GERBILS IN SPACE: PERFORMANCE ON THE 17-ARM RADIAL MAZE

DONALD M. WILKIE AND PETER SLOBIN

THE UNIVERSITY OF BRITISH COLUMBIA

In Experiment 1 six hungry gerbils received six trials per day on a 17-arm radial maze. During each trial the subjects were allowed to choose freely among the arms, each of which contained a food pellet, until each arm had been visited once or until eight minutes had elapsed. An error was recorded when the subject entered a previously visited arm. The gerbils quickly learned not to re-enter previously visited arms and generally made errors on fewer than 15% of entries, performance comparable to that of the rat and superior to that of other species tested in the radial arm maze. The intertrial-interval duration did not affect accuracy of arm choices during acquisition but did influence asymptotic accuracy. Accuracy did not change systematically over the six trials. A high proportion of arm entries were to nearby arms. Errors occurred most often towards the end of a trial. Odor cues were not important. When the number of trials per day was reduced from six to one, accuracy deteriorated slightly. In Experiment 2 neither the transposition of extramaze cues nor the placement of the maze in a different room had large disruptive effects on accuracy. In Experiment 3 the addition of three explicit intramaze brightness cues aided accuracy, perhaps by permitting the subjects to decompose the large maze into three smaller mazes, although there was no direct evidence that this was the case. Implications of a number of these results for models of spatial maze performance were discussed.

Key words: radial arm maze, spatial memory, foraging, gerbil

The radial arm maze (Olton, 1979; Olton & Samuelson, 1976) consists of a central area from which several identical arms radiate, like the spokes of a wheel. The distal end of each arm contains a small well, baited with a piece of food. A hungry rat (*Rattus norvegicus*) placed in the maze quickly learns the optimal strategy of visiting each arm only once. In a 17-arm maze, rats reach an asymptotic level of entering about 15 baited arms during the first 17 choices (88% correct) after about 50 trials (Olton, Collison, & Werz, 1977) and do even better on smaller versions of the maze (Olton, 1978).

Although there are several mechanisms (e.g., odor cues emanating from the food, odor trails left by the passage of the rat, response strategies such as entering only adjacent arms) that

could produce accurate arm choice, the rat's performance seems to be memory based (cf. Olton & Samuelson, 1976). That is, the rat seems to remember, and subsequently avoid, the arms that have been entered previously.

Only four other species—the ringdove, *Streptopelia risoria* (Wilkie, Spetch, & Chew, 1981); the domestic pigeon, *Columba livia* (Bond, Cook, & Lamb, 1981); the Siamese fighting fish, *Betta splendens* (Roitblat, Tham, & Golub, 1982); and CD-1 mice, *Mus* (Mizumori, Rensensweig, & Kermisch, 1982)—have been systematically tested in the radial arm maze. Performance of all these species was inferior to that of the rat, and in the cases of the pigeon and Siamese fighting fish evidence for response strategies was noted.

Although field observations of nectar-feeding birds (e.g., Kamil, 1978) and laboratory studies of food-caching birds (e.g., Shettleworth & Krebs, 1982) suggest that other species do have good spatial memories, because of procedural differences it is as yet unclear how these species compare to the rat. Accordingly, it is still not known with any degree of certainty if accurate memory-based performance

This research was supported by the Natural Sciences and Engineering Research Council of Canada. Richard Taki assisted with testing the animals and Richard Wright and Jean Murdock assisted with the data analysis and graphs. Reprints may be obtained from Donald M. Wilkie, Department of Psychology, The University of British Columbia, Vancouver, B.C., Canada V6T 1W5.

in the radial arm maze is not simply some peculiarity of the laboratory rat.

There are several approaches available to explain differences between species in performance in the radial arm maze (cf. Roitblat et al., 1982). One appeals to a phylogenetic scale of ability (cf. Bitterman, 1965). A second appeals to adaptive specializations in cognitive abilities (Roitblat et al., 1982) such as spatial memory. A third suggests that a species' foraging ecology and the resulting foraging patterns (e.g., a "win-shift" strategy—Olton & Schlosberg, 1978) are prime determinants of accurate radial arm maze performance. In order to evaluate these hypotheses, which are not necessarily mutually exclusive, comparable data from many species are required.

Consequently, there are two reasons for systematically studying the radial arm maze performance of new species. Here we report some of our studies of the Mongolian gerbil (*Meriones unguiculatus*). Many of the natural activities of this small seed- and plant-eating rodent from a desert ecosystem have been described by Roper and Polioudakis (1977).

