

Olfactory Discrimination of Urine Odors from  
Five Species by Tufted Capuchin  
(*Cebus apella*)

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**ABSTRACT.** Urine collected from New World monkeys (tufted capuchin, squirrel monkey, cotton-top tamarin) and Old World monkeys (rhesus macaque, Japanese macaque), was used as the odor stimuli. Two adult tufted capuchins were trained on a successive odor-discrimination task with two odors, 30 trials each, in one session per day. Responses to one of the two odors (S + ) were reinforced by sweet water. The monkeys failed to discriminate between the urine from the two species of macaques but could discriminate among the urine from the three species of New World monkeys. Furthermore, similarity of urine odors was analyzed by multi-dimensional scaling (MDS) and a cluster analysis. These analysis suggested that the tufted capuchin can distinguish differences among New World monkeys but not between the macaques. The natural distribution of the tufted capuchin overlaps with that of other New World monkeys, but it does not overlap with those of Old World monkeys. Consequently, it can be concluded that this difference in olfactory recognition in the tufted capuchin reflects their sympatric and allopatric relationships with other species.

**Key Words:** Species discrimination; Olfactory discrimination; *Cebus apella*; Urine odor.

## INTRODUCTION

Our knowledge of olfactory communication in primates lags far behind that of visual and auditory modalities. This is understandable, taking it into consideration the limitation placed on the human observer by his own sensory capacities. Because of his relatively poorly developed olfaction, the human observer is much more inclined to record a visual or auditory pattern of communication than an olfactory pattern. Therefore, much of the olfactory communication occurring in primate groups escapes notice during direct observation. Also, it may be the fact that primate olfaction itself arouses less of an interest in researchers than the visual and auditory senses. One reason for this is that they might predict that olfaction is not a very important sense for primates, since the degree of development of the primate olfactory system tends to decrease relative to other cortical structures. Another reason is the prediction that olfaction is not a very important sense for communication in the human researcher himself, because, for abstract and logical thinking, olfactory information is not as meaningful as information from the visual and auditory senses (SCHLEIDT et al., 1988).

Recently researches have shown evidence that prosimian and simian primates use olfaction for communication. Even in humans, olfactory communication has been suggested. In addition to prosimians, the New World monkey is well-known to have scent glands and a repertoire of marking behavior, i.e. behavior in which a trace of the glandular secretions and/or excretion is left in the environment or on the body. Further, the vomeronasal organ and accessory olfactory bulb are relatively well developed in the prosimian and the New

World monkey (JORDAN, 1972; BAILEY, 1978; EPPLE & MOULTON, 1978; WORHRMANN-REPENNING, 1984), and these organs probably have a chemosensory role different from the primary olfactory system. For example, ESTES (1972) hypothesized that the vomeronasal organ of mammals are involved in the perception of signals that are significant in intra-species communication.

Several species of primate have been investigated concerning what information they can use for communication through odors from glandular secretions and excretion. For example, the ring-tailed lemur (*Lemur catta*) has a brachial gland, an antebrachial gland, and a circumgenital gland (MONTAGNA & YUN, 1962). Based on such odors, they can discriminate the difference between individuals (MERTL, 1975) and between sexes (DUGMORE et al., 1984). Moreover, they probably use that odor for territorial demarcation (MERTL, 1977; MERTL-MILLHOLLEN, 1988). Similarly, the brown lemur (*Lemur fulvus*) has several scent glands and can also discriminate between individuals and the sexes from the odors (HARRINGTON, 1976, 1977). The marmoset and the tamarin, which are New World monkeys, also have various glands such as the suprapubic gland, the genital gland, and the anogenital gland (EPPLE & LORENZ, 1967; EPPLE, 1986), the odors from which are used for individual discrimination, sex discrimination, species discrimination, signal of ovulation, and so on (EPPLE, 1972, 1974a, b, 1976, 1986; ZIEGLER et al., 1993).

