Exchange of Objects Between Humans and Captive Western Lowland Gorillas

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ABSTRACT. An experiment was carried out to assess the ability of captive western lowland gorillas (*Gorilla g. gorilla*) to exchange objects with a human partner. Before the exchange itself, individuals had to learn to give an item to the experimenter. Four individuals out of nine performed active giving. After that familiarization with giving behaviour, two kinds of exchanges, of increasing complexity, were tested with gorillas. Simple exchange (give C to obtain D) was the first procedure and six gorillas out of nine succeeded. Double exchange (give B to receive C, then give back C to obtain D) was performed only by three individuals and triple exchange (give A to receive B, give back B to receive C, then give back C to obtain D) was performed only by two individuals. Different types of errors were scored, as well as social constraints on learning. Results showed that (1) naive gorillas are able to get a reward (D) in an experimental exchange situation; and (2) the complex rules of multiple successive exchanges were not easily understood by gorillas.

Key Words: Exchange; Intentional giving; Sharing; Gorillas.

INTRODUCTION

The gorilla has recently been called the "misunderstood ape" (BYRNE, 1996) from a cognitive point of view. Indeed, the number of cognitive studies performed on gorillas is much smaller than that with chimpanzees. Gorillas sometimes failed to perform like chimpanzees and orangutans when confronted to similar cognitive tasks. In this regard, self-recognition has been more controversial to demonstrate in gorillas than in the other great apes (SUAREZ & GALLUP, 1981; LEDBETTER & BASEN, 1982). Recently, some gorillas formally passed the mark-test (PATTERSON & COHN, 1994; PARKER, 1994) and were considered to be capable of self-recognition (BYRNE, 1996). The fact that some of them failed to display self-recognition could be considered as a consequence of the low number of gorillas tested in front of a mirror.

The cognitive skills of gorillas seem to resemble those of orangutans in other domains, such as intentional communication, true imitation and tool-use (RUSSON et al., 1996) and strengthen the hypothesis of cognitive homogeneity among the great apes. However, in order to give further support, the cognitive skills of gorillas should be investigated in several domains such as those tested with chimpanzees. Intentional giving of an object is considered to have played an important role in the evolution of hominidae (STOCZKOWSKI, 1994). This type of behaviour makes it possible for complex social rules of exchange based on reciprocity to emerge (MAUSS, 1950). In this context, exchange of objects could be considered as an aspect of complex socio-cognitive abilities in humans.

Active giving and gifts *a fortiori* does not seem to be as usual in non-human primates societies. In the living great apes, active sharing is restricted to a few occurrences in chimpanzees and may imply reciprocal obligations (DE WAAL, 1989). In cooperative hunting by wild chimpanzees, several authors have observed passive sharing between individuals while active sharing remained a rare pattern (GOODALL, 1963, 1986; TELEKI, 1973; BOESCH & BOESCH, 1989). Active sharing and gifts of meat accounted for 7% of all the occurrences of sharing observed during hunts and concerned adult males more frequently than adult females (BOESCH & BOESCH, 1989).

In orangutans, active food sharing has been observed in the wild between mothers and infants (MACKINNON, 1974; HORR, 1977; GALDIKAS & TELEKI, 1981). The development of active giving has been investigated in the mother-offspring pair (BARD, 1990). Active giving and allowing the infant to take food items accounted for 14 to 35% of maternal responses. This proportion was higher than that observed in chimpanzees and capuchin monkeys but it was restricted to mother-offspring relationships (DE WAAL, 1989; DE WAAL et al., 1993).

Active sharing was finally the least frequent pattern of food sharing behaviour whatever the primate species under consideration. For example, among all the different sorts of sharing observed, passive sharing represented the most frequent type in capuchin monkeys while active sharing represented only 0.5% of all the possible food interactions scored (DE WAAL, 1993).

Some authors have experimentally investigated the basic behaviour which allows active sharing to occur, i.e. the ability to actively give. This kind of behaviour has been studied in a nursery raised chimpanzee *Pan troglodytes* (LEFEBVRE, 1982), in a home-raised pigtail macaque *Macaca nemestrina* (BERTRAND, 1976) and in a mangabey *Cercocebus t. torquatus* (COUSSI-KORBEL, 1993). The results showed that the macaque and the mangabey, as well as the chimpanzee, readily exchange non-preferred items with the experimenter. Moreover, when prized objects were involved, subjects have learned to give as little as possible in exchange. Although the results appeared to be relatively similar for all subjects, important differences in the time required to learn specific rules were apparent.

