

Comparison of Object Manipulation Among 74 Species of Non-human Primates

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ABSTRACT. Seventy-four primates species (24 genera of six families) were presented with a nylon rope and a wooden cube, and their subsequent manipulations were recorded in detail. Five hundreds and six manipulation patterns were distinguished on the basis of the actions performed, body-parts used and relations to other objects. Inter-specific comparisons revealed three groups: (1) lemurs, marmosets, spider monkeys and leaf-eaters; (2) Old World monkeys except leaf-eaters; and (3) cebus monkeys and apes. The first group had the smallest repertoire of manipulations, in which only a few types of actions and body-parts were involved. The second and third groups had more varied modes of manipulation. Actions such as Roll, Rub and Slide, and use of fingers characterized these groups. Except for the lesser ape, their manipulations were frequently related with other objects. Moreover, actions such as Drape, Drop, Strike, Swing and Throw were typical of the third group. The factors producing such inter-specific differences in manipulations and the relations to tool use are discussed.

Key Words: Object manipulation; Inter-specific comparison; Phylogeny; Tool use.

INTRODUCTION

The variety, versatility and skillfulness of manipulation of non-edible environmental objects by primates are the most characteristic features which sharply distinguish them from non-primate mammals. Many researchers of primate behavior have investigated this subject theoretically and empirically (CANDLAND & JOHNSON, 1978; CONNOLLY & ELLIOTT, 1972; DERIAGINA, 1982; JORDAN, 1982; MASON, HARLOW & RUEPING, 1959; MENZEL, 1966; PARKER, 1973, 1974a, b, 1978; PARKER & GIBSON, 1977; VAUCLAIR & BARD, 1983). However, from the standpoint of making inter-specific comparisons, few empirical data were obtained systematically under comparable conditions over a wide range of species (except by PARKER, 1974a, b). Comparative evidence is needed in order to elucidate the evolution of object manipulation in primates.

Generally speaking, the similarities observed among species reflect a common ancestor or similar environmental pressures (WILSON, 1975). The detection of manipulation patterns specific to a given species or to a given species group can thus serve to clarify factors contributing to the evolution of object manipulation. Comparative evidence of manipulation is also needed for placing our own species within the framework of primates: object manipulation has been assumed to be a precursor of tool use, which was and is one of the most effective strategies of adaptation to the environment especially among human beings. Intensive and extensive analyses of object manipulation in primates may thus help to elucidate the conditions and restrictions underlying the occurrence of tool use and may suggest factors which have made our own species the most eminent tool-user.

PARKER (1974a, b) observed the object manipulation of as many as 11 species of primates

ranging from the lemur to chimpanzee under comparable conditions and analyzed qualitatively the various aspects of their modes of manipulation. Some of his data indicated species-specific modes of manipulation. However, from these data, it is not possible to distinguish a species-specific pattern from a species group (e.g., genus)-specific one, since he employed only one species in each group except for the great apes. For example, he reported that rolling the manipulandum back and forth by the palmar hands was specific to capuchins, whereas it may not be specific to capuchins but common to all cebus species. In addition, ITANI (1957) has reported that rolling objects were frequently observed in Japanese monkeys.

The present study extends the work of PARKER. As many as 74 species (covering 24 genera of 6 families) were observed under conditions similar to PARKER's, in an attempt to reveal the characteristic nature of object manipulation in primates and to provide a comprehensive and exhaustive framework for further comparative studies on manipulation.

METHOD

SUBJECTS AND HOUSING CONDITIONS

This study was performed at the Japan Monkey Centre (JMC) and Primate Research Institute of Kyoto University, Inuyama, Japan.

Table 1 provides a list of the species employed and the numbers of subjects observed in this study. All subjects were housed in outdoor cages in groups of two to seven members, including at least one adult male and one adult female, of an identical species, except for

Table 1. Species observed. The numbers of subjects are indicated in parentheses.