The tufted capuchin, a New World monkey, often urinates on its hands, and the urine is then washed over the soles of the feet or rubbed elsewhere on its body. At that time, the monkey leaves the urine trace on the perch. This behavior is called "urine-washing." Previous studies have proposed different assumptions concerning the function of this behavior. These assumptions can be roughly divided into those related to communication and those related to nonsocial-environmental factors (see OPPENHEIMER, 1973, 1977; HARCOURT, 1981; ROEDER & ANDERSON, 1991).

UENO (1994a) reported that the tufted capuchin can discriminate conspecific odors from other species' odors. However, that report could not clarify how tufted capuchins perceive or recognize the odors from other species. The present experiment investigated whether tufted capuchins can discriminate among five different species odors. The five species for urine donors were chosen with consideration of their ecological relationship with the tufted capuchin. A urine odor should be able to provide various forms of information such as species discriminability, discriminability of individuals, and/or gender difference and so on.

In this experiment, I focused on species discriminability. Therefore, the tufted capuchins were trained to transfer their ability to differentiate among stimuli as a function of odor cues common to different individuals of the same species versus those of other species. Additionally, in order to examine species recognition by odor, the distribution of the odors in olfactory perceptual space was analyzed by the method of multivariate analysis (nonmetric multidimensional scaling: MDSCAL, KRUSKAL, 1964, hierarchical cluster analysis, JOHNSON, 1967). These methods have been used in analyzing data on the perception of various sensory modalities in humans (e.g. PODGORNÝ & GARNER, 1979) and nonhuman animals (TOMONAGA & MATSUZAWA, 1992; DOOLING et al., 1990).

If urine-washing functions as a means of communication, the tufted capuchin should be able to process information from urine odors. That is, the tufted capuchin should show different responses to odors. From the viewpoint that urine-washing is a marking behavior, UENO (1991, 1994a) investigated the response to the urine odors from different species using the habituation-dishabituation task. The tufted capuchin responded only to the odor from another conspecific group, but not to those of other species groups. This suggested

that the tufted capuchin can discriminate between conspecific groups and between conspecific and other species.

However, when using the habituation-dishabituation task, the absence of response to an odor may show that the odor is not detectable or discriminable, but a lack of response may also indicate that the odor is not interesting to the animal, that the animal is not motivated to search for the odor, or that the odor is aversive and is avoided. Therefore, it was impossible to investigate how the tufted capuchin can discriminate between the odors from other species by the habituation-dishabituation method.

Such uncertainty can be resolved by using operant conditioning techniques. In this method, the subject is reinforced for responding, and its responses including its ability to discriminate may be quantified. Consequently, it is possible to determine whether the subjects can discriminate between odors. The present study was designed to use an operant conditioning method to investigate whether the tufted capuchin can discriminate between the urine odors from five different species.

## METHOD

### SUBJECTS

Two tufted capuchins (*Cebus apella*), which were born and reared in the Primate Research Institute of Kyoto University, were used as subjects. *Prim* was an 8-yr-old female and *Seg* was a 7-yr-old male. *Seg* had received artificial nursing as a neonate. They had previously received odor discrimination training involving several artificial food flavors (UENO, 1994b). However, *Prim* could not participate in the present experiment in its entirety, because of her health. They were deprived of water for approximately four hours before every session of the experiment, but otherwise they could get water without restriction.

The New World monkeys were individually caged during this experiment. They each got a daily ration of monkey chow biscuits, apples, bananas, and a quail egg. The macaques were fed a daily ration of monkey chow biscuits and sweet potatoes.

### APPARATUS

The monkeys were trained in an operant chamber modified from those which were designed to study olfactory stimuli in rats by SLOTNIC and PTAK (1977), and DAVIS (1973). A detailed description was given in a previous study (UENO, 1994b).

### ODOR STIMULI

Stimuli were the urine odors of the following five species of monkeys: tufted capuchin (*Cebus apella*), cotton-top tamarin (*Saguinus oedipus*), squirrel monkey (*Saimiri sciureus*), rhesus macaque (*Macaca mulatta*), and Japanese macaque (*Macaca fuscata*). Every donor species involved both male and female individuals. The squirrel monkeys and the cotton-top tamarins were caged in pairs, and the other monkeys were individually caged.

