is a significant aspect in attaining higher rank by a male.

Bonobo rank relations differ from the chimpanzee patterns in several ways, as could be expected since there is less Conflict over sex, more positive social relations with migrants, and less overt kin support. Males and females groom each other more

frequently and spend more time in association than do common chimpanzees. All of these factors impact on each other to influence the behavioral diversity between the two species, in addition, both forms show a high level of behavioral flexibility when social situations are in a state of flux. There is very little evidence on captive bonobos, but the differences apparent in captive groups of chimpanzees and the fact that longer established captive populations are more similar to wild ones than to still unstable captive groups, suggest that it is the chimpanzees response to the fluctuating social stress which can occur in captivity, rather than the state of captivity itself which is most relevant in influencing their behaviour.

The third section of this book is focused on culture and cognition. The discussions of various behaviours in this book have been building towards the argument that while some behavioral variability is based on morphological and ecological factors, and some on differential responses to demographic and social variables, there are still other aspects of behaviour which seem to rest on a cognitive base. Cognition is defined as an animal's ability to represent relevant aspects of the world in which it lives in mental schemes that can be manipulated in simulation types of procedures. On the basis of this ability the animal can design its behaviour and make choices about its course of actions; in other words it can behave intentionally." (Dickinson 1988 in this volume pg:267). The animal can reflect on itself and the conditions of its own functioning. If an animal is self reflective it must have some knowledge about itself, a self awareness, which has been the focus of considerable study since Gallup's early work with mirrors. The attribution of self recognition is confused by inconsistent evidence, but it seems that once chimpanzees pass 6 years of age they usually can respond to a mirror image as a representation of self. The question then becomes is meta-knowledge of the self a prerequisite for the capacity to attribute knowledge and intentions to others? This is often tested by examining deception, but one experiment was set up so that the chimpanzee could see which human knew the correct answer to which can held the food treat, and had the opportunity to trust that person or a blind folded observer about the location of the food. The animal did not see which can was baited, but was able to attribute the knowledge to the correct human. This is quite an interesting result, because only the most advanced of the 4 levels of deception discussed by Mitchell, requires that the deceiver act on the basis of knowledge about the receiver's beliefs. There has been a lot of discussion about whether animals can be aware of another's beliefs. DeWaal suggests that in animals as closely related to us as chimpanzees, postulating a cognitive explanation for such complex behaviours is the most parsimonious explanation, since we use it for ourselves. As an example he cites the ability to attribute beliefs and intentions to other individuals as the foundation for efficient alliance formation. On the other hand, baboons and macaques also use complex and shifting alliances, which other animals seem to manipulate, so would the argument attributing a cognitive basis to this behaviour have to refer to them as well?

Another research technique which can be used to address issues of cognitive abilities is the language and symbol learning work. Two important factors which have been revealed during research on bonobo's acquisition of lexigrams and comprehension of spoken English are relevant. The first is that bonobos can learn these systems without formal training although the rate does differ between individuals. This removes one of the major differences between language learning in children and most common chimpanzees who have learned language skills. The second is an elaboration of earlier discoveries that there is considerable separation between comprehension and production in symbol use. At age 22 months Mulika, a young female bonobo could only use 6 lexigrams, but was receptive to 42 symbols, 30 of

which she had only used once. Kanzi, a 10 year old male responded correctly to over 300 of 400 novel requests in English, which, of course, he can not produce. The learning pattern seems to occur by observing others and seeing the consequences of symbol use and results. Thus the evolution of culture could have been patterned on an increased ability to concentrate.

This brings us to the topic of imitation versus other mechanisms of observational learning. A list of 14 different levels of social learning is provided from Whitten and Ham (1992) ranging from social and response facilitation, through stimulus enhancement, emulation and imitation to imitative learning. The difference between the last two appears to be that some behaviours can be imitated but learning only occurs when you understand why you are imitating an action. Tomasello argues that children understand what they are doing when they imitate language, but I think that the initial stages of word copying is an imitation of sound, without attendant meaning. Many young children can say the words from one to ten, but have no idea of the correct answer when you hold up seven fingers and ask how many there are. Tests comparing children with chimpanzees who have the task of bringing food within reach using a rake reveal that children do copy the motor actions of the non verbal demonstration more closely than the chimpanzees do. Several authors conducting different studies in this book conclude that chimpanzee show more emulative rather imitative behaviour in that they associate two parts of a problem and work at a solution, but don't necessarily solve the problem exactly as they observe it being done. Imitation is defined as "modelling of a behaviour pattern by copying the example set by another," (276) while emulation involves "learn(ing) the connection between a simple procedure and meaningful consequence" (276). Learning through emulation rather than imitation could be advantageous as in the case of two young wild chimpanzees whose mothers had not mastered nut cracking using a stone hammer and anvil. The youngsters, however, grew up to be successful nut crackers without their mothers as models, presumably by watching others. In some cases actual teaching of correct hammer grip and relation of the nut to the anvil has been observed from a mother chimpanzee to her infant. In my opinion, the ability to move back and forth from imitation to emulation, means that the cognitive aspect of problem solving is more clearly understood. There are many ways to solve most problems and the wide variability in behaviours revealed by chimpanzees and bonobos in this volume suggests that a number of successful approaches have been tried and many levels of association can contribute to completion of a task. Galef argues that Japanese macaque potato washing was not learned by true imitation but can be explained more parsimoniously by local enhancement and stimulus enhancement. Tomasello argues, however, that an increase in focus of attention can transform emulation into imitation. In fact when human acculturated chimpanzees are compared with children and mother-raised conspecifics, the effect of human rearing is to produce copying behaviour in chimpanzee youngsters much more parallel to that found in children than to that found in mother-reared chimpanzees. This study comparing 2 year old human children, human enculturated chimpanzees and mother-raised captive chimpanzees who were exposed to 24 novel actions, tested whether the subjects scored successfully reproduced the action. The enculturated chimpanzees and human children scored about equally well and better than mother-reared apes. This research reinforces the suggestion that focus of attention and by implication a social organization that reinforces focused attention is of prime importance in shifting the learning pattern from emulation to imitation .