<i>Lemur catta</i> (5) <i>L. macaco</i> (2) <i>L. variegatus</i> (2)
<i>Callithrix penicillata</i> (2) <i>C. jacchus</i> (3) <i>C. argentata</i> (2)
<i>Saguinus weddelli</i> (4) <i>S. labiatus</i> (3) <i>S. mystax</i> (2) <i>S. midas</i> (2)
<i>Ateles geoffroyi</i> (2) <i>A. belzebuth</i> (2) <i>A. paniscus</i> (1)
<i>Lagothrix lagothricha</i> (2)
<i>Cebus nigrivittatus</i> (5) <i>C. capucinus</i> (3) <i>C. apella</i> (7) <i>C. albifrons</i> (5)
<i>Saimiri sciureus</i> (6)
<i>Callicebus moloch</i> (3)
<i>Aotus trivirgatus</i> (2)
<i>Macaca sylvanus</i> (3) <i>M. fuscata fuscata</i> (3) <i>M. f. yakui</i> (4) <i>M. arctoides</i> (3) <i>M. thibetana</i> (2) <i>M. nemestrina</i> (2) <i>M. mulatta</i> (3) <i>M. assamensis</i> (2) <i>M. cyclops</i> (4) <i>M. sinica</i> (2) <i>M. radiata</i> (4) <i>M. fascicularis</i> (4) <i>M. silenus</i> (2) <i>M. maura</i> (2)
<i>Cercopithecus hamlyni</i> (3) <i>C. petaurista</i> (3) <i>C. aethiops</i> (5) <i>C. albogularis</i> (2) <i>C. ascanius</i> (2) <i>C. lhoesti</i> (3) <i>C. talapoin</i> (2) <i>C. cephus</i> (2) <i>C. neglectus</i> (2) <i>C. mona</i> (4)
<i>C. nigroviridis</i> (2)
<i>Cercocebus torquatus</i> (2) <i>C. t. lunulatus</i> (5) <i>C. atys</i> (2) <i>C. albigena</i> (1) <i>C. galeritus</i> (2)
<i>C. g. chrysogaster</i> (2)
<i>Erythrocebus patas</i> (2)
<i>Mandrillus leucophaeus</i> (5) <i>M. sphinx</i> (2)
<i>Papio hamadryas</i> (2) <i>P. cynocephalus</i> (2) <i>P. anubis</i> (4)
<i>Theropithecus gelada</i> (2)
<i>Colobus guereza</i> (1)
<i>Presbyris francoisi</i> (2) <i>P. obscurus</i> (2) <i>P. pileatus</i> (2) <i>P. entellus</i> (3) <i>P. cristatus</i> (5)
<i>Nasalis larvatus</i> (5)
<i>Hylobates lar</i> (2) <i>H. agillis</i> (2) <i>H. moloch</i> (1) <i>H. klossii</i> (2)
<i>Symphalangus syndactylus</i> (2)
<i>Pongo pygmaeus</i> (4)
<i>Pan troglodytes</i> (5)
<i>Gorilla gorilla</i> (2)

Ateles paniscus, *Colobus guereza*, and *Hylobates moloch* which were housed individually, and *Cercocebus albigena* and *C. galeritus* which were housed in a cage. Some groups included infants (less than one year old), the data of which were excluded from analysis, since a pilot study on Japanese monkeys had indicated that the manipulation patterns of infants were qualitatively different from those of other members.

The standard home cage measured about $2 \times 2 \times 3$ m, varying according to the group size and species concerned: it was larger for a great ape and smaller for a marmoset. The floor and one of the walls of the cage were made of concrete and the ceiling and other three walls were made of wire-mesh. All cages were equipped with a water vessel and some wooden perches. The subjects were fed daily in the morning and late afternoon.

PROCEDURES

The observational procedures were similar to those of PARKER (1974a, b), except for the manipulanda and the observational setting. Two manipulanda were employed in the present study. One of them consisted of a white three-strand nylon rope with two knots made at each end to prevent loosening, measuring 120 cm in length and 10 mm in diameter for great apes, 60 cm in length and 4 mm in diameter for marmosets, and 90 cm in length and 7 mm in diameter for other species. The rope was not attached to the cage, in contrast to PARKER's studies, since a pilot study had indicated that an unattached rope elicited a greater variety of manipulation patterns than an attached one. The other manipulandum was a wooden cube measuring $3 \times 3 \times 3$ cm for great apes, $1 \times 1 \times 1$ cm for marmosets and $2.5 \times 2.5 \times 2.5$ cm for other species.

The experiments were performed in a social setting, which was also shown in the pilot study to inhibit or eliminate neophobia towards novel objects placed in the cage. The experimenter placed the manipulandum in the group cage, and recorded the subject manipulating it and the mode of manipulation in detail for 45 min. Only qualitative aspect of the manipulation were recorded: quantitative aspects such as frequency or duration were not recorded. When the manipulandum was left alone for more than 20 min, the observation was brought to an end. Data were obtained from as many subjects of the species concerned as possible. Therefore, second and, if necessary, third manipulanda of the same kind were placed in the cage and focused on, in cases where one subject held the manipulandum exclusively for more than 20 min. Subjects were neither deprived of food before the experiment nor rewarded for manipulations carried out. Each species received one session with each manipulandum.