The trays, which were put under the respective home cages, collected urine. The trays were covered with meshes to minimize contamination from feces and foods. The collected urine from each individual or pair was stored at  $-30^{\circ}\text{C}$ , and was restored to room

temperature immediately before the experiment. This urine was used for stimulus odor without any preparation. It was frozen and stored again after each experiment. The stimulus set was changed one once every two, three, or four sessions (chosen in random order), that is, the stimulus set was changed three times within every ten sessions. The urine from the same individual was never used in successive sessions. The odor of the tufted capuchin was always used as the stimulus for which the response was reinforced.

Odorous air was generated by bubbling the filtered air through the urine (30 ml) contained in a gas-washing bottle which was retained at 25°C in a water bath. This saturated odorous air was used as odor stimuli, and it was presented to the subjects at the volume of 5 l/min.

#### PROCEDURE

A session consisted of 60 trials, that is, 30 trials for each stimulus. The sequence of two odor stimuli were changed in a quasi-random manner every session. A trial was 20 sec, and the odor stimulus was presented throughout the trial. The room lamp was onset during a trial. Between each trial, was 10-sec intertrial interval (ITI), where the room lamp was offset and filtered air (10 l/min) was pumped into the chamber through the stimulus nozzle.

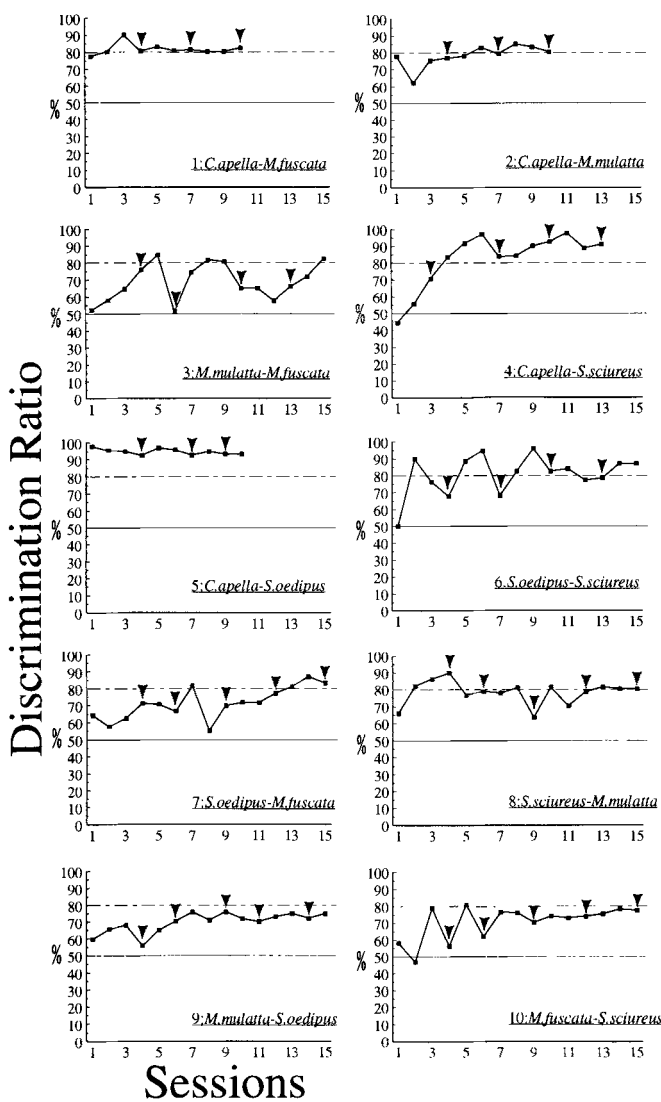
The monkeys were trained on the successive discrimination of a pair of odor stimuli. If the monkeys responded to the lever on the positive stimuli (S+), they could drink sweet water containing 5% sucrose (0.25 ml/times) as a reinforcer once in 20 sec on the average (i.e. VI 20 sec). On the other hand, if the monkeys responded to the lever during the presentation of negative stimuli (S-), they were not reinforced (i.e. Extinction). This reinforcement schedule may be described of mult VI 20 sec EXT, ITI 10 sec.

