

# Use of Olfactory Cues in Foraging by Owl Monkeys (*Aotus nancymai*) and Capuchin Monkeys (*Cebus apella*)

Rosina H. Bolen and Steven M. Green  
University of Miami

The authors tested free-ranging New World monkeys (nocturnal owl monkeys [*Aotus nancymai*] and diurnal capuchin monkeys [*Cebus apella*]) to determine the extent to which they use olfactory cues to locate food hidden in containers at 2 of 6 feeding sites within a 1½-ha forested enclosure. These 2 sites were selected randomly for each trial and then were baited with banana and banana peel residue. The 4 other sites were unbaited and unscented. In trials in which the food was not visible to the monkeys, *Aotus* monkeys located the baited sites at a level greater than expected by chance, whereas *Cebus* monkeys did not. Use of olfactory information by *Aotus* monkeys in foraging may be an adaptation for nocturnal foraging because olfactory cues are more salient than visual cues at low light levels.

Information regarding identity, reproductive condition, and social status in primates can be transmitted through olfactory signals (for reviews, see Epple & Moulton, 1978; Zeller, 1987; also see Ueno, 1994b, 1994c), but the extent to which nonhuman primates use olfactory cues to locate foods and to decide which foods to eat is relatively unknown. Most studies of food-related olfaction in primates have focused on their ability to discriminate among odors (Hudson, Laska, & Ploog, 1992; Laska & Hudson, 1993a, 1993b; Ueno, 1994a). In the present study, we examined the use of olfactory cues to locate food in two species of New World monkeys, the nocturnal owl monkey (*Aotus nancymai*) and the diurnal capuchin monkey (*Cebus apella*).

## Food-Related Olfactory Discrimination in New World Monkey Species

At least two species of New World monkeys have been tested for food-related olfactory discrimination in a laboratory environment. Ueno (1994a) investigated the ability of *Cebus apella* to discriminate between novel odors from two different categories: fruity (e.g., guava, strawberry) and fishy (e.g., seaweed, salmon). The monkeys achieved better discrimination when both odors were from the fruity cate-

gory than when they were both from the fishy category. The fruity odors represent palatable foods, whereas the fishy odors represent nonpalatable foods for *Cebus*. Hudson et al. (1992) and Laska and Hudson (1993a, 1993b) found that squirrel monkeys (*Saimiri sciureus*) were able to identify containers baited with food on the basis of an odor cue unrelated to the food. Their testing apparatus consisted of 1.5-ml opaque cups containing one eighth of a peanut as a food reward placed upon an artificial "tree" consisting of five horizontal bars (limbs) attached to a vertical bar (trunk). The cups were equipped with absorbent paper that had been immersed in various solutions of odorants (e.g., banana or aniseed aroma) that signaled the presence or absence of a food reward.

Discrimination ability, as demonstrated in these experiments, does not necessarily imply that odor cues are used naturally in foraging. In addition, it is not clear whether the concentrations of odors used in these studies were comparable with olfactory cues present in a natural foraging situation.

## Species Differences in Use of Olfactory Cues in Foraging

Species differences in the structures associated with olfaction and differences in activity patterns (nocturnal vs. diurnal) suggest that nonhuman primate species may differ in their use of olfactory cues in foraging. In pilot work by Garber, Bolen, and Evans (1993), captive New World monkeys were presented with three containers (one baited and two unbaited) in which olfactory cues (presence vs. absence of food scent) were manipulated. Nocturnal foragers, *Aotus nancymai*, used a scent cue more effectively to choose the baited container than did the diurnal foragers (*Cebus apella*, *Saimiri boliviensis peruviansis*, *Callithrix jacchus*, and *C. penicillata*). The applicability of these results to a natural foraging situation is limited, however, because the baited and nonbaited containers were placed only 20 cm apart. At such close distances, the spatial location of the scent could

---

Rosina H. Bolen and Steven M. Green, Department of Biology, University of Miami.

This research was supported by a Grant-in-Aid of Research from the National Academy of Sciences, through Sigma Xi, The Scientific Research Society; the Department of Biology at the University of Miami; and the DuMond Conservancy for Primates and Tropical Forests, Miami, Florida. We thank the staff of Monkey Jungle in Miami, Florida, for their assistance in animal handling and care and for their permission to conduct the study. We also thank Matthias Laska for providing helpful comments on the manuscript. Useful suggestions were received from Keith Waddington, C. Mindy Nelson, and other members of the Behavior Group at the University of Miami.