RESULTS

CATEGORIES OF MANIPULATION PATTERNS

In this study, manipulation was defined as any physical contact with the manipulandum placed in the cage, except for incidental contact. Therefore, visual exploration and sniffing without making physical contact were not recorded as manipulations. Each manipulation pattern consisted of three components: actions performed, body-parts used and the relation to other objects or the substrate.

Five hundreds and six manipulation patterns were identified, of which 254 were observed only for the rope, 157 only for the cube, and 95 for both.

The third component involved two types of manipulation: primary manipulation and secondary manipulation. The former was defined as object manipulation with no relation to another object or in global relation to the substrate. The latter was defined as object manipulation in relation to some specific feature of the environment. For example, rolling the manipulandum on the floor was classified as primary, while rolling it in the water vessel was classified as secondary. Two body-parts pulling the rope in opposition to each other was classified as primary, while the same action by way of the wire-mesh was classified as secondary. Of the 506 manipulation patterns, 449 were primary and 57 were secondary manipulations.

Table 2 shows the kinds of actions and the numbers of kinds of primary manipulation patterns in which each action was performed. Twenty-one actions were distinguished, of which one was only for the wooden cube, six were only for the rope, and the others were for both. Most of the secondary manipulations included the same actions as the primary ones, while some were specific to the secondary manipulations, as described elsewhere in this paper.

Table 2. Categories of actions and their definitions. The numbers of manipulation patterns are indicated in parentheses.

Drape (16):	placing the manipulandum over a body-part
Drop (4):	releasing the manipulandum, not including passive dropping
Flip (9):	flipping the manipulandum sideways or upward with rapid finger action, little or no arm movement
Mouth (13):	touching orally, biting or licking the manipulandum
Passive hold (10):	holding, resting on or sitting on the manipulandum without movement
Pick up (19):	lifting the manipulandum up off the floor
Pull (19):	two or more body-parts pulling the manipulandum in opposition to each other
Push or Press (19):	applying pressure on the manipulandum with a body-part without moving it
Roll (43):	rolling the manipulandum against the floor, wall or a body-part
Rotate (3):	turning the manipulandum in the hands or lips
Rub (60):	rubbing the manipulandum against the floor, wall or a body-part
Shift (29):	moving the manipulandum on the floor without picking it up off the floor
Slide or Stroke (71):	moving a body-part along the surface of the manipulandum or sliding the manipulandum across a body-part by pulling it
Strike (26):	striking the manipulandum with a body-part or striking something with it
Swing (28):	waving or shaking the manipulandum in an alternating or circular motion
Throw (14):	throwing the manipulandum
Touch (18):	touching the manipulandum without manipulating it further
Transfer (9):	changing the holding state, e.g., from oral holding to manual holding
Transport (24):	locomotion while holding the manipulandum
Untwist (14):	untwisting the rope strands, including actions attempting to untwist and actions with a strands-untwisted rope
Wad (1):	making a compact mass or wad

The body-parts were classified into 18 categories. Table 3 shows the numbers of kinds of manipulation patterns in which each body-part was engaged. The sum of the manipulation patterns exceeds 506 because most of the manipulation patterns were related with two or more bodyparts.

COMPARISON OF MANIPULATION PATTERNS

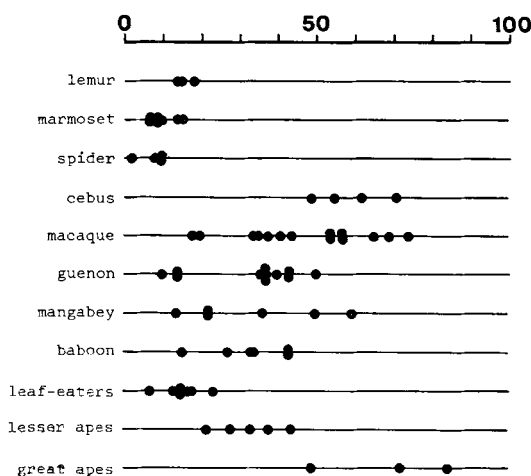
In the following analysis, an inter-species group comparison was performed for each

Table 3. Categories of body-parts used and the numbers of kinds of manipulation patterns in which each body-part was engaged.