In captivity, giving has been observed in many species for which it has not been reported in the wild (BERTRAND, 1976). Sharing did not seem to be naturally exhibited by the gorilla unlike the other great apes (BOESCH & BOESCH, 1989; BARD, 1990). The present study was an attempt to investigate active giving and exchange of objects between captive gorillas and humans.

SUBJECTS AND METHODS

SUBJECTS AND HOUSING

Two groups of western lowland gorillas (*Gorilla g. gorilla*) were housed in the CIRMF (Department of Primatology in Franceville, Gabon). Each group lives in an indoor area for feeding and sleeping (see FONTAINE et al., 1995). An outdoor area was available once a day for one group (*Djoutou*) and twice a day for the other group (*Mabéké*). The experiment reported here was run from October to November 1996 when ten individuals were present (see Table 1). However, only nine individuals were potentially capable of participating to the experiment because one gorilla (*Tani*) was too young.

In order to assess the ability of exchange the test sessions should have been carried out with a single subject at a time. However, it was very difficult to separate the individuals for several technical reasons. (1) First of all, it was not easy to isolate one individual from his social group. (2) The medical cages (in which one individual may be isolated) adjacent from the indoor area are not large enough to allow such experiments. The individual subjects have to go away from the experimental area to search objects requested for the exchange. (3) Social tensions between two adult males in group A forced the keepers to let the door between the indoor and the outdoor area open as often as possible (CHALMEAU & PEIGNOT, in press).

Name	Age (years)	Sex	Status
Group A			
Mabéké	16	М	Young silverback
Cola	15	М	Young silverback
Omoye	12	М	Adolescent
Kessala	9	F	Adult
Group B			
Djoutou	18	М	Fully adult silverback
Typhen	24	F	Adult
Caroline	13	F	Young adult, daughter of Typhen
Dian	8	F	Adolescent, daughter of Typhen
Zvé	16	F	Adult
Tani	0.5	?	Typhen's infant

 Table 1. Name, age, sex, and status of the two groups of gorillas.

Table 2. Procedure used in the exchange experiments.

Procedure	Success	Objects
Familiarization	Actively giving into human's hand	Twig and palm nut
Simple exchange	Gorilla gives T-> human gives P	T: twig; P: peanut
Double exchange	Gorilla gives F-> human gives T->	F: piece of fruit
_	Gorilla gives back T-> human gives P	-
Triple exchange	Gorilla gives L-> human gives F->	L: leaf
-	Gorilla gives back F-> human gives T->	
	Gorilla gives back T-> human gives P	

T, F, and L were available in the indoor room.

PROCEDURE

Each group was tested in its social situation in order to note social factors such as monopolizing the experimental area and social tolerance in front of the experimenter. The experiment was run in four successive steps: familiarization, simple, double, and triple exchange (Table 2). For each step, the experimenter initiated each exchange with the following behavioural sequence: the experimenter presented an object A in his left hand while the other hand was empty and directed towards the individual. The individual had to give an object B to the experimenter's empty right hand to obtain object A in exchange. The nature of the objects depended on the type of exchange (simple, double, and triple exchange). If the gorilla presented an object other than the expected object B, the experimenter simply closed his empty hand indicating a refusal.

Familiarization

This period consisted of habituating the individuals to actively put an object in the human's hand through the wire mesh (4 hr). It was a necessary step before investigating the gorillas' ability to exchange objects. Spontaneous behaviour exhibited by the gorillas facilitated familiarization. Indeed, they used sticks as tools to reach vegetables or pieces of fruit outside their cages and otherwise inaccessible (FONTAINE et al., 1995). The experimenter benefited from this behaviour which facilitated exchange procedures. The goal was to test as many individuals as possible. Qualitative data were scored for each individual to describe the development of active giving behaviour as precisely as possible.