Correspondence concerning this article should be addressed to Rosina H. Bolen, Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, Florida 33124.

have been difficult to pinpoint. An incorrect choice delayed access to food by only a few seconds, so the cost of delayed reinforcement may have been insufficient to motivate the diurnal species to learn the cue that indicated the correct choice.

The goal of the present study was to examine species differences in use of olfactory cues to locate food in a natural social and environmental setting. *Aotus nancymai* and *Cebus apella*, free-ranging within a 1½-ha forested enclosure, were tested to determine if they could use a scent cue to locate hidden food. In addition, the search patterns of the monkeys in the experiment were examined to determine if strategies other than the use of olfactory cues could account for their performance. These strategies include the formation of a positional habit, namely always search the same place first, as well as win-stay and win-shift strategies (e.g., MacDonald, 1994; MacDonald, Pang, & Gibealt, 1994).

## Method

### Subjects

A mated pair of adult *Aotus nancymai* (Niko and Jenny) and a *Cebus apella* group consisting of 2 adult males, 4 adult females, 1 subadult female, and 1 infant male were tested at Monkey Jungle, a zoological park located south of Miami, Florida. All subjects reside there in a 1½-ha forested enclosure (henceforth referred to as the *rainforest*) with a vegetation and structural profile similar to natural rainforests (DuMond, 1968). The subjects' diet of naturally occurring fruits, vegetation, and insects is supplemented by commercial monkey chow, fruits, and vegetables. For the duration of this study, the monkeys received this provisioned diet in addition to the small amounts of banana provided during the experiments. Banana was chosen as the food reward for the experiments because it is a highly preferred fruit for both species (personal observation [pers. obs.]).

### Experimental Apparatus

Six wooden platforms (1.60 m [height] × 1.23 m [length] × 0.6 m [width]) were placed in the rainforest in an oval array (7 m × 5 m, major × minor axes) with approximately 3 m between adjacent platforms. A rigid plastic box (0.12 m [height] × 0.65 m [length] × 0.21 m [width]; Toolmaster truck/van box) with a hinged lid was attached to the top of each platform. A 17-cm length of 5-cm diameter opaque gray polyvinyl chloride (PVC) pipe, capped on one end, was fastened horizontally lengthwise in the center of the bottom of each box. When the boxes were in place on the platforms, their lids were attached together by ropes to allow simultaneous opening of all boxes. The six platforms remained in the rainforest for the duration of the experiments. The boxes were removed from the rainforest enclosure at the end of the trials each day.

### Training Procedures

The monkeys completed the following training procedures to ensure that they were proficient at retrieving food from the pipes in the boxes on all six platforms.

*Aotus.* Initially, the *Aotus* monkeys had difficulty traveling

from one platform to another and retrieving food from the pipes. They used only certain travel routes among the platforms (i.e., only adjacent platforms were visited sequentially). Consequently, walkways were added to connect each platform to every other platform. These walkways were constructed of plastic chain threaded through PVC pipes and attached to the platforms. After the walkways were added, the *Aotus* traveled from any one platform to any other platform.

The *Aotus* did not reach inside the pipes spontaneously to retrieve the food. This behavior was shaped over 3 nights by placing banana slices first in the box, then at the edge of the pipe in the box, then further back inside the pipe.

Ten training trials over 3 nights were conducted after the walkways had been constructed and after the monkeys had learned to retrieve the food from the pipes. During these trials, the pipes in all six boxes were baited with banana. Both *Aotus* monkeys showed flexibility in the order in which they visited platforms, and both retrieved food from the pipes readily.

*Cebus.* Most of the monkeys in the *Cebus* group had been exposed to a similar experimental apparatus during an earlier unrelated experiment. To reacquaint the group with the trial procedure and to train them to expect the trials in the early morning (around 7:00 a.m.), we conducted 21 training trials over 7 days. As in the *Aotus* training trials, all six feeding sites were baited with banana.

### Experimental Trials: General Procedures

After the training procedures were complete, the experimental trials began. Three trials were conducted daily for each species. In each trial, two of the six platforms contained scented and baited boxes, whereas four platforms contained unscented and unbaited boxes.

*Preparation of apparatus for each day of trials.* Prior to the start of each day's trials, and before the boxes were placed on the platforms, the 6 boxes to be baited (2 baited boxes for each of three daily trials) were chosen randomly from the total of 18 cleaned boxes. Three banana slices were placed inside the pipes of these boxes. The pipes in these baited boxes were also heavily scented with banana residue (see below). The residue was allowed to dry before the trials began. The other 12 boxes remained unbaited and unscented. Scented and unscented boxes could be olfactorily but not visually distinguished by human observers.