Gerbils and rats have been tested in two other situations involving spatial cues; in both spontaneous alternation (Dember & Kleinman, 1973; Dennis, 1939) and thymotaxy (Nauman, 1968) differences have been found. Thus, it was by no means clear how the gerbil would perform in the radial arm maze.

EXPERIMENT 1

In this experiment we examined acquisition and asymptotic performance in a 17-arm radial maze. We also examined the effect of varying the interval between trials and a number of dependent variables previously measured for other species (e.g., Olton, 1978; Olton & Samuelson, 1976). Because gerbils have a very distinctive scent-marking response (Thiessen & Yahr, 1977), we observed if they marked visited (and consequently depleted) arms and we included procedures to discount the possibility that the gerbils used "odor trails" to avoid repeating empty arms. Because there is ample evidence that some rodents can locate hidden food by olfactory detection (e.g., Reichman, 1981), procedures were also included to rule out the possibility that gerbils simply entered arms in which they could smell food.

METHOD

Subjects

Six experimentally naive adult male Mongolian gerbils, offspring of parents obtained from Tumblebrook Farms, were housed individually in translucent plastic cages containing Sanicel bedding. The colony room had a reversed 12-hr light/12-hr dark cycle. The gerbils had free access to water but received only enough food during and after test sessions to maintain them at about 85 to 90% of their free-feeding weights.

Apparatus

The apparatus was a 17-arm radial maze. The circular central platform, 70 cm in diameter, was constructed of sheet metal (floor) and galvanized wire mesh (walls and ceiling). The arms radiated from the central area. The space between the arms was equal (approximately 21°). A circular sheetmetal insert, slightly smaller in diameter than the central platform area, could be raised and lowered to control access to the arms. The arms, constructed of wire mesh, were 45 cm long, 6 cm high, and 6 cm wide. A black plastic food cup was recessed approximately 2 cm into the floor at the distal end of each arm.

Testing Room

The maze was placed on a table top approximately 80 cm above the floor in a room approximately 2.1 m wide by 2.8 m long. The walls of the room were painted an off-white color. The room was illuminated by two banks of overhead fluorescent lights, each containing four 40-W cool white lamps. One side wall contained a green door; the opposite side wall contained a window, covered by beige drapes. Five cardboard posters, about 25 cm in diameter and 90 cm above the floor, were located on three walls of the room. The posters contained the following designs: cross, circle, triangle, S, and square, in blue on a white background. Going clockwise around the room starting at the door, the following items were visible to the gerbil: the experimenter, cross poster, circle poster, triangle poster (on middle of drape wall) air inlet, S poster, electrical outlet, square poster, and coat rack.

Procedure

All subjects were tested during the last 3 hr of the colony room dark cycle. The experiment consisted of six phases. In the first two phases, acquisition and the effect of intertrial interval were examined. During the third, fifth, and sixth phases an attempt was made to mask odor cues. During the fourth phase, data were collected under conditions that permitted some degree of comparison with the results reported by Olton and Samuelson (1976) for the rat.

Phase 1 (Days 1 to 21). No preliminary training was given. Each arm was baited with a 45-mg Noyes food pellet. The gerbil was put in the central area and the barrier was raised. The gerbil was allowed to enter arms until all 17 arms had been visited or until 8 min had elapsed. An entry into an arm was defined as placing all four paws within the arm. If the subject turned around in an arm and did not proceed to the food container, a choice was still recorded. (This happened only rarely.)

All gerbils received six trials per day. For three gerbils (numbers 3, 4, and 5) the intertrial interval (ITI) of approximately 2 min was spent confined to the central area (barrier down). For the other three gerbils (numbers 7, 8, and 9) the approximately 22-min ITI was spent in the home cage.

Phase 2 (Days 22 to 28). The ITI value for the two sets of gerbils was reversed.

Phase 3 (Days 29 and 30). With the ITI the same as during Phase 2, the central platform area was sprinkled with Mennen Aftershave Lotion during each of two test days.

Phase 4. Each gerbil received one trial per day for 15 days.

Phase 5. In chronological order this and the next phase followed Experiment 3 by several weeks. Gerbil 9 did not participate in these phases. The baseline phase (4 days) was identical to Phase 4. During the 4 tests a single unobtainable Noyes pellet was hidden immediately beside each food well. This manipulation should have disrupted accurate performance if the gerbils were relying upon food odors emanating from the food wells.