Simple Exchange

Seven successive sessions were run in each group. A session lasted 30 min. Success was defined as follows: the experimenter presented a peanut to the individual which had to find a twig in the indoor area and give it to the human to receive the peanut. The procedure was repeated after each success until the end of the session so the number of trials in each session depended on the activities of the gorillas during the sessions.

Double Exchange

Six successive sessions were run in each group (30 min each). The level of complexity had risen since a second exchange was required to receive the peanut. Success was defined as follows: the experimenter presented a twig and the gorilla had to find a piece of fruit in his cage to receive the twig. Then, the experimenter presented a peanut. To receive the peanut, the gorilla had to give back the twig he had just received. In this procedure, the novelty was the first part of the double exchange while the second part was the same as in the simple exchange. For one session (S3), two experimenters conducted the exchanges simultaneously from two opposite places to allow the participation of subordinate individuals in Group A.

Triple Exchange

One 30-min session was run in each group. Another exchange was added and success defined as follows: the experimenter presented a piece of fruit. The individual had to give a leaf for the piece of fruit. Then the experimenter gave a twig against the piece of fruit and finally the peanut for the twig.

ANALYSES

The number of successes was scored for each individual. Some acts of social behaviour were recorded such as monopolizing the experimental area (with or without success) and stealing an item (twig or peanut) from a cagemate. Errors made during the exchange were also scored. Two major types of error are distinguished: (1) error of exchange gesture, i.e. throwing an item (the right one) through the wire mesh and not putting it in the human's hand; and (2) error in the procedure, i.e. finding a wrong item and giving it to the experimenter. In this case, the experimenter did not take it and closed his hand to indicate that the item was not the expected one. This kind of error could be performed by solver as well by non-solver individuals.

RESULTS

FAMILIARIZATION

Group A

Three individuals out of four participated in familiarization. *Cola*, the second silverback male, never approached the experimental area due to social tension with the dominant male, *Mabéké* (CHALMEAU & PEIGNOT, in press). Furthermore, he did not participate in the following experiments (simple, double, and triple exchange).

Omoye was the first individual in the group to perform active giving with the experimenter: Omoye put a twig through the wire mesh, the experimenter took it and give a palm nut to Omoye. Then, the experimenter presented his empty hand to Omoye. Less than one minute later, Omoye picked up a twig from the ground and put it through the wire mesh into the human's hand. He received a palm nut in exchange. Thirteen exchanges followed with Omoye before the arrival of Mabéké, the dominant silverback male.

Familiarization with *Mabéké* was not successful because he never put a twig through the wire mesh by himself. So, the experimenter tried to give him a twig to be used for exchange with a palm nut. However, *Mabéké* never took the twig.

Kessala, the only female in the group, gave actively eight times. When the experimenter presented a palm nut in one hand while the other empty hand was directed toward her, she went to search for a twig and came back to give it to the experimenter. Even though several other objects were present on the ground (pieces of different fruits, pieces of wood, etc), she spontaneously took a twig and came back to exchange it against palm nut.

To summarize, two individuals out of four rapidly performed giving behaviours in Group A.

Group B

Djoutou, the dominant silverback male, came in front of the experimenter. Even though he put a twig through the wire mesh, he pushed it so hard that the experimenter could not take it. The rest of the time, he showed little interest in what was going on, even when some of his cagemates earned palm nuts.

Typhen and Dian performed giving behaviour quite easily. More precisely, they let the experimenter take the twig without any resistance. *Caroline* on the other hand often put twigs through the wire mesh, but she never let the experimenter take them. *Zoé*, the subordinate female in the group, never came to the experimental area because the other individuals prevented her from coming (CHALMEAU & PEIGNOT, in press). To summarize, two individuals out of five performed active giving in Group B.

EXPERIMENT 1: SIMPLE EXCHANGE

During experiment 1, other individuals learned to give and participated in simple exchange: *Mabéké* in Group A and *Caroline* in Group B. Finally, three individuals in each group succeeded in the simple exchange. The total number of exchanges was respectively 129 in Group A (*Omoye*: N=12; *Kessala*: N=32; *Mabéké*: N=86) and 153 in Group B (*Typhen*: N=40; *Caroline*: N=42; *Dian*: N=70). In Group A the order in which the individuals performed simple exchange is the following: *Omoye* (S1), *Kessala* (S1), and *Mabéké* (S4). As soon as the dominant male learned to exchange a twig against a peanut, he monopolized the experimental area and prevented other individuals from coming. In Group B, *Dian* had performed the great majority of her exchanges (80% from S1 to S4) before *Typhen* and *Caroline* learned to do it. The order of access to the experimenter area was the same as rank in access to food between the females: *Typhen, Caroline*, and *Dian* (PEIGNOT, pers. obs.). Monopolization of the experimental area was not as clear as in Group A because changeover occurred frequently between the three females.