Head and Neck	20
Face, excluding mouth	4
Body trunk	17
Feet and Legs	73
Mouth and Lips	75
Arms	19
Hands and/or fingers not moving independently or used non-opposably	
Palmar side	393
Radial side	4
Ulnar side	6
Dorsal side	16
Fingers moving independently or used opposably	
Finger I	12
Finger II	21
Finger III	1
Fingers I-II	12
Fingers II-III	7
Fingers III-IV	2
Finger V	1
Fingers I-V	4

component as well as an inter-specific one. For the former analysis, 11 groups of species were selected mainly on the basis of genus: (1) lemurs (*Lemur*), (2) marmosets, including *Callithrix* and *Saguinus*; (3) spider monkeys, including *Ateles* and *Lagothrix*; (4) cebus monkeys (*Cebus*); (5) macaques (*Macaca*); (6) guenons (*Cercopithecus*); (7) mangabeys (*Cercocebus*); (8) baboons, including *Papio*, *Mandrillus* and *Theropithecus*; (9) leaf-eaters including *Colobus*, *Presbytis* and *Nasalis*; (10) the lesser apes, including *Hylobates* and *Symphalangus*; and (11) the great apes including *Pongo*, *Pan* and *Gorilla*. *Saimiri sciureus*, *Callicebus moloch*, *Aotus trivirgatus* and *Erythrocebus patas* did not belong to any of these species groups. The species groups corresponded partially to the ten species observed by PARKER (1974a, b).

Figure 1 shows the numbers of kinds of manipulation patterns observed in each species.

**Fig. 1.** Numbers of kinds of manipulation patterns observed in each species. Each dot represents a single species.

The score for each species was counted from the pooled data for the subjects of the species concerned. (Similarly, the scores for each species described below were calculated from the pooled data for subjects of that species.) The results indicate that the great apes and cebus monkey have the most varied repertoire of manipulations. The lesser apes, macaque, guenon, mangabey and baboon form the next group having various modes of manipulation, although there is great variety within each species group. The lemur, marmoset, spider monkey and leaf-eaters have the fewest modes of manipulation. The rank order of the species groups resembles that of the diversity measures reported by PARKER (1974a, b), except that the cebus monkey and guenon occupy a higher rank and the lemur a lower rank.

Actions

Figure 2 shows the median numbers of kinds, for each species group, of manipulation patterns, in which each action was performed. Pick up, Mouth and Transport were observed in all of the species groups, suggesting that these actions are primate-common ways of manipulation. Rotate, Transfer, Pull and Passive hold are also considered to be primate-common, since these actions were observed in 9 or 10 out of the 11 species groups. The lemur, marmoset, spider monkey and leaf-eaters performed exclusively these primate-common actions and very rarely other actions.

Roll, Slide and Rub are dominant actions in Old World monkeys (except for leaf-eaters), the cebus monkey and great apes (apart from Roll). In addition, some details of manipulation differed among these groups. For example, rolling the manipulandum on the floor, back and forth, with one hand or with both hands in coordination formed common manipulation patterns in these groups, while rolling in an alternate motion of both hands was typical of the macaque and guenon. Rubbing the manipulandum against the substrate with a palmar hand pressing the substrate was commonly observed in four species groups of Old World monkeys and the cebus monkey, but rarely in the great apes, in which rubbing against the subject's own body parts was typical.

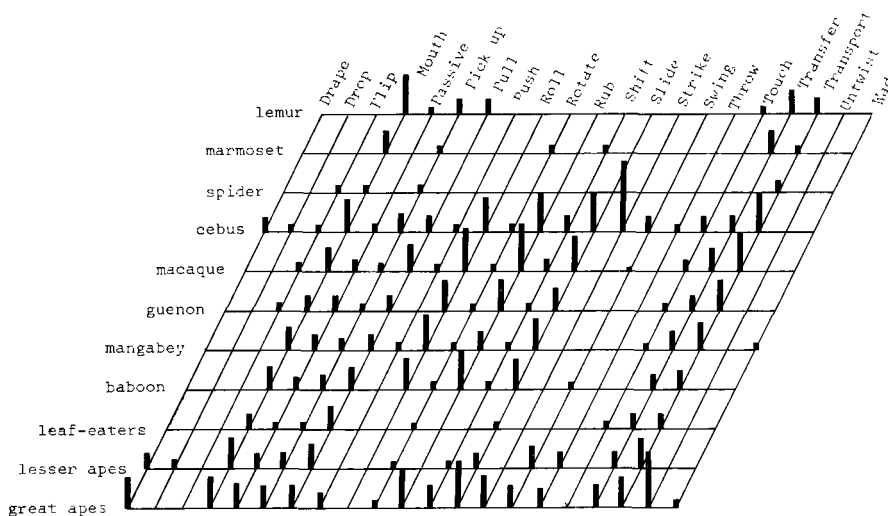


Fig. 2. Median numbers of kinds of manipulation patterns in each action.