The number of responses to the lever was counted on each trial, and the response latency of the first response in each trial was measured. A discrimination ratio was determined by dividing the mean of response rate for S+ trials by the sum of the response rate for both S+ and S- trials. The mean of response rate prior to the first reinforcement on both S+ and S- trials was calculated from the responses prior to the first reinforcement every session. Although the responses were actually not reinforced on S- trials, the time for reinforcement was calculated logically as having the same frequency as on S+ trials: once in 20 sec on the average.

The criterion for the end of training was the following. 1) If there was a statistically significant difference ( $p < 0.01$ : Mann-Whitney's *U* test) between the mean response latency on S+ and S- trials, the subject was considered to have acquired the discrimination and training was continued for ten more sessions. 2) If there was no statistically significant difference ( $p < 0.01$ : Mann-Whitney's *U* test) between the mean response latency on S+ and S- trials by the 15th session, the monkey was considered to have not acquired the discrimination and the training was stopped.

#### RESULTS

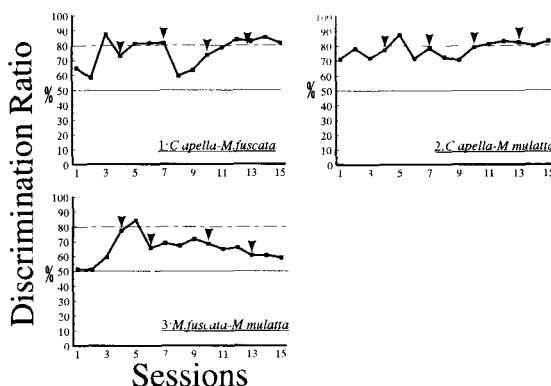
The capuchins learned to discriminate differentially among urine odors of the New World monkeys and between the New World monkeys and macaques. However, they failed to discriminate the urine odors of the Japanese macaque and the rhesus macaque. When the urine from tufted capuchins was used, there was a tendency for rapid acquisition of



**Fig. 1.** The learning curve for *Seg*. Arrows show sessions in which stimulus set was changed. Solid rectangles show the discrimination ratio which is calculated by the mean response rate of S+ and S- trials in a whole session. Open lozenges show the discrimination ratio which is calculated by the mean response rate before the first reinforcement on S+ and S- trials in a whole session.

the odor-discrimination. For example, when *Seg* was trained to discriminate between the urine odors from the tufted capuchin and squirrel monkeys, a discrimination ratio greater 90% was achieved in the first session. Figures 1 and 2 show the discrimination acquisition curves for the stimuli pairs for *Seg* and *Prim*, respectively.

As described above, the odor discriminanda were switched to new ones three times during ten sessions. The first, second, and third switched sessions were used for comparison. The mean response rate of S+ and S- trials in these three switched sessions was calculated



**Fig. 2.** The learning curve for *Prim.* Arrows show sessions in which stimulus set was changed. Solid rectangles show the discrimination ratio which is calculated by the mean response rate of S+ and S- trials in a whole session. Open lozenges show the discrimination ratio which is calculated by the mean response rate before the first reinforcement of S+ and S- trials in a whole session.

**Table 1.** Matrix of the mean response rate ratio of the three sessions in which stimulus sets were changed for ten sessions.

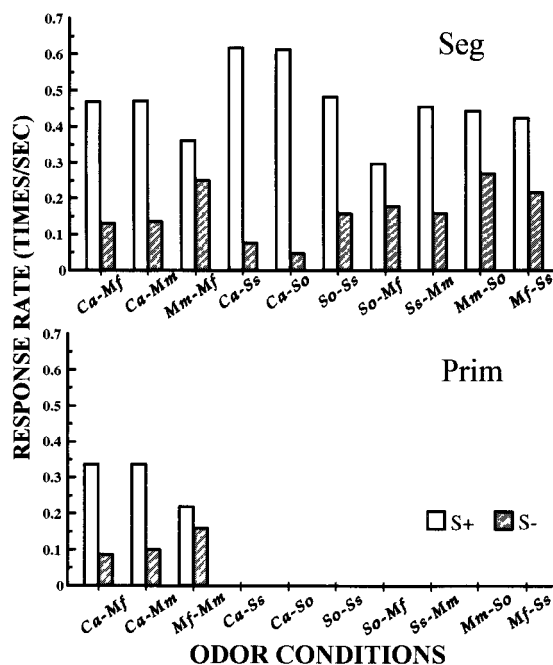
	<i>Cebus apella</i>	<i>Saimiri sciureus</i>	<i>Saguinus oedipus</i>	<i>Macaca mulatta</i>	<i>Macaca fuscata</i>
<i>Cebus apella</i>					
<i>Saimiri sciureus</i>	0.890				
<i>Saguinus oedipus</i>	0.929	0.753			
<i>Macaca mulatta</i>	0.776	0.740	0.621		
<i>Macaca fuscata</i>	0.781	0.589	0.627	0.590	

The relation of S+ and S- was neglected.

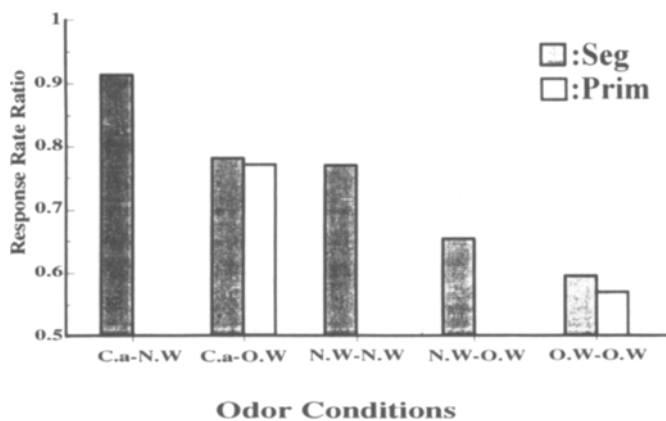
under every stimulus condition. Results for both subjects are shown in Figure 3. There was no significant difference in the mean response rate preceding the first reinforcement between S+ and S- trials on the stimulus sets of the urine from Japanese macaques and rhesus macaques ( $U=1, p>0.1$ : Mann-Whitney's *U* test). However, there was a significant difference of that between S+ and S- trials for the other stimulus sets ( $U=0, p<0.05$ , respectively).

The mean response rate ratio (RRR) was calculated from the response rates for *Seg* under every condition. The RRR was obtained by dividing the mean response rate for S+ trials by the total mean response rate of S+ and S- trials (Table 1). The species of the odor donors could tentatively be classified into the three categories: 1) Conspecific-tufted capuchin; 2) New World monkey-squirrel monkey and cotton-top tamarin; and 3) Old World monkey-Japanese macaque and rhesus macaque. On the basis of these three categories, the stimulus conditions used in this experiment were classified into the following five types: 1) Conspecific-New World monkey (Ca-NW); 2) Conspecific-Old World monkey (Ca-OW); 3) New World monkey-New World monkey (NW-NW); 4) New World monkey-Old World monkey (NW-OW); and 5) Old World monkey-Old World monkey (OW-OW).

This classification of stimulus set types was independent of which species was used as S+ or S-. The mean of response rate ratio was plotted according to these five stimulus set types (Fig. 4). The OW-OW type showed a significantly lower score on the response



**Fig. 3.** The mean response rate to the first reinforcement of each trial on each stimulus condition. Odor conditions were arranged in the order of presentation. Ca: *Cebus apella*; So: *Saguinus oedipus*; Ss: *Saimiri sciureus*; Mm: *Macaca mulatta*; Mf: *Macaca fuscata*.



**Fig. 4.** The mean of the response rate ratio. Conditions were rearranged by stimulus categories. Ca: Tufted capuchin; N.W: New World monkeys (cotton-top tamarin, squirrel monkey); O.W: Old World monkeys (rhesus macaque, Japanese macaque).

rate ratio than the other types. The statistical analysis using the *U* test showed the following: 1) Ca-NW,  $U=0, p<0.05$ ; 2) Ca-OW,  $U=0, p<0.05$ ; 3) Nw-Nw,  $U=0, p<0.05$ ; and 4) Nw-Ow,  $U=1, p<0.05$ . The Ca-NW comparison showed a significantly higher response rate ratio than the other types ( $U=0, p<0.05$ , respectively). There was not a significant difference between the Ca-OW and NW-NW types ( $U=3, p>0.1$ ).

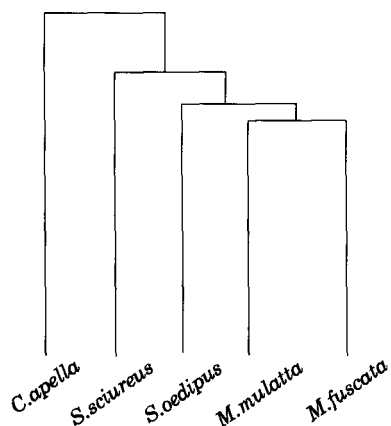


Fig. 5. Hierarchical cluster analysis of the perceived similarity of odors. Data are based on the mean of the response rate ratio.

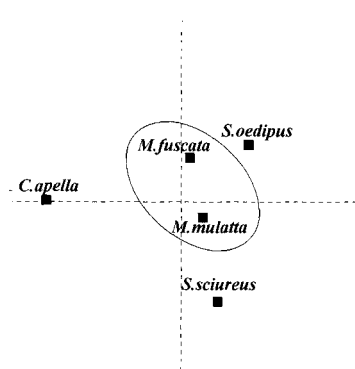


Fig. 6. Two dimensional representation of the solution of the multidimensional scaling (MDS) showing the perceived similarity of odors. Data are based on the mean of the response rate ratio. Eclipse shows the cluster obtained at the lowest part of the tree by the hierarchical cluster analysis.

Further, in order to examine the distribution of each species in the olfactory perceptive space of the tufted capuchin, multivariate analysis was applied. The response rate ratio could be regarded as an index of similarity. Hence, the response rate ratios were used as input for nonmetric multidimensional scaling: MDSCAL (KRUSKAL, 1964) and hierarchical cluster analysis (JOHNSON, 1967). MDSCAL can represent the psychological relationship among the stimuli as the spatial distance among the stimuli in the multidimensional psychological space. The more similar two stimuli are, the nearer they are represented in that space. Cluster analysis can also represent the psychological relationship among the stimuli in a hierarchical tree pattern. More similar stimuli form groups (called clusters) at the lower part of the tree, and on the contrary less similar stimuli form groups at upper part of the tree. Figure 5 shows the results of the cluster analysis. Japanese macaques and rhesus macaques were included in the cluster which was divided at the most bottom node. Figure 6 shows the two dimensional representation of the solution by MDSCAL. The stress was 0.100. Both Japanese macaques and rhesus macaques were close to the center of the two dimensional plot of MDSCAL. The other three species were far from each other, and on the periphery of the two dimensional space.

## DISCUSSION

This experiment showed that the tufted capuchin could discriminate among urine odors



collected from five different species, including its own. However, they could not necessarily easily recognize the features of the odor of every species, because they showed no reliable evidence of discriminating between the Japanese macaque and the rhesus macaque.

The response rate ratio to the first reinforcement varied with respect to the odor conditions. The reason for this variation of efficiency of discrimination could not be determined unconditionally from the comparison of the response rate among the odor conditions. Therefore, ten odor conditions were sorted according to five stimulus types, using various combinations of the three categories (conspecific, New World monkey, and Old World monkey). This arrangement showed that there were consistent differences among odor discriminanda among the stimulus types.

The response rate ratio can be regarded as an index for the efficiency of discrimination. That is, the value reflects the perceived distance between two stimuli. Therefore, on the basis of the difference of the response rate ratio among the combinations of the three species categories (Fig. 4), the following interpretations are suggested. 1) The tufted capuchin was able to discriminate between the odors from a conspecific and other New World monkeys very well. This suggests that each of these odors has a very distinctive feature for the tufted capuchin. 2) They discriminated better between tufted capuchins and New World monkeys as compared to discriminating only between New World monkeys. This suggested that the features of the odor from a conspecific are more distinctive for the tufted capuchin than those of New World monkeys. 3) When the odor from Old World monkeys were paired with the odors from the tufted capuchin or the other New World monkeys, the discrimination of the stimulus pairs became more difficult for the tufted capuchin. This suggests that the odors of Old World monkeys lacks the distinctive features for the tufted capuchin. 4) *Seg* showed the discrimination ratio exceeding 80% three times on the two-macaque comparison. However, it did not show the generalization of discrimination among the stimulus sets of macaques. The tufted capuchin might not be able to detect discriminable features of each species. Therefore, the tufted capuchin failed to discriminate between the odors collected from Old World monkeys (the Japanese macaque and the rhesus macaque). This suggests that there is not a distinctive feature, which the tufted capuchin can perceive, between the odors from these two macaques.

The subjective classification of five species, which was determined by MDSCAL and cluster analysis, corroborates the interpretation described above, concerning the psychological relations of the species categories (Fig. 5). That is, the odors from conspecifics and two New World monkeys were very different from each other in the perception of the tufted capuchin. On the other hand, the odor from two macaques were not only quite similar to each other, but also ambiguous or featureless in comparison with the other three species. These two macaques formed a group at lowest part of tree by cluster analysis and were plotted close to the center of the two dimensional space of MDSCAL (Fig. 6). This psychological distance among the five species is at variance with their phyletic distance.

What causes this subjective classification of the tufted capuchin? Does this reflect directly the similarity of odor stimuli themselves? Or, does this depend on the olfactory cognitive system of the tufted capuchin? Does this classification suggest that the tufted capuchin is not sensitive to the features of macaques because of a species-specific recognition property?

The similarity of urine odor might be affected by diet. In the present study, three New World monkeys and two Old World monkeys were constantly got same diet each other. Although tufted capuchins could not discriminate between Old World monkeys, they could discriminate among New World monkeys. Therefore, in the present study, diet presumably did not contribute to the urine odor directly.

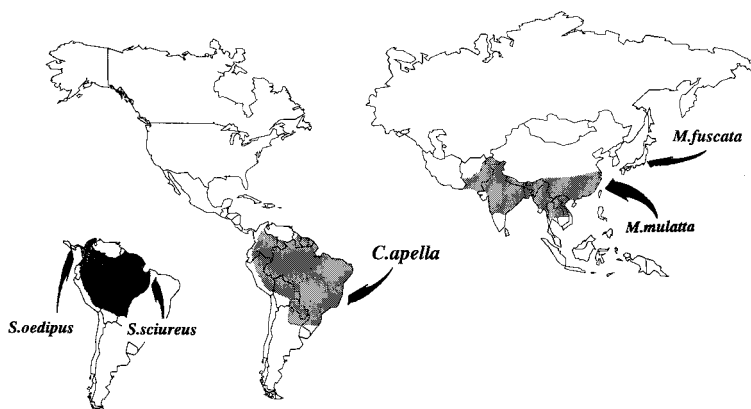
Japanese macaques and rhesus macaques belong to the same genus *Macaca*, so that the relationship of these species is phylogenetically closer than that of the other species. Therefore, there is a possibility that the chemical components of the odor may be so similar to each other that the tufted capuchin could not distinguish them.

However, if the difficulty of discrimination of two macaques arose from the similarity of chemical components, this cannot explain why the tufted capuchin perceived the odor of macaques as ambiguous or featureless in comparison to that of conspecifics or New World monkeys. Besides, DEMARIA and ROEDER (1989) reported that the stumptailed macaque (*Macaca arctoides*) and the pigtailed macaque (*Macaca nemestrina*), both of which belong to the same genus, were able to discriminate their urine odors. This supports the assumption that the urine from Japanese macaques and rhesus macaques must have discriminable differences in their odors, although they belong to the same genus. Therefore, we are able to consider that the results of this experiment were caused not simply by the similarity of chemical components of the urine odors, but also by the olfactory cognitive system of the tufted capuchin. In order to clarify this problem more strictly, however, we are also proceeding to compare the odor profiles of these five species by chemical component analysis.

The existence of a subjective cognitive system of a species as shown in this experiment is not specific to olfaction. Previous studies concerning other sensory modalities also showed a discrepancy between subjective classification and phyletic classification. For example, FUJITA (1987) investigated how five species of *Macaca* discriminate among each other using photographs as discriminative stimuli, on the basis of the paradigm of sensory reinforcement. All five species showed that the psychological distance between their own species and the other species was wide in comparison to that between other species. Further, the result suggested that these monkeys generally tended to discriminate their own species from other sympatric species more clearly than from other allopatric species. It is regarded as general, not only for primates, but also for many other animals, to be able to discriminate their own species from other species quite well. The subjective cognitive system of a species can function adaptively to maintain interspecific and/or intraspecific social relations, or to perform efficient reproduction, as suggested by YOSHIKUBO (1987) and FUJITA (1989).

Previous studies showed that the social response of primates was affected by innate and/or learned factors. The response to the urine odors shown in this experiment was not acquired through the social interaction with other species. The subjects were born in the Primate Research Institute, so they have not directly experienced interspecific social interaction. Furthermore, they have not interacted with squirrel monkeys or cotton-top tamarins even indirectly. Therefore, the property of discrimination of urine odors from several species must not be due to an acquired factor but an innate one.

This property of olfaction may reflect the biological/ecological relationship of the tufted capuchin with the other species. Figure 7 shows the distribution of habitat of the five species used in this experiment (WOLFHEIM, 1982). The tufted capuchin is distributed widely in South America, and its habitat overlaps or is adjacent with that of the squirrel monkey and the cotton-top tamarin. This implies that tufted capuchins probably have some interaction or social relationship with these two species. If so, it must be biologically/ecologically important for the tufted capuchin to be able to discriminate or recognize these sympatric monkeys. In contrast, Japanese macaques and rhesus macaques are distributed in Asia, so that their habitats do not overlap with that of the tufted capuchin at all. Hence, tufted capuchins do not have any social interaction with these macaques in nature. There-



**Fig. 7.** Schematic map showing the distribution of the habitat of five species. The habitat of the tufted capuchin (*C. apella*) overlaps with that of the cotton-top tamarin (*S. oedipus*) and the squirrel monkey (*S. sciureus*).

fore, the biological importance of these macaques for tufted capuchins is doubtlessly very small. Accordingly, we can propose that the results of this experiment arose from the property of the olfactory cognitive system of the tufted capuchin.

In conclusion, the tufted capuchin can discriminate not only between conspecific urine odor and other species' odor, but also between other species' odors. However, the tufted capuchin cannot discriminate equally well the odor of every species. The difficulty of discrimination increased in the following order: tufted capuchins, New World monkeys, and Old World monkeys. This order of difficulty is consistent with the proximity of ecological relationship with the tufted capuchin. That is, the closer the biological/ecological relationship the tufted capuchin has with a species, the more sensitive the tufted capuchin will be to its odor. In conclusion, the tufted capuchin is more sensitive to the odors of species with overlapping ecology. Additionally, it is suggested that the property of species-odor discrimination, shown in the present study, is due to an innate olfactory cognitive system in the tufted capuchin.

**Acknowledgment.** The author is grateful to the staff of the Psychology Department of Primate Research Institute, Kyoto University. Thanks are also due to Dr. ROGER THOMAS for crucial comments on the manuscript.

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— Received: October 10, 1993; Accepted: December 24, 1993

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