*Description of a typical trial.* In a typical trial, a closed box was placed on top of each of the six platforms. Two platforms received baited boxes, and four platforms received unbaited boxes. The particular platforms on which the baited boxes were placed were chosen randomly (using a roll of dice) for each trial, within the constraint that the same platform was not baited in more than two consecutive trials within a day.

At the start of the trial, the boxes were opened simultaneously, and the monkeys approached the platforms. Identity and behavior of each monkey visiting a platform were recorded continuously within consecutive 15-s intervals. Behaviors recorded were presence at site (monkey touched the platform) and probing a pipe. Probing a pipe was scored when a monkey (a) pressed its face to the opening of the pipe (*nontarp* trials only; see below), (b) removed a covering on the outside of the pipe opening (*tarp* trials only; see below), or (c) reached inside the pipe.

The trial ended when the food was gone (usually in less than 3 min). The boxes were then removed from the platforms and were replaced with six new boxes and pipes to start the next trial. Intertrial intervals were approximately 10 min.

*Cleaning of apparatus at the end of each day's trials.* At the end

of each day's trials, all 18 boxes were cleaned thoroughly with high-pressure water. The pipes were cleaned with bleach and rinsed with water.

### Experimental Trials: Schedule

Two series of experimental trials were conducted for each species. Each series consisted of 10 days or nights of 3 trials each for a total of 30 trials.

**Nontarp trials.** The first series of 30 trials for the *Cebus* group occurred on 10 mornings between June 23 and July 3, 1994. The first series of 30 trials for the *Aotus* pair occurred on 10 evenings (at dusk) between October 19 and October 29, 1994. For the scenting procedure, the baited pipes were smeared on the inside and outside with banana residue from the inside of the peel to increase the amount of scent present at the baited platforms.

**Tarp trials.** On many occasions during the nontarp trials, subjects of both species were observed to press their faces to the opening of the pipe and to reach inside the pipe or to move to a different platform. It was unclear whether the monkeys were using a scent cue, a visual cue, or both in making the decision whether to reach inside the pipe. It did seem, however, that the *Cebus* monkeys oriented their faces so that their eyes were looking into the pipe and that the *Aotus* monkeys oriented their noses to the pipe opening (e.g., on some occasions their eyes were above the opening). To determine whether each species was olfactorily or visually inspecting the pipe, we placed a visual but not olfactory obstruction (nylon tarp) over the opening of the pipe for a second series of 30 trials for each species. The tarp was attached by rubber bands to the hardware that attached the pipe to the box and had to be removed by the monkeys before reaching inside the pipe. Both species received a brief training period with the tarp in place (2 trials for the *Cebus*, which spontaneously removed the tarp, and 4 trials for the *Aotus*, which had some difficulty learning to do so).

This second series of 30 trials for both the *Aotus* and *Cebus* monkeys occurred on 10 days between November 10 and December 6, 1994. *Cebus* trials and *Aotus* trials were run on the same days, with the *Cebus* trials occurring in the late afternoon and the *Aotus* trials occurring at dusk. For the scenting procedure, in the tarp trials, the inside of the baited boxes (rather than the pipes) was smeared with actual banana rather than residue from the peel to increase the amount of banana scent at the sites.

### Scoring of Performance

For both series of trials, the first two choices of each monkey for each trial were used to measure performance on the task. For Series 1 (nontarp trials), a choice was scored if a monkey either pressed its face to the opening of a pipe or reached its hand in the pipe. For Series 2 (tarp trials), a choice was scored if a monkey removed the tarp covering the pipe opening. For both series of trials, a *correct* choice was scored if the pipe chosen was baited (i.e., contained banana slices).

To avoid the influence of social factors in the analysis of performance, we scored visits to baited pipes as choices only if that pipe had not been previously visited in that same trial by any other monkey. Therefore, if a monkey's first choice was a baited pipe that had already been visited by one or more monkeys in that same trial, this choice was not included in the scoring of performance. If the monkey's next visit was to a pipe previously unvisited in that trial, then that choice would be scored as that monkey's second choice. If a monkey visited only previously visited pipes in a particular trial, it would be recorded as having made no scored

choices in that trial. Second visits to the same pipe by the same monkey were also not scored as choices. These procedures disregard choices potentially influenced by the presence of other monkeys at a pipe.