Drop, Drape, Swing and Throw are typical of the cebus monkey, the lesser and the great apes (apart from Drop). In these actions, some differences were observed among the species groups. Swing can be divided into rapid movement or shake (17 kinds of manipulation patterns) and slow movement or wave (11 kinds). Shake was rather dominant in the lesser apes (the median number of kinds of manipulation patterns in the species of that group was 11) and in the great apes (median number, six kinds), as opposed to the cebus monkey (three kinds). On the other hand, wave was dominant in the cebus monkey (five kinds) as opposed to the lesser and the great apes (one and two kinds, respectively). Another difference was that the cebus monkey threw the manipulandum mainly upwards with the elbow stretched; the lesser apes with the wrist dorsiflexed or adducted; and the great apes with a swinging arm.

Strike is another characteristic action observed in the cebus monkey and the great apes. This action can be further divided into two categories: striking the manipulandum with the body-parts (7 kinds of manipulation patterns) and striking the substrate with the manipulandum grasped (19 kinds). In the cebus monkey, the latter category showed a greater variety of manipulation patterns (17 kinds) than the former (2 kinds), in contrast to the great apes (6 and 3 kinds, respectively).

The next step in the analysis examined the relations among the species groups on the basis of the occurrence of each action. A 74 (species) \times 21 (actions) one-zero matrix was subjected to HAYASHI's quantification model III analysis¹⁾ (HAYASHI, 1952), which is a useful tool for rearranging similar items nearer and different items farther away in a multi-dimensional space. Two axes were extracted, whose eigenvalues were 0.1514 and 0.1002 (the correlation coefficients between species and actions were 0.389 and 0.316, respectively). Figure 3 shows the distribution of actions in the two-dimensional space. The primate-common actions described above were distributed around negative values of axis I and positive values of axis II. Drape, Drop, Strike, Swing, Throw and Untwist were distributed around positive values of both axes. The other actions were distributed around negative values of axis II.

Each species was also plotted in this two-dimensional space. For information reduction, the mean normalized score in each species group is plotted in Figure 4. The 11 species groups can be classified further into three groups: first, the lemur, marmoset, spider monkey and leaf-eaters; second, macaque, guenon, mangabey and baboon; and third, cebus monkey, and lesser and great apes. Axis I is similar to the rank order of diversity measures reported by PARKER (1974a, b). This axis was therefore assumed to reflect the diversity of manipulation. Axis II was unique in the present study. Most of the actions distributed around negative values of axis II were actions in relation to the substrate, such as Shift, Rub, Flip, Roll and Push. On the other hand, most of the actions distributed around positive values of axis II did not necessitate the substrate. This axis can therefore be said to reflect substrate-related or substrate-non-related actions.

Body-parts

Figure 5 shows the percentages of body-parts used in relation to the total kinds of manipulation patterns observed in each species. The palmar side of the hand was involved most dominantly; roughly 90% of the manipulation patterns were performed by this body-part.

1) This analysis was performed with HITAC M-180 at the Information Processing Center of Hiroshima University, using the Program Package for Social Science II (PPSS II).

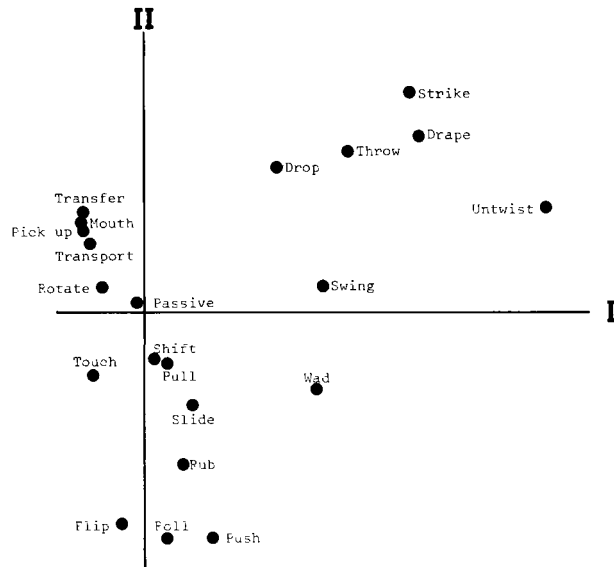


Fig. 3. Distribution of actions in two dimensions extracted by HAYASHI's quantification model III analysis.

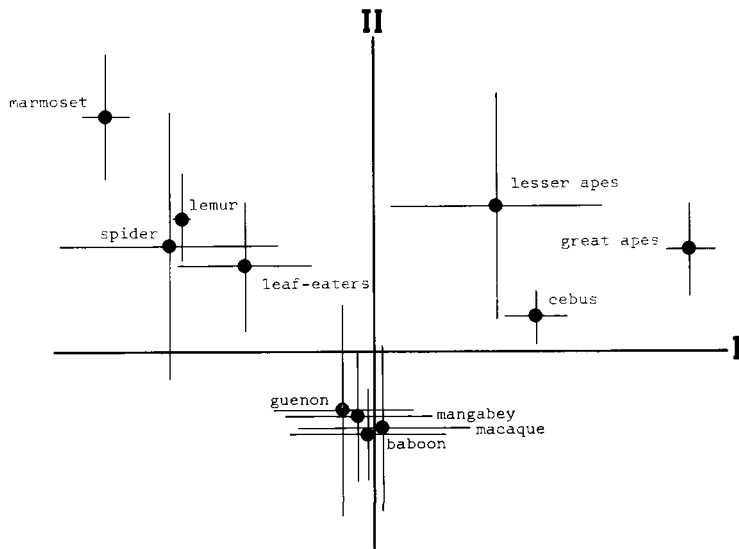


Fig. 4. Distribution of species groups in two dimensions extracted by HAYASHI's quantification model III analysis. The horizontal and vertical lines across each dot represent 2 SDs of the normalized scores.

Little difference among species group was noted. The mouth was also used dominantly by all species. In particular, the marmoset and lemur tended to manipulate orally more dominantly than the other groups. The feet were markedly used by the lesser apes. They grasped, picked up, mouthed, transported, transferred, etc., by feet frequently, in contrast to other species performing the same actions commonly by hand.

Use of the fingers moving opposably to or independently of each other was frequently

observed in the macaque, guenon, mangabey, baboon, lesser ape and great ape species. The most popular mode of finger use was that involving the thumb and index finger or thumb and other fingers opposably. Of 48 species in which finger use was recorded, 35 species utilized this mode most dominantly. As for the other finger uses, that involving the index finger alone was characteristic of the gelada baboon (14%) and chimpanzee (11.9%), as opposed to other species (less than 7%). For example, fixing the manipulandum with the index finger followed by mounting was observed in the chimpanzee; picking the manipulandum up with the index finger was observed in the chimpanzee; pressing it with the index finger in the gelada baboon and chimpanzee; pressing the edge of the cube against the floor with one index finger or both, and making it roll in the gelada baboon; and touching and shifting it with the index finger in the chimpanzee.

As for the other body-parts, use of the head and neck was typical in the cebus monkey, the lesser and the great apes (3.3, 5.3 and 4.8%, respectively; 0% for others); arm use was typical in the cebus monkey, the lesser and the great apes (3.9, 2.3 and 5.6%, respectively;

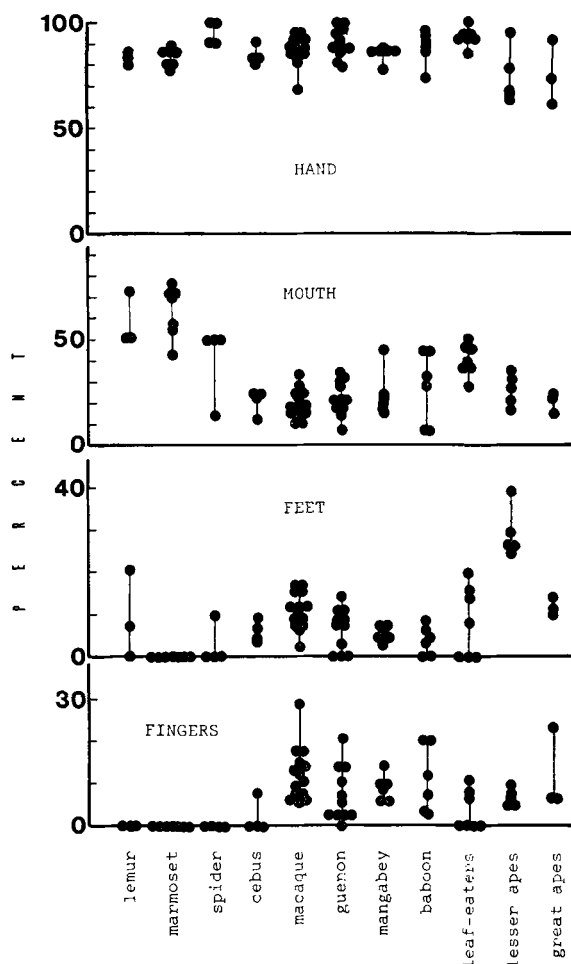


Fig. 5. Percentages of occurrence of body-parts to the total numbers of kinds of manipulation patterns. Each dot represents a single species.

0% for others); use of the body trunk in the cebus monkey and the great apes (0.8 and 3.6%, respectively; 0% for others); face use in the great apes (2.4%; 0% for others); use of the ulnar side of the hand in the cebus monkey (1.4%; 0% for others); and use of the back of the hand in the cebus monkey and the great apes (0.7 and 5.6%, respectively; 0% for others). Thus, the great apes and cebus monkey manipulated the manipulandum with the most varied parts of the body; and the lesser apes with more varied parts than other species groups except the great apes and cebus monkey.

Secondary manipulations

Figure 6 shows the numbers of kinds of secondary manipulations observed in each species. The rank order is similar to that of the other manipulation parameters described above: the great apes show the highest rank; the next ranking group consists of the cebus monkey and Old World monkeys except leaf-eaters; and the lemur, marmoset, spider monkey and leaf-eaters show the lowest ranks. It should also be noted that the lesser apes did not perform this type of manipulation.

The main features of the environment, in relation to which subjects acted on the manipulandum, were wire-mesh (20 kinds of manipulation pattern) and water (28 kinds). Most of the secondary manipulations in relation to wire-mesh or water involved the same actions as the primary manipulations. However, some actions were unique to the secondary manipulations: chimpanzees floated the cube on the water and poked it with their finger tips; a toque monkey pushed the end of the rope out of the wire-mesh and pulled it through at another place in the wire-mesh, repeating these actions as if sewing the wire-mesh with the rope; and an orang-utan held both ends of the rope with each hand through the wire-mesh and twisted the rope, making another rope.

The remainder of the secondary manipulations were related to rather accidental objects which were not available to all of the species: one orang-utan placed the cube repeatedly into and out of a suspended tire; the same subject put the food on the cube; one chimpanzee

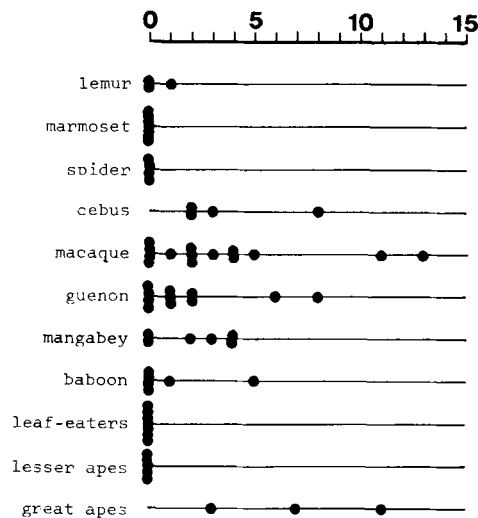


Fig. 6. Numbers of kinds of secondary manipulations observed in each species. Each dot represents a single species.

pressed feces with the cube held manually; and a juvenile *Cercopithecus hamlyni* wrapped the cube with a cabbage leaf which had been placed in the cage for food.

DISCUSSION

CHARACTERISTIC NATURE OF MANIPULATIONS

The object manipulation of 74 primate species was observed under comparable conditions, and 506 manipulation patterns were distinguished on the basis of the actions performed, body-parts used, and relations to other objects.

The results of an inter-species group comparison showed that the 11 groups of species could be further classified into three groups: first, the lemur, marmoset, spider monkey and leaf-eaters; second, the Old World monkeys except leaf-eaters; and third, the cebus monkey, the lesser and the great apes. The first group had the smallest repertoire of manipulations. The primate-common actions, such as Pick up, Mouth and Transport, and the body-parts commonly used by all the species, such as the hand and mouth, were mainly involved in the manipulation modes displayed by this group. In addition, such manipulation patterns were directed only towards the manipulandum presented, and in no relation to other environmental objects. In this group, differences among species groups and within each species group were not eminent.

The second group had more varied modes of manipulation than the first. The actions characterizing this group were Roll, Slide and Rub, although some details of the manipulation patterns produced by these actions differed among the species groups. Use of the fingers moving opposably to or independently of each other was also typical of this group.

The third group displayed the most varied repertoire of manipulations. Almost all the actions and body-parts were involved in their manipulations. In particular, Drape, Drop, Strike, Swing and Throw characterized this group. In addition, their manipulations were frequently related to other environmental objects, although the lesser apes were an exception.

Some species-specific features of the manipulations were also indicated. For example, use of the index finger was typical of the gelada baboon and chimpanzee; use of the ulnar side of the hand was typical of some species of cebus monkeys; and most of the secondary manipulations were species-specific as reported by PARKER (1974b). In addition, a species-specific manipulation pattern could be distinguished from a pattern specific to a species group. PARKER (1974b) reported that rolling a rope on the floor, back and forth, with palm was specific to capuchins; however, the results of the present study showed that this manipulation pattern is observed not only in other species of cebus monkeys, but also in most of the old world monkeys.

EVOLUTION OF MANIPULATIONS

The next step is to attempt to specify those factors responsible for the differences and similarities in manipulations among the species revealed in the present study. Anatomical differences among species can be considered to account for some of the differences in manipulation. For example, the lemur and marmoset cannot move each finger independently because of their anatomical restrictions. The leaf-eaters and spider monkey have shortened thumbs or no thumb at all, which are disadvantageous for complex manipulations (CONNOLLY & ELLIOTT, 1972; NAPIER, 1961). However, anatomical restrictions cannot account for

all the differences among species. It is unlikely, for example, that macaques do not strike the object against the floor as cebus monkeys do because of some anatomical constraint.

PARKER and GIBSON (1977) reported that the apes and cebus monkeys were superior in object manipulation and tool use to other primate species and discussed their evolution from the standpoint of feeding adaptation. PARKER (1978) assumed that the great diversity of manipulation in great apes had evolved through feeding adaptation as generalists. The findings of the present study support this assumption in part because many of the manipulation patterns described here occur really in the feeding context: Pick up, Mouth, Transport, Transfer and Rotate are commonly observed when animals treat their food and eat; some cebus monkeys strike hard-shelled nuts against wood trunks and open them before eating the contents in their natural habitat (IZAWA & MIZUNO, 1977); and Japanese monkeys may roll or rub their food frequently before eating it (ITANI, 1957; KAWAI, 1965). Nevertheless, it is unlikely that other manipulation patterns such as Throw, Drape and Drop are related to feeding. In chimpanzee, throwing or dropping an object was not observed in the context of hunting prey animals or cracking objects, but was in the agonistic context (PARKER & GIBSON, 1979; SUGIYAMA & KOMAN, 1979). Orang-utans were found to swing on some artificial objects or branches for locomotion (CHEVALIER-SKOLNIKOFF, GALDIKAS & SKOLNIKOFF, 1982; LETHMATE, 1979). It is clearly more appropriate to regard species-specific or species group-specific features of object manipulation as having evolved not only through feeding adaptation, but also in other behavioral contexts. Thus, multiple factors must be considered when examining the evolution of manipulation. Observations of manipulation in various behavioral contexts within the natural habitat are needed in order to specify the precise factors contributing to the evolution of species-specific modes of manipulation.

PRECURSORS OF TOOL USE: SECONDARY MANIPULATIONS

Object manipulation is assumed to be a precursor of tool use (PARKER, 1974b). In order that an object can serve as a tool, the animal must relate the object with another unfixed object (BECK, 1980). In this respect, the secondary manipulations occupy the nearest place to tool use.

One of the principal findings concerning secondary manipulation was that lesser apes did not perform this type of manipulation. ABORDO (1976) noted the rarity of tool use in lesser apes and concluded that this was due to their limited manipulative dexterity. However, the present study and the work of PARKER (1973, 1974a, b) have demonstrated a great variety of manipulation in them comparable to that of the great apes and the Old World monkeys except leaf-eaters. It may be more appropriate therefore to consider that tool use does not arise from the variety of manipulations but from the extent to which the animal relates the object with other objects. There were only a few unfixed objects available to be related to the manipulandum in the observational setting of the present study. Data should therefore be obtained systematically under a more complex setting concerning how the animal relates the manipulandum to environmental features. Inter-species comparisons based on such data would contribute to clarifying the new aspects of tool use and tool manufacture.

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