Phase 6. During the 4 baseline days the animals were allowed to make four normal arm choices; they were then briefly confined to the fifth arm for about 120 sec. During the 4

test days, the first four (depleted) arms were switched with four as yet unentered arms during confinement. Arm switching should have disrupted accurate choice if odor cues in visited arms were important.

RESULTS AND DISCUSSION

Figure 1 shows percentage of trials each gerbil chose a correct (baited) arm during Phase 1 (Days 1 to 21) and Phase 2 (Days 22 to 28). Percentages are averages of the six trials conducted each day. Except for the first day, accuracy of arm choice by all gerbils clearly was above the level expected if they chose arms randomly (64.3%—e.g., Spetch & Wilkie, 1980). The gerbils trained with the short ITI (numbers 3, 4, and 5) acquired the task as quickly as those trained with the long ITI [$F(1,4) = 7.06$, $p > .05$ for group by week interaction in an analysis of variance of average first- and average third-week accuracy scores].

Although ITI value did not appear to affect accuracy during acquisition, it did affect asymptotic accuracy to some extent. The accuracy of the short-ITI gerbils increased (from $M = 88.7$ to $M = 91.7$) when the ITI was lengthened during Phase 2. The long-ITI gerbils' accuracy decreased (from $M = 91.3$ to $M = 87.7$) when the ITI was shortened. The group by ITI-value interaction was significant [$F(1,4) = 57.1$, $p = .003$] when the average last-week accuracy scores of Phase 1 and Phase 2 were analyzed.

At no time during this or subsequent experiments was ventral rubbing scent-marking behavior observed in the maze. Although the accuracy of Gerbils 3, 4, and 5 decreased during Phase 3 odor days, performance still remained well above chance and the decreases observed for these subjects were matched by slight improvements by the remaining subjects. The percentage of trials on which each gerbil chose a correct (baited) arm during the last two days of baseline and the two odor days of Phase 3 were: Gerbil 3—86.5 (baseline), 77.5 (odor); Gerbil 4—94, 89.5; Gerbil 5—96.5, 87.5; Gerbil 7—89, 95; Gerbil 8—85.5, 93.5; Gerbil 9—89, 93.

Hiding food at the end of each arm (Phase 5) also was without effect. The 4-day baseline scores and 4-day test percentage-correct scores for each gerbil were: Gerbil 3—84.0 (baseline), 84.3 (test); Gerbil 4—88.0, 92.5; Gerbil 5—86.8,

Fig. 1. Percentage of trials in Experiment 1 on which each gerbil chose a correct (baited) arm during Phase 1 (Days 1 to 21) and Phase 2 (Days 22 to 28). The intertrial interval was varied between phases (see text for details). Percentages are averages of the six trials conducted each day.

83.3; Gerbil 7—86.5, 86.5; Gerbil 8—89.3, 90.5.

Switching visited and unvisited arms (Phase 6) did not affect accuracy. The 4-day baseline and 4-day test percentage-correct scores for each gerbil were: Gerbil 3—81.5 (baseline), 86.5 (test); Gerbil 4—86.5, 89; Gerbil 5—83.5, 81.5; Gerbil 7—82.5, 82; Gerbil 8—84, 83.

Figure 2 shows performance over the six trials conducted each day during the first, third, and fourth weeks of Phases 1 and 2. There was no systematic tendency for the gerbils' accuracy to improve or deteriorate over the six trials in either early or late stages of acquisition. These results for the short-ITI gerbils (3, 4, and 5) provide another piece of evidence that "odor trails" are unimportant. If depleted arms had been marked with an odor recognizable to a gerbil as its own from the first trial, performance on second and subsequent trials should have suffered; clearly it did not.

The fact that performance did not decrease from Trial 1 to Trial 6 does not indicate that proactive interference was absent. Like Roberts and Dale (1981), we found that the gerbils tended to rely more upon the response strategy of choosing nearby arms on later trials. For example, on Trial 1 the gerbils chose a nearby arm (i.e., an arm less than three arms away from the current arm) on 67% of the oppor-

tunities, whereas on Trial 6, 76% of choices were nearby arms.