A proportion correct (PC) score was calculated for each monkey for each daily set of three trials. PC is equal to the number of correct choices (out of the first two choices for each trial) divided by the total number of (first two scored) choices for each daily set of three trials. The denominator of the PC score could range from one, if only one choice was scorable (e.g., the monkey only made one choice or the other choices were to previously visited pipes), to six (all first and second choices in each trial were scorable). Daily PCs ranged from zero (all choices were incorrect, i.e., unbaited pipes) to one (all scored choices were correct: e.g., 1/1, 2/2, 3/3, and so on).

In addition to analyzing each monkey's performance individually, we calculated a daily PC score for each species as a group. This group score was computed by summing the numerators of all PC scores for a species and dividing that by the sum of all of the denominators of all PC scores for that species.

### Analysis of Observed Versus Expected Performance

For each monkey, the binomial probability ( $P$ ) of obtaining by chance a result at least as good as each daily performance in each series was determined, given that two out of six sites were baited. Fisher's method for combining probabilities was used to calculate  $\chi^2$  (equal to  $-2 * \sum \ln P$ , where  $P$  is each binomial probability), which is compared with a  $\chi^2$  distribution ( $\alpha = .05$ ; Sokal & Rohlf, 1981), to determine the overall likelihood of obtaining results at least as good as each subject's performance level within a series. In similar fashion, the combined probability of obtaining the results achieved from each species for each series of trials was also determined using Fisher's method.

The fact that more individual *Cebus* than *Aotus* monkeys were tested could potentially influence the scored performance of individual monkeys. The expected chance level performance of individual monkeys is different from one third (two of six pipes) if more than 2 monkeys are choosing simultaneously so that some pipes are unavailable. Because there are only two baited sites, only 2 monkeys can possibly score correctly on each trial. Because the *Cebus* group is larger than the *Aotus* group, any difference in performance between the species could possibly be attributed to this effect rather than to differences in the use of olfactory cues in locating the food.

To take this effect into consideration in comparing the results between the two species, we also analyzed the data in the following way. Computer simulations, written in MS-DOS QBasic, were designed to generate results that would be obtained if the monkeys were choosing platforms randomly. The program generated "trials" of two to four unique random integers from one through six to simulate two to four choices of one of six labeled "platforms." The number of choices (two, three, or four) represents the number of monkeys observed to have chosen simultaneously. The number of trials in which two, three, and four choices were so generated equaled the actual number of trials in the experiment with the corresponding number of monkeys choosing. (For example, if in the *Cebus* tarp trials, in 12 of the 30 trials, 3 monkeys chose at once, the computer simulation would then generate 12 trials. In each trial, three choices would be generated.) Within each category of "number of monkeys choosing," the procedure of producing trials (e.g., 12 of them in this example) was repeated 1,000 times.

Two of the six possible choices of platforms were always identified *pre hoc* as the correct choices for all trials. For each trial,

the number of correct choices generated by the simulation (zero, one, or two) was determined and then tallied for all trials within each category of number of monkeys choosing (e.g., 12 results tallied for 3 monkeys choosing). This tallying procedure was performed for each of the 1,000 sets of results, which were then ranked from worst possible performance (e.g., all 12 trials had zero choices correct) to best possible performance (e.g., all 12 trials had two choices correct).

The actual results obtained in the experiment were located in the list of 1,000 results generated by the simulation. If the actual results matched one represented in the best 25 or the worst 25, then the actual results were in the 5% most outlying and thus were significantly different than expected by chance at the .05 level.

### Analysis of Performance Differences

For both series of trials, daily PC scores were compared using a Mann-Whitney *U* test on (a) the 2 *Aotus* monkeys and (b) the *Cebus* group versus the *Aotus* group. A Kruskal-Wallis single-variable analysis of variance (ANOVA) by ranks was used to determine if individual *Cebus* monkeys differed in performance within each series of trials. A Newman-Keuls test by ranks was used to determine the source of any individual effects found in the Kruskal-Wallis test. The alpha level for all hypothesis testing was .05.

### Analysis of Spatial Strategies

**Positional habits.** To determine if monkeys exhibited preferences for choosing particular platforms first, we compared the distribution of first choices made to each platform per monkey in each series of trials against an expected uniform distribution (i.e., absence of positional habits) using a log-likelihood ratio test (Zar, 1974).

**Win-stay/win-shift strategies.** The results were examined to determine if win-shift or win-stay strategies were used by the monkeys in choosing platforms. Monkeys using a win-stay strategy will preferentially choose platforms baited in the previous trial. Monkeys using a win-shift strategy will preferentially choose platforms unbaited in the previous trial. For this analysis, only data from the second and third trials in each day were used to examine application of these strategies only within a day because if these strategies are used at all, they are more likely to be used within a 10-min interval than over a 24-hr interval.