In Group A, when an individual performed exchanges, no other individuals were in proximity. If a more dominant individual approached, the first one left the area. In Group B however, there was tolerance between *Typhen* and *Caroline* because for the last three sessions, they continued to perform exchanges alternately. The Spearman correlation between time spent and success was high for *Omoye, Kessala, Mabéké*, and *Dian* (respectively: 0.98; 0.86; 0.93; 0.96; p < 0.05, two-tailed). For *Typhen* and *Caroline*, rho was lower than 0.5 (p > 0.05, two-tailed). This result indicated that *Typhen* and *Caroline* stayed for a long time even though they achieved few successes. For subordinate individuals (*Omoye, Kessala*, and *Dian*), the correlation was high because as soon as they had the opportunity to come and perform exchanges, they did so as much as possible.

Even though the subordinate individuals frequently monitored the distance between them and dominant individuals, some occurrences of stealing peanuts were observed: *Mabéké* stole two peanuts from *Kessala, Typhen* stole four peanuts from *Dian* and *Caroline* stole two peanuts from *Dian*. It should be mentioned that *Djoutou*, the dominant male, was never seen stealing peanuts from the females, even when he was close to them. In Group B, some individuals also stole a twig from a cagemate when it was in arm's reach rather than leaving the experimental area to search for a twig in the indoor room and coming back in front of the experimenter with it.

EXPERIMENT 2: DOUBLE EXCHANGE

This experiment required individuals to search for an item other than the one used previously to initiate the exchange. Before, they learned to find a twig for exchange against a peanut. Here, they had to learn to give something else, like piece of fruit which was the item requested by the experimenter before he gave them a twig. Several individuals, especially in Group B, showed some difficulty to stop giving twigs to the experimenter while he also presented a twig. However, three individuals out of the six performed the double exchange correctly: Mabéké (N=101), Kessala (N=24), and Typhen (N=52).

In fact, without the simultaneous presence of a second experimenter, only two individuals, the dominant male in Group A and the dominant female in Group B would have monopolized access to the experimental area. It should be noticed that *Typhen* and *Caroline* still stole twigs from *Dian* even though a twig was not required to initiate the double exchange (N=2 for each individual).

EXPERIMENT 3: TRIPLE EXCHANGE

Two individuals performed the triple exchange. Even though the complexity seemed to be increased in this situation, *Mabéké* and *Typhen* were not disturbed by having to add a new exchange to get a reward. *Typhen* performed 19 triple exchanges and *Mabéké* 20. This level of performance was similar to that reached in the last sessions of the double exchange experiment, i.e. it did not take much more time to succeed. As for double exchange, other individuals only had limited access to the experimental area and so were unable to perform any trials. In fact, *Mabéké* and *Typhen* monopolized the experimental area during the entire session.

ANALYSIS OF THE NUMBER OF ERRORS

Simple Exchange

Some individuals displayed a few type I errors because they tended to give a twig as soon as they found it even before the experimenter had his hands in the right position. In fact, they put the twig through the wire mesh (and sometimes threw it) without taking the experimenter's position into account. In this case, the item fell to the ground and the experimenter waited for

another item. The number of type I errors was very low: two for *Mabéké* and *Typhen*, one for *Dian*, and zero for the other individuals. Concerning type II errors in Group B, all the individuals spontaneously give a twig against a peanut. In Group A, *Mabéké* and *Omoye* made one type II error and *Kessala* made 12 type II errors, particularly in the first sessions. Overall, the total number of errors (N=19) according to the number of successful exchanges (N=282) was very low (6.3%).