Figure 3 shows a more detailed analysis of each gerbil's spatial distribution of choices. The arm entered on any particular choice during the 15 trials of Phase 4 was designated as arm 0. The next arm entered was given a score ranging between ± 8 . The adjacent arm in the clockwise (counterclockwise) direction was designated as +1 (−1), etc. Choosing the same arm again was scored as 0. Some gerbils (numbers 3, 5, and 8) turned predominately clockwise, the others counterclockwise. Most choices of all gerbils were either to the adjacent or second or third nearest arm. There was sufficient variability in the distribution of choices for each gerbil to reject the hypothesis that the gerbils solved the maze problem by acquiring a stereotyped response strategy (e.g., visiting every second arm) that would lead to accurate performance. Gerbil 9, whose behavior was the most stereotyped, chose the adjacent arm on only about 40% of trials.

Figure 4 shows the transformed probability of a correct arm choice as a function of successive choices. The percentages of arm choices made on the first, second, third, etc. choice over the 15 sessions of Phase 4 that were correct were transformed according to the formulae of Olton and Samuelson (1976, p. 105-106)

Fig. 2. Percentage of trials on which each gerbil chose a correct (baited) arm on each of the six daily trials during first, third, and fourth week of Experiment 1.

to control for the changing probability of a correct choice by chance over a series of choices. The transformed scores can range from 1.0, indicating the maximum number of correct choices, through 0, indicating random choice, to -1.0, indicating the maximum number of incorrect choices. All transformed scores for all of the gerbils were above 0, even on the 17th choice. In general, the likelihood of making an error increased with the number of

choices. No gerbil made an error in the first four choices. Although the scores were somewhat variable, there was a gradual but steady increase in the probability of an error after about the fourth choice.

Average accuracy during the one-trial-per-day procedure of Phase 4 was compared to the accuracy during Week 4 of Phase 1 (six trials per day). Surprisingly, the gerbils did slightly less well on one trial per day (i.e., a 24-hr ITI)

Fig. 3. Percentage of arms chosen by each gerbil in Experiment 1 at each distance and direction (— is counter-clockwise) from the currently chosen (0) arm. Data are from all 15 sessions of Phase 4.

than on six trials per day (i.e., ITIs of a few minutes). The difference of means (M one trial = 82, M six trials = 89.7) was significant in a repeated measures analysis of variance [$F(1,5) = 18.1, p = .009$].

EXPERIMENT 2

Although blind rats perform above chance in the radial arm maze (Zoladek & Roberts, 1978), accuracy is better when extramaze cues are available to locate the arms (Suzuki, Augerinos, & Black, 1980). The purpose of this experiment was to determine if extramaze cues are important for gerbils' radial arm maze performance. Two types of tests were performed. First, certain prominent extramaze cues were transposed (cf. Suzuki et al., 1980). Second, a completely new set of extramaze cues was introduced.

METHOD

Subjects and Apparatus

Same as in Experiment 1.

Procedure

The experiment consisted of two phases. During the first, extramaze cues were transposed. During the second, the maze was moved to a new room.

Phase 1. This phase lasted 8 days during which time the gerbils received one trial per day. During Days 2, 4, 5, 6, and 8 (baseline) the procedure was the same as during Phase 4 of Experiment 1. During the other 3 days the extramaze cues were changed in the following fashion: (1) the experimenter stood in the diagonally opposite corner of the room from usual, (2) the cross poster was replaced by the S poster, (3) the circle poster was replaced by the cross poster, (4) the S poster was replaced by the square poster, and (5) the square poster was replaced by the circle poster.

Phase 2. This phase lasted 10 days during which time the gerbils received one trial per day. During Days 1, 2, 3, 4, 5, 7, and 9 (baseline) the conditions were identical to those of Phase 4 of Experiment 1. During the remain-

Fig. 4. Transformed probability of a correct choice by each gerbil in Experiment 1 as a function of choice sequence. Data are from all 15 sessions of Phase 4.

ing days the maze was moved to a new room. The maze rested on the floor of the new room which was about four times as large as the old room and had undraped windows across one long wall. On the other long wall were two doorways. The room contained several cabinets, benches, compressed gas tanks, chairs, floor-standing surgical lamps, and other miscellaneous items.

RESULTS AND DISCUSSION

Overall, extramaze cues seemed to be of minor importance. Accuracy of some gerbils deteriorated slightly when the room cues were transposed; for others, however, accuracy increased slightly under the same conditions. The percentage of trials on which each gerbil chose a correct arm during baseline (average last five days) and test (average of three trans-

position sessions) were: Gerbil 3—89.5 (baseline), 76.0 (test); Gerbil 4—77.2, 72; Gerbil 5—79.8, 82; Gerbil 7—83.2, 74; Gerbil 8—77.2, 80; and Gerbil 9—77.2, 84.