First, the platform choices of each individual monkey were examined for consistent use of win-stay or win-shift strategies. For each platform, we calculated the proportion of first choices made to that platform in trials in which the monkey (a) had received food from that platform in the previous trial and (b) had not received food from that platform in the previous trial. These proportions should not differ if neither strategy is used. The proportions were compared using a Wilcoxon paired sample test.

Because the monkeys were tested in their social groups, the performance of any individual monkey using either of these strategies could be based on whether any monkey received or did not receive food from a particular platform on the preceding trial. To consider this possibility, we calculated the proportion of first choices made to each platform by any monkey when the platform (a) had been baited in the previous trial and (b) had not been baited in the previous trial. These proportions should not differ if the choice of a platform is unaffected by monkeys having discovered whether that particular platform was baited or unbaited in the previous trial.

## Results

### Participation of Monkeys in the Trials

Both *Aotus* monkeys participated in all trials. Only 4 of the *Cebus* monkeys participated on enough days to analyze daily PC scores: Willy (the dominant male, all days), Paul (subordinate male, all days), and Charlie (all except 1 tarp day) and Carol (all except 4 nontarp days, both adult females).

### Nontarp Trials

**Observed versus expected performance.** In the series of trials without tarp covering the opening of the pipes (nontarp trials), performance by all monkeys and both species groups within the entire series was not greater than expected by chance (see Figure 1a; binomial probabilities combined by Fisher's method; all  $X^2 < \chi^2_{crit}$ ; all  $ps > .05$ ). The observed results for the *Cebus* nontarp trials and the *Aotus* nontarp trials were not significantly different at the .05 level from those generated by the computer simulation (see Table 1).

**Individual and species differences in performance.** The daily PC scores for this series did not differ in a comparison of (a) the 2 *Aotus* subjects (Mann-Whitney *U* test,  $U = 51.5$ ,  $p > .05$ ), (b) the 4 *Cebus* subjects (Kruskal-Wallis ANOVA,  $H_c = 7.066$ ,  $p > .05$ ), and (c) the *Cebus* group versus the *Aotus* group (Mann-Whitney *U* test,  $U = 38.5$ ,  $p > .05$ ).

### TARP Trials

**Observed versus expected performance.** In the series of trials in which a tarp covering was placed over the opening of the pipes, the performance of the individual *Aotus*, as well as the *Aotus* group as a whole, was significantly greater than expected by chance (see Figure 1b; binomial probabilities combined by Fisher's method; both  $X^2 > \chi^2_{crit}$ ; both  $ps < .05$ ). None of the 4 *Cebus* subjects or the *Cebus* group as a whole performed at a level greater than chance (see Figure 1b; binomial probabilities combined by Fisher's method; all  $X^2 < \chi^2_{crit}$ ; all  $ps > .05$ ). The observed results for the *Aotus* trials, but not the *Cebus* trials, were significantly different from those generated by the computer simulation ( $p < .05$ ; see Table 2).

**Individual and species differences in performance.** The daily PC scores of the *Aotus* group and the *Cebus* group differed significantly in the tarp trials (Mann-Whitney *U* test,  $U = 100$ ,  $p < .05$ ). No individual differences were found in comparing daily PC scores between the *Aotus* subjects (Mann-Whitney *U* test,  $U = 62.5$ ,  $p > .05$ ). The main effect of identity was found to be significant in the Kruskal-Wallis ANOVA comparing the PC scores of individual *Cebus* in the tarp trials ( $H_c = 9.478$ ,  $p < .05$ ). The Newman-Keuls test by ranks determined that the daily PC scores of Paul ( $Mdn = 0.417$ ) and Carol ( $Mdn = 0.000$ ) were significantly different: calculated  $q(4.06) > critical q_{0.05, \infty, 4}(3.633)$ ,  $p < .05$  (Zar, 1974).