If cultural phenomena are defined by their universality in a group, their uniformity in nature and some level of time depth, then it is clear why such a transition to imitative

behaviour could be regarded as important in establishing truly cultural behaviour. However, if culture is represented by behaviours passed on by learning and modified in response to differing situations, responding to various functional requirements, then the question of distinguishing between emulation and true imitation seems less important. Certainly chimpanzees are capable of both, but current research suggests that there is little true imitation in free ranging chimpanzees. However, since it is clear that a lot of human behaviour does not occur at a conscious level, does a lack of learning by exact copying of behaviour, rather than learning by attending to the relevant cues and desired out- come of procedure mean that behaviours should not be considered to be culturally transmitted? The general conclusions of this book are not strongly stated. Jane Goodall's Post Script is more concerned with the future of chimpanzee populations in Africa, than as an editorial commentary on the book's conclusion. However, a tremendous quantity of information about a wide range of chimpanzee and bonobo behaviours should help to stimulate a lot of thought about the potential for cultural behaviour in the genus Pan.

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More on Apes: From Incest to Deception

Chimpanzees of the Mahale Mountains. Sexual And Life History Strategies. Edited by Toshisada Nishida. Tokyo: U. of Tokyo Press. 1990. (ISBN: 4-13-068153-2)

This study provides a fascinating comparison to Jane Goodall work on the Gombe chimpanzees. For at least 25 years the two studies ran in parallel in similar habitats, less than 200 kilometres apart on the shores of Lake Tanganyika. Together they

provide us with a broad spectrum of information allowing us to ascertain and assess the similarities and differences between two chimpanzee populations. This is important because we are learning that in spite of underlying similarity of demographic pattern and environmental exploitation, there are important differences between populations in their biocultural relationships with each other and their habitat.

Since Goodall's work was mainly published in English and has received support from organizations promoting the use of film, such *National Geographic*, most people are much more aware of her work than they are of the Japanese research program. Nishida's book is an effort to collect and make available in English a comparable set of data on the male chimpanzees. All the articles have been written especially for this book, but they refer to material previously published in a wide variety journals, directing the reader to sources describing work earlier in detail.

The eleven authors who are represented in this collection are not all of those who have conducted work at Mahale Mountains. Chapters 4 through 15 were very specific studies well bolstered with statistical support for the questions examined. These covered a wide range, from age differences in consumption of ants, sex differences in ranging patterns, sperm competition, and mating behaviours, to adult male social relations with adult females.

Among the more fascinating chapters is the material on demographic and reproductive profiles which can only come from a long term study of known animals, and is so important for our understanding of life history patterns and conservation. The information that over a 10 year period in one group of these chimpanzees deaths equalled births (74) in a population which is not hunted for food and living in a National Park, reinforces the realization that chimpanzee populations are basically in a no growth stage. Of 107 animals born in 22 years, 56, or 52% died before weaning of a combination of disease, aggression, death of mother and unknown causes. As a matter of fact, chimpanzee intra-species aggression, particularly infanticide by males, was responsible for 18% of the deaths, and may be a major factor in holding the population size constant. A confounding factor in determining precise population size is emigration of females, often at about age 11 ± 1.5 years and the return immigration of other females of unknown age. Because of this there are no known ages at first birth. Although these can be closely estimated, one notable difference between this population and the situation at Gombe, is that a number of natal females remained in the Gombe population to breed, and had their first live offspring at 13-14 years of age. The information from Mahale suggests that it takes immigrant females an average of about 3 years to become pregnant. They must establish relationships with males, learn a foraging area and develop relationships with other animals. During this period they run the risk of being attacked by females, disease, exhausted by stress, failure to consort and the possibility that they will leave this community, and go through the same process in attempting to move into another one. As a result the estimated age at first birth is about 14-15 years -- range 12 to 20.