Double Exchange

The number of errors (types I and II) was enhanced in double exchange compared to simple exchange. Overall, the total number of errors accounted for a large proportion of the trials. With a total of 454 errors and 178 successes, the overall percentage of errors reached 72% of all trials. The main solvers, *Mabéké* and *Typhen* continued to present a twig against a twig, i.e. when the experimenter was waiting for a piece of fruit (type II errors: N=150 for *Mabéké*; N=11 for *Kessala*; N=146 for *Typhen*). Other non-solver individuals like *Caroline* and *Dian* still presented a twig against a twig and did not succeed in the double exchange (N=73 for *Caroline*; N=25 for *Dian*). It should be mentioned that they only had limited access to the experimental area which *Typhen* tended to monopolize.

Type II errors were the most frequent (64% of all trials). It seemed that the learning rule acquired in the simple exchange still persisted for all the individuals as revealed by the high proportion of type II errors. Note that *Typhen* did not succeed in the last session because she still presented or threw twigs and leaves through the wire mesh while the experimenter wanted a piece of fruit against the twig he presented. This particular and repeated type of error (observed also for Mabéké) was used to investigate triple exchange.

Triple Exchange

The main result was that type II errors decreased drastically since triple exchange was initiated using spontaneous errors in double exchange. The overall proportion of errors reached 31% for *Mabéké* and only 5% for *Typhen* (error I: 0 for *Typhen*, 2 for *Mabéké*; error II: 1 for *Typhen*, 10 for *Mabéké*). In fact, as revealed by the type of errors, the difficulty for solvers was to select the expected first item rather to add a new exchange. *Mabéké* still threw peanut shell rather often (N=10) compared to *Typhen* even though this behaviour was never reinforced.

DISCUSSION

The experiment was conducted to investigate giving abilities of gorillas in successive exchange procedures. The results showed that gorillas quickly learned to give an object to receive a reward. Moreover, active giving did not seem to be difficult to learn since the majority of the subjects acquired it in only a few sessions [this was not the case in COUSSI-KORBEL's study (1993) with a mangabey]. Two different reasons can be proposed to explain why three gorillas out of nine did not learn to give. For two of them, *Cola* (Group A) and *Zoé* (Group B), the main reason was social constraints: *Zoé* was the most subordinate female in the group and had no access to the experimental area; *Cola* was an adult male who was inhibited by *Mabéké*'s presence (CHALMEAU & PEIGNOT, in press). For *Djoutou*, the third non-solver gorilla, the reason was less trivial. He had free access to the experimental area due to his social status (dominant male) but only showed little interest for the experiments and never stole an item (even a peanut)

from cagemates. This relative lack of interest was also evident in various other tasks (PEIGNOT & CHALMEAU, unpubl. results).

Even though only four individuals learned to give an item in the familiarization step, two others (Caroline and Mabéké) showed regular success during the simple exchange procedure. The learning rule, which consisted in giving a specific item to obtain a reward, seemed to be acquired by gorillas quite easily and without numerous errors. Qualitative data on giving by a home-raised Macaca nemestrina have shown that the willingness or reluctance with which the individual monkey gave an object on command (vocal and visual) depended on the attractiveness of the object (BERTRAND, 1976). Spontaneous giving is much less frequent than giving on command and occurred in two situations: (1) to acquire something or to ask for help; and (2) as an exchange for something else that the monkey cannot get in another way. The author concluded that the monkey appeared to perform giving as a social technique (BERTRAND, 1976). A more quantitative study by COUSSI-KORBEL (1993) with a mangabey showed that exchange occurred when a desired item cannot be acquired by means of dominance. The period during which the exchange was achieved (two months) was much longer than with gorillas (few hours). Moreover, the procedure involving the mangabey concerned simple exchange only in which the first object was given to the monkey. Concerning gorillas, even for simple exchange, the individual had to go to search for the requested object within the indoor area before the exchange itself.