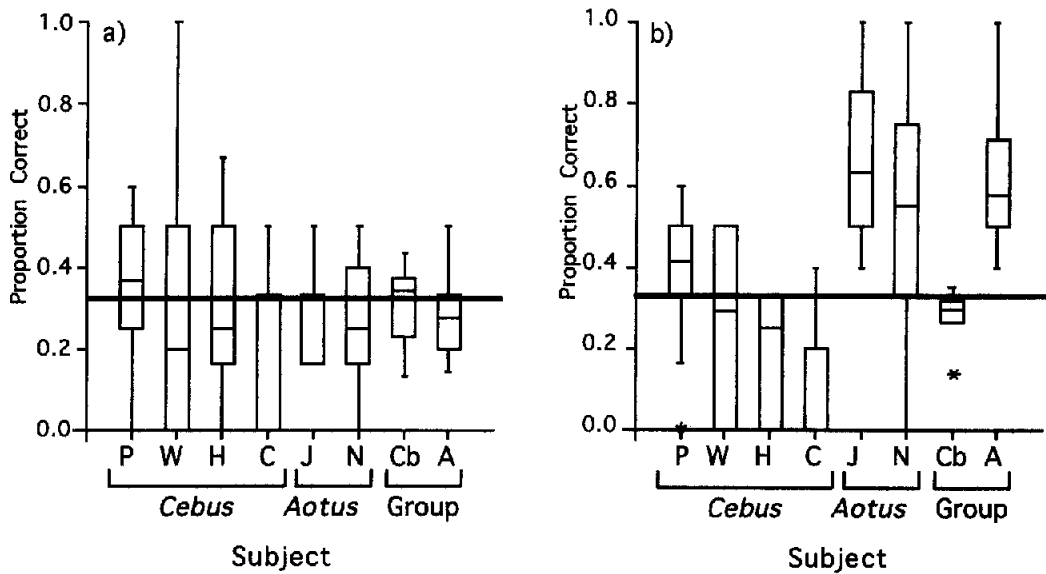


Figure 1. Box plots of proportion correct (PC) of first two choices made in each of three daily trials for 10 days per subject and per species group in two series of trials: (a) nontarp trials and (b) tarp trials. In the box plots, the horizontal lines in the boxes are the medians, and the hinges of the boxes are the quartile scores. The vertical lines extending from the boxes encompass scores that fall within 1.5 interquartile ranges from the hinges. The asterisks indicate scores falling between 1.5 and 3 interquartile ranges from the hinges (Wilkinson, 1990). The solid horizontal line indicates chance level performance (PC = 0.33). Letters below the plots indicate monkeys represented: *Cebus*: P = Paul, W = Willy, H = Charlie, C = Carol; *Aotus*: J = Jenny, N = Niko; *Group*: Cb = all *Cebus* combined, A = both *Aotus* combined.

Spatial Strategies

**Positional habits.** A positional habit is revealed if a particular platform is a monkey's first choice more than one sixth of the time. Percentage of first choices made to one particular platform ranged from 48% to 100% in individual *Cebus* and from 31% to 58% in individual *Aotus*. Positional habits were weaker in the *Aotus* tarp trials (31%–33% of choices made to one platform). All individual monkeys in all series of trials exhibited significant preferences for choosing certain platforms first (log-likelihood ratio tests,

all  $ps < .05$ ). Individual monkeys differed in the particular platforms preferred. The platforms preferred by each monkey remained constant throughout the two series for the *Cebus* but not for the *Aotus*.

**Win-shift/win-stay strategies.** For each monkey, there was no difference in the proportion of choices made to each platform when that monkey had as opposed to had not received food from that platform in the previous trial on the same day ( $p > .05$ , Wilcoxon paired sample test). In addition, the proportion of first choices made to each platform did not differ whether that platform had been baited versus left unbaited in the previous trial on the same day ( $p > .05$ , Wilcoxon paired sample test).

Table 1  
Comparison of Observed Results to Simulated Expected Results for Nontarp Trials

Species/ $n^a$	Observed results <sup>b</sup>			Location of observed result <sup>c</sup>
	0	1	2	
<i>Aotus</i>				
2	8	9	2	436–471
<i>Cebus</i>				
2	3	3	1	483–581
3	4	8	3	235–278
4	0	2	1	324–650

<sup>a</sup> Number of monkeys choosing at once in the simulation. <sup>b</sup> Number of trials in which 0, 1, and 2 correct choices were scored. <sup>c</sup> From the list of 1,000 groups of simulated trials ranked from worst (1) to best (1,000) performance.