The median number of births per female was 3 with a median number surviving to reproduction of 2 offspring per female. It is also not clear that if the females who disappear from a group survive long enough to establish themselves in a new group, so the death rate may be even higher than estimated. These figures reinforce the information of stable population size from Gombe, even though there is an argument that human disease (polio) disrupted the normal demographic pattern at Gombe. The

mounting tide of statistics on population size is clearly relevant in decisions about "harvesting" wild chimpanzees for use in medical and behavioural research. Nishida does not comment on this problem.

However, the overview of chimpanzee behaviour at Mahale in the first chapter by Nishida is a fine summary and will permit easy comparison with other material on chimpanzees. Nishida notes some of the most salient comparisons with material from Gombe and the Budongo forest such as material on incest, tool use and greeting gestures. The primate background to mother-son, brother-sister and father-daughter mating has long been an interesting focus for those investigating the human condition. Many aspects of group formation are considered to be adaptations to prevent serious levels of inbreeding in primates. These include offspring dispersal in monogamous forms, male emigration in multi-male groups, periodic male replacement in single male groups, and, among chimpanzees, female emigration. The most clearly recognizable incest is between mothers and sons, since in most cases fathers of offspring are not known with accuracy. Mother-son mating does occur with pre and post post-weaning offspring, both in chimpanzees and rhesus macaques (Fedigan 1982). Nishida reports pairs of mothers and immature sons in which he says mating was often seen, but that in the only case of a mature son mounting his mother, she threw him out of the tree, and he didn't try it again. Goodall in contrast, reported some episodes of mothers mating with mature sons (1986). This behaviour may have had other relevance than reproductive. For example it may have allowed the son the opportunity to assert himself over a female in the presence of other males. Brother-sister and father-daughter mating was not seen in Mahale because all natal females emigrated as late adolescents. In Gombe, Fifi was seen to scream and attempt to fight off her brothers when they tried to mate with her, even though she persistently solicited mating from all the other males. These observations of a persistent, but not universal avoidance of incest, and its variability by age suggest that the inhibitors tend to be social rather than biological factors which come into play when the relations between adult males and females are confounded by the relations between mothers and offspring.

Another area in which comparisons with the Gombe material are interesting is the variability in subsistence activities. Of particular interest is the difference in ant fishing techniques and the species of ants eaten. Gombe chimps eat driver ants which they fish for using a long stick. Mahale chimps eat a number of species of *Camponotus* and *Crematogaster* ants which they lick up after chewing into nests. However, Mahale chimps occasionally use long sticks for extracting a nesting bird from a hole in a tree. Differences in culturally transmitted behaviours such as these are indicative of the behavioural plasticity of chimpanzees, but the uniformity of prey species and extraction techniques within communities, suggests a basic conservatism. Nishida notes that in spite of the thousands of hours of chimpanzee observation, the adoption of a new habit has not been seen. New foods have been added to the food list after humans were translocated, leaving cultigens behind. In some cases adult females were observed to initiate their use, unlike the patterns reported for some macaques.

Greeting and grooming gestures also show some differences between the two populations. The mutual grooming hand clasp is an unusual behaviour seen among Mahale chimpanzees, and not seen among other groups. Other aspects of coupleship behaviour such as a leaf clipping display were also used in different contexts among Mahale chimpanzees. These comparisons help us to understand where areas of variability occur in the behavioural template of chimpanzees. However a more

organized presentation of these areas of comparison, with input from all available studies of free ranging chimpanzees would have turned some very interesting comparisons into a truly valuable tool to explore the ranges of labile behaviours.

The only summarizing essay, after the background of the study and the ecological parameters of the region are explored, is the final piece on deception in chimpanzees, which brought together some of the anecdotal material involving deception seen by various researchers over the years and compared them with some other published accounts. In this I feel that the book has not lived up to the exhortation by Itani "not to forget the Kyoto University African Primatological Expedition tradition of extensive study from a "birds eye view" (Preface). It is Goodall's ability to move back and forth from the specific to the general which makes her work so readable to the non-specialist. Nishida's book is very valuable in the detail and insight provided in discussing particular research questions, but it lacks the overview from a population perspective. A concluding chapter which referred to the studies presented in the book and summarized their content, drawing general insights into Mahale chimpanzee behaviour would have been very useful it would have permitted rapid comparison to be drawn between this population and others which have been studied, and contributed to a general understanding of chimpanzee behaviour.

Nonetheless this book provides an excellent compilation of material some of which was previously unavailable to western researchers. The history of establishing the study site is a clear example of how perseverance can eventually result in longterm success. The major advantage of this material is its long time span which allows comparisons to be drawn with both the type of data short studies provide and other long term ape research.

The tables, photographs and maps included also contribute substantially to the overall appeal and usefulness of this book. It will serve as a valuable addition to the resources of those engaged in studying primates' social life and communication.

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