Replacement of all of the extramaze cues (by moving the maze to a new room) had a more consistent deleterious effect (Figure 5). Still, accuracy in the new room was not always poorer than that in the old room, and for one gerbil (number 9) accuracy seemed to be even a bit better in the new room. In all cases, accuracy remained well above chance levels. Average old-room accuracy (mean of three baseline days prior to three test days: $M = 90.2$) was slightly but not significantly [$F(1,5) = 5.08$, $p > .05$] higher than accuracy on new-room days (mean of three test days: $M = 84.3$).

These results are relevant to evaluation of the two predominant conceptualizations of

Fig. 5. Percentage of trials on which each gerbil chose a correct (baited) arm when tested in old and new rooms in Experiment 2.

radial arm maze performance. These two views (O'Keefe & Nadel, 1978; Olton, 1978) have been reviewed elsewhere (e.g., Olton, Becker, & Handelman, 1979; Suzuki et al., 1980) and are only outlined here. Briefly, Olton's model assumes that accurate radial arm maze performance depends upon storage of discrete spatial-location information in working memory. As the trial proceeds, the animal stores a list of places that have been visited and which are not to be repeated on that trial. During the ITI the memory is cleared. O'Keefe and Nadel (1978), elaborating on the "cognitive map" notion originated by Tolman (1948), proposed that animals do not treat stimuli segmentally but rather form a representation in which places are located relative to each other (i.e., a map). The two approaches make different predictions about the effect of manipulating extramaze cues. Transposition of extramaze cues and substitution of a completely new set of cues both should severely disrupt maze performance according to the map hypothesis. Although Suzuki et al. (1980) found that trans-

position disrupted rats' maze performance, such was not the case for our gerbils and further, substitution of the complete set of extramaze cues was without major effect. These results, although inconsistent with the map hypothesis, do not necessarily refute it because animals are likely to use several types of cues, including proprioceptive and intramaze cues, to solve maze problems (cf. Restle, 1957); it is possible that cues other than extramaze visual cues are what are represented in the map. Such a possibility is suggested by the findings that both blind rats (Zoladek & Roberts, 1978) and blind children (Landau, Gleitman, & Spelke, 1981) can solve spatial problems.

EXPERIMENT 3

Gerbils seem not to rely exclusively upon extramaze visual cues for accurate arm choice in the radial arm maze. Although it is possible that gerbils, like blind rats, rely upon kinesthetic cues (cf. Zoladek & Roberts, 1978), it is also possible that they use subtle intramaze

cues. Although radial mazes are constructed so that arms are as identical as possible, it is still possible that subjects discriminate slight variations in arm cues. If animals discriminated differences in all 17 arms, a seemingly unlikely possibility, choices could be guided simply by intramaze cues. A perhaps more likely possibility is that certain arms appear more similar than other sets of arms. If this were the case the animals might "chunk" (Miller, 1956) or "decompose" the large maze into several smaller mazes, each consisting of a few arms.

In the present experiment we sought to determine if the addition of explicit and salient intramaze cues would facilitate accurate choices. One of three brightness cues was placed at the entrance to each arm.

METHOD

Subjects

Same as in Experiments 1 and 2.

Apparatus

The maze used in the previous experiments was modified after Phase 1 in the following fashion: A piece of heavy cardboard was mounted in front of each arm entrance; each piece had a door which could be raised to permit entry to that arm. Six entrances had white (W) cardboard, six had black (B), and five had grey (G). The arms, numbered 1 to 17, had the following colors: W, B, G, W, G, B, W, B, W, B, G, W, B, W, G, B, and G.

Procedure

The experiment consisted of four phases.

Phase 1—Baseline. For 15 days the gerbils were tested as in Phase 4 of Experiment 1 (i.e., there were no explicit intramaze cues).

Phase 2—Free Choice with Intramaze Cues Present. For 15 days the gerbils were permitted to choose among the arms as in the baseline conditions in Experiment 2.

Phase 3—Forced Choice. During each of 30 sessions the gerbils were given access (i.e., doors opened) to only one color of arm at a time. The order in which the colors were made available varied randomly from day to day. The gerbils were confined in the last chosen arm of a particular color for the few seconds it took to close one color of arm and open the next color of arm.

Phase 4—Free Choice. This phase, which lasted 5 days, was identical to Phase 2.

RESULTS AND DISCUSSION

Accuracy of arm choice during Phase 2 when explicit intramaze cues were present (average correct $M = 85.8$) exceeded that when