Discussion

The nocturnal *Aotus* monkeys used the olfactory cues to locate the baited pipes at a level greater than chance in the tarp trials, whereas the *Cebus* monkeys did not. Both *Aotus* and *Cebus* have been observed to smell foods before tasting them (Wright, 1985; pers. obs.). However, there is little evidence from field studies that *Cebus* monkeys use olfactory cues in foraging and only indirect evidence that *Aotus* monkeys do so. Foraging *Aotus* tend to reuse the same paths night after night (Peru and Paraguay: Wright, 1985; in the rainforest enclosure: pers. obs.), suggesting possible route memorization and potential scent marking of trails for navigational purposes (Wright, 1989). This study provides the

Table 2  
Comparison of Observed Results to Simulated Expected Results for Tarp Trials

Species/n <sup>a</sup>	Observed results <sup>b</sup>			Location of observed result <sup>c</sup>
	0	1	2	
Aotus 2	1	11	6	>1,000 <sup>d</sup>
Cebus 2	3	6	1	738-811
3	1	5	4	858-895
4	1	3	0	26-69

<sup>a</sup> Number of monkeys choosing at once in the simulation.

<sup>b</sup> Number of trials in which 0, 1, and 2 correct choices were scored. <sup>c</sup> From the list of 1,000 groups of simulated trials ranked from worst (1) to best (1,000) performance. <sup>d</sup> The observed result was better than the best simulated result ( $p < .05$ ).

first documentation that free-ranging *Aotus* can use olfactory information to locate food.

Given the olfactory anatomy of *Aotus* monkeys, this difference in performance is not surprising. In relation to body and brain size, the olfactory bulb, the accessory olfactory bulb, and the volume of the lateral olfactory tract nucleus are larger in *Aotus* than in other New World monkeys (Stephan, 1972; Stephan, Frahm, & Baron, 1981). The relationship between nocturnal activity and increased olfactory bulb size has also been found across the entire primate order (Barton, Purvis, & Harvey, 1995) and in birds as well (Healy & Guilford, 1990). Increased size of olfactory structures may indicate a greater reliance on olfactory cues in a foraging (and/or social) context. It has been noted, however, that the size of olfactory structures does not necessarily correlate with olfactory performance in odor detection. Laska (1990) found that short-tailed fruit bats (*Carollia perspicillata*), which have reduced olfactory structures compared with rats, outperformed rats by many orders of magnitude in the detection of fruity esters.

The *Cebus* monkeys in this study may have performed poorly in both series of trials because they were relying on a visual cue rather than an olfactory one. In the nontarp trials, *Cebus* monkeys were observed to press their faces close to the opening of every pipe visited. In the tarp trials, the *Cebus* monkeys tore the tarp off almost every pipe visited, whether it was baited or not. They looked inside, then reached inside and retrieved the food only if the pipe was baited. They did not discriminate between baited and unbaited pipes before tearing off the tarp, thus lowering their performance scores.

The tendency of the *Cebus* monkeys to tear off the tarp is probably greater than that of *Aotus* monkeys because of their normal modes of foraging. In the wild (Terborgh, 1983) and in the rainforest enclosure (pers. obs.), *Cebus apella* commonly extract prey hidden in tough substrates, such as deep within the wood of large dead branches. This foraging mode requires the use of force and manipulation of the substrate by the hands and teeth. *Aotus*, on the other hand, catch insects in flight or scrape them off leaves or

branches (Peru: Wright, 1985; rainforest enclosure: pers. obs.) rather than extensively and destructively manipulating substrates. The fact that the *Aotus* but not the *Cebus* required training to pull off the tarp is consistent with their differences in foraging style.

In the tarp trials, the *Aotus* monkeys removed the tarp at baited sites but not at unbaited sites, resulting in higher performance scores. This result indicates that the decision to reach inside the pipe was made before the banana slices were visible. The poor performance of *Aotus* in the nontarp trials was probably a consequence of the scoring procedure, because the *Aotus*, like the *Cebus*, pressed their faces close to the opening of every pipe visited. In the nontarp trials, this behavior was scored as a choice, and performance by both species was at chance level.

It is not surprising that neither the *Cebus* nor the *Aotus* monkeys appeared to be using a win-stay or a win-shift strategy in choosing platforms. Because we baited platforms randomly within the constraint that the same platform was not baited more than twice in a row within a day, consistent use of these strategies would not have improved performance above chance levels.

Instead of using these spatial strategies, each monkey tended to specialize on one particular platform to choose first, which also did not increase performance. Certain platforms were favored, perhaps because of the travel paths used by different monkeys to the site of the array of platforms, or because of the natural asymmetries in substrate support (i.e., tree branches) near the platforms. The positional habit may have been more pronounced in the *Cebus* because more monkeys were choosing simultaneously, so that the platform preference of one individual, such as the dominant male, affected the choices of platforms available to other monkeys. There is a strong tendency for positional habits in both species, but *Aotus* monkeys' performance using olfactory cues in the tarp trials was sufficiently good to overcome these habits.