The experiment is growing into complexity with the double exchange procedure applied to gorillas. When that procedure was set up, a lot of errors appeared for all the individuals. In particular, all of them persisted in presenting the object which had been reinforced in the simple exchange, i.e. giving a twig to obtain a reward. Even after the experimenter had refused the exchange on numerous occasions, solvers persisted in throwing items like twig or peanut shell when a piece of fruit was expected. For two individuals, the dominant male in one group, and the dominant female in the other group, it seemed easier to perform triple exchange than double exchange. In the double exchange, Typhen still presented leaves torn from twigs first. This behaviour was previously scored as a type II error in the double exchange while it was required to initiate the triple exchange. This could explain why the number of errors was lower for Typhen (compared both to Mabéké in the same procedure and to her own performance in the double exchange) even if the complexity of the task was considered as being greater for the experimenter. In fact, the exchange itself was not so difficult, the individuals simply had to learn to give back what the experimenter had just given them. The main difficulty was to select the first item which initiated the exchange: in double and triple exchanges, type II errors revealed that individuals did not associate what was presented by the experimenter with the item they had to give. From the moment they got the first item, they just had to keep on giving items back until they obtained the peanut.

In gorillas, active giving has never been observed in the wild (BARD, 1990), but it seemed relatively easy to acquire in an experimental situation. The natural feeding behaviour in gorillas, which consists in "solitary" foraging may not facilitate the occurrence of active giving. Hence, the silverback leads his group to a place with abundant fruit and each individual gathers for itself. For chimpanzees, active giving could be promoted by particular situations such as cooperative hunting in which a small amount of prized food items (meat) is available (BOESCH & BOESCH, 1989). Consequently, it could be more difficult to observe active giving in wild gorillas because their feeding behaviour does not favour such activities. Although active giving between group members has not been observed in the wild, it was observed once when *Typhen* had just put a peanut in her mouth and *Dian* approached to beg for it, *Typhen* showed the peanut between her lips and *Dian* took it with her own mouth. Tolerated taking was also observed once

when Typhen let her daughter Dian take a peanut she had just gained from an exchange. For numerous primate species, giving has been much more frequently observed in captivity than in the wild and occurs mostly in apes (BERTRAND, 1976). Similarly, several other studies have shown that some species have the potential to perform in captivity behaviour unknown in the wild. Sophisticated tool-use skills were, for many years, the considered the sole attribute of chimpanzees until experiments demonstrated that other great apes are able to make and use tool as well as chimpanzees (PARKER & GIBSON, 1977; BECK, 1980; LETHMATE, 1982; GALDIKAS, 1989; FONTAINE et al., 1995). In the same way, chimpanzees are the only apes known to display cooperative hunting in the wild (BOESCH & BOESCH, 1989). In an experimental situation, captive chimpanzees are able to solve a cooperative task; orangutans are too although they have never been observed to participate in cooperative hunting (CHALMEAU, 1994; CHALMEAU & GALLO, 1996; CHALMEAU et al., 1997). In a feeding context in the wild, gorillas have never been observed to give food items unlike to chimpanzees. Experiment on giving and exchange modify this view since in a particular situation, gorillas are able to exhibit behaviour belonging to the most complex form of sharing. Because active giving is assumed to play an important role in early hominids, we suggest that the living great apes may share this ability although, as yet, it seems that only chimpanzees, due to their specific socio-ecological selection pressures, display it naturally in the wild.

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REFERENCES

- BARD, K. A. 1990. "Social tool use" by free-ranging orangutans: a Piagetian and developmental perspective on the manipulation of an animate object. In: "Language" and Intelligence in Monkeys and Apes, PARKER, S. T.; GIBSON, K. R. (eds.), Cambridge Univ. Press, New York, pp. 356–378.
- BECK, B. B. 1980. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. Garland STPM Press, New York.
- BERTRAND, M. 1976. Acquisition by a pigtail macaque of behavior patterns beyond the natural repertoire of the species. Zeitsch. Tierpsychol., 42: 139–169.
- BOESCH, C.; BOESCH, H. 1989. Hunting behavior of wild chimpanzees in the Taï national park. Amer. J. Phys. Anthropol., 78: 547-573.
- BYRNE, R. W. 1996. The misunderstood ape: cognitive skills of the gorilla. In: *Reaching into Thought: The Minds of the Great Apes*, RUSSON, A. E.; BARD, K. A.; PARKER, S. T. (eds.), Cambridge Univ. Press, Cambridge, pp. 111–130.
- CHALMEAU, R. 1994. Do chimpanzees cooperate in a learning task? Primates, 35: 385-392.
- CHALMEAU, R.; GALLO, A. 1996. Cooperation in primates: critical analysis of behavioural criteria. *Behav. Process.*, 35: 101–111.
- CHALMEAU, R.; LARDEUX, K.; BRANDIBAS, P.; GALLO, A. 1997. Cooperative problem solving by orangutans (*Pongo pygmaeus*). Int. J. Primatol., 18: 23-32.
- CHALMEAU, R.; PEIGNOT, P. in press. Inter-individual spatial proximity in two captive groups of western lowland gorillas (*Gorilla g. gorilla*). Folia Primatologica.
- COUSSI-KORBEL, S. 1993. Influences sociales sur l'acquisition et l'utilisation d'informations relatives à la recherche de nourriture dans un groupe de Cercocèbes (*Cercocebus t. torquatus*). Ph.D. thesis, Univ. de Rennes I.

- DE WAAL, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. J. Human Evol., 18: 433-459.
- DE WAAL, F. B. M. 1992. Appeasement, celebration, and food sharing in the two Pan species. In: Human Origins, NISHIDA, T.; MCGREW, W. C.; MARLER, P.; PICKFORD, M.; DE WAAL, F. (eds.), Univ. of Tokyo Press, Tokyo, pp. 37–50.
- DE WAAL, F. B. M.; LUTTRELL, L. M.; CANFIELD, M. E. 1993. Preliminary data on voluntary food sharing in brown capuchin monkeys. *Amer. J. Primatol.*, 29: 73-78.
- FONTAINE, B.; MOISSON, P. Y.; WICKINGS, E. J. 1995. Observations of spontaneous tool making and tool use in a captive group of Western Lowland Gorillas (*Gorilla gorilla gorilla*). Folia Primatol., 65: 219-223.
- GALDIKAS, B. M. F. 1989. Orangutan tool use. Science, 243: 152.
- GALDIKAS, B. M. F.; TELEKI, G. 1981. Variation in subsistence activities of female and male pongids. Cur. Anthropol., 22(3): 241-256.
- GOODALL, J. 1963. My life among wild chimpanzees. Nat. Geogr., 124: 272-308.
- GOODALL, J. 1986. The Chimpanzees of Gombe. Belknap Press, Cambridge.
- HORR, D. 1977. Orangutan maturation: growing up in a female world. In: *Primate Biosocial Development*, CHEVALIER-SKOLNIKOFF, S.; POIRIER, F. (eds.), Garland Press, New York, pp. 289-321.
- LEFEBVRE, L. 1982. Food exchange strategies in an infant chimpanzee. J. Human Evol., 11: 195-204.
- LETHMATE, J. 1982. Tool-using skills of orang-utans. J. Human Evol., 11: 49-64.
- MACKINNON, J. 1974. The behaviour and ecology of wild orangutans (Pongo pygmaeus). Anim. Behav., 22: 3-74.
- MAUSS, M. 1950. Sociologie et Anthropologie. Presses Universitaires de France, Paris.
- PARKER, S. T. 1994. Incipient mirror-self-recognition in zoo gorillas and chimpanzees. In: Self-awareness in Animals and Humans: Developmental Perspectives, PARKER, S. T.; MITCHELL, R. W.; BOCCIA, M. L. (eds.), Cambridge Univ. Press, New York, pp. 301–307.
- PARKER, S. T.; GIBSON, K. R. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. J. Human Evol., 6: 623-641.
- PATTERSON, F. G. P.; COHN, R. H. 1994. Self-recognition and self-awareness in lowland gorillas. In: Selfawareness in Animals and Humans: Developmental Perspectives, PARKER, S. T.; MITCHELL, R. W.; BOCCIA, M. L. (eds.), Cambridge Univ. Press, New York, pp. 273-290.
- RUSSON, A. E.; BARD, K. A.; PARKER, S. T. 1996. Reaching into Thought: The Minds of the Great Apes. Cambridge Univ. Press, Cambridge.
- STOCZKOWSKI, W. 1994. Anthropologie Naïve, Anthropologie Savante. CNRS Editions, Paris.
- SUAREZ, S. D.; GALLUP, G. G. 1981. Self-recognition in chimpanzees and orangutans but not gorillas. J. Human Evol., 10: 175–188.
- TELEKI, G. 1973. The Predatory Behavior of Wild Chimpanzees. Bucknell Univ. Press, Lewisburg.

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