A combination of differences between the *Aotus* and *Cebus* monkeys contributed to the better performance of *Aotus* monkeys in using the olfactory cues to locate food. The diurnal and extractive foraging style of the *Cebus* monkeys may predispose them to access and use visual information (i.e., tearing off the tarp in this experiment) rather than to rely on olfactory information. To nocturnal foragers, however, olfactory cues are more salient than visual cues. Greater utilization of olfactory information is associated with larger olfactory structures and may be an adaptation for nocturnal foraging.

## References

- Barton, R. A., Purvis, A., & Harvey, P. H. (1995). Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 348, 381-392.
- DuMond, F. V. (1968). The squirrel monkey in a seminatural environment. In L. A. Rosenblum & R. W. Cooper (Eds.), *The squirrel monkey* (pp. 88-146). New York: Academic Press.
- Epple, G., & Moulton, D. (1978). Structural organization and

- communicatory functions of olfaction in nonhuman primates. In C. R. Noback (Ed.), *Sensory systems of primates* (pp. 1–22). New York: Plenum Press.
- Garber, P. A., Bolen, R. H., & Evans, S. (1993, August). *The use of color and odor cues in primate decision-making*. Paper presented at the meeting of the American Society of Primatologists, Sturbridge, MA.
- Healy, S., & Guilford, T. (1990). Olfactory bulb size and nocturnality in birds. *Evolution*, *44*, 339–346.
- Hudson, R., Laska, M., & Ploog, D. (1992). A new method for testing perceptual and learning capacities in unrestrained small primates. *Folia Primatologica*, *59*, 56–60.
- Laska, M. (1990). Olfactory sensitivity to food odor components in the short-tailed fruit bat, *Carollia perspicillata* (Phyllostomidae, Chiroptera). *Journal of Comparative Physiology A: Sensory, Neural and Behavioral Physiology*, *166*, 395–399.
- Laska, M., & Hudson, R. (1993a). Assessing olfactory performance in a New World primate, *Saimiri sciureus*. *Physiology and Behavior*, *53*, 89–95.
- Laska, M., & Hudson, R. (1993b). Discriminating parts from the whole: Determinants of odor mixture perception in squirrel monkeys, *Saimiri sciureus*. *Journal of Comparative Physiology A*, *173*, 249–256.
- MacDonald, S. E. (1994). Gorillas' (*Gorilla gorilla gorilla*) spatial memory in a foraging task. *Journal of Comparative Psychology*, *108*, 107–113.
- MacDonald, S. E., Pang, J. C., & Gibealt, S. (1994). Marmoset (*Callithrix jacchus jacchus*) spatial memory in a foraging task: Win-stay versus win-shift strategies. *Journal of Comparative Psychology*, *108*, 328–334.
- Sokal, R. R., & Rohlf, F. J. (1981). *Biometry: The principles and practice of statistics in biological research* (2nd ed.). San Francisco: Freeman.
- Stephan, H. (1972). Evolution of primate brains: A comparative anatomical investigation. In R. H. Tuttle (Ed.), *The functional and evolutionary biology of primates* (pp. 155–174). Chicago: Aldine-Atherton.
- Stephan, H., Frahm, H., & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica*, *35*, 1–29.
- Terborgh, J. (1983). *Five New World primates: A study in comparative ecology*. Princeton, NJ: Princeton University Press.
- Ueno, Y. (1994a). Olfactory discrimination of eight food flavors in the capuchin monkey (*Cebus apella*): Comparison between fruity and fishy odors. *Primates*, *35*, 301–310.
- Ueno, Y. (1994b). Olfactory discrimination of urine odors from five species by tufted capuchin (*Cebus apella*). *Primates*, *35*, 311–323.
- Ueno, Y. (1994c). Responses to urine odor in the tufted capuchin (*Cebus apella*). *Journal of Ethology*, *12*, 81–87.
- Wilkinson, L. (1990). *SYGRAPH: The system for graphics*. Evanston, IL: SYSTAT.
- Wright, P. C. (1985). *The costs and benefits of nocturnality for Aotus trivirgatus (the night monkey)*. Unpublished doctoral dissertation, City University of New York.
- Wright, P. C. (1989). The nocturnal primate niche in the New World. *Journal of Human Evolution*, *18*, 635–658.
- Zar, J. H. (1974). *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall.
- Zeller, A. C. (1987). Communication by sight and smell. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 433–439). Chicago: University of Chicago Press.

Received June 29, 1996

Revision received October 21, 1996

Accepted October 22, 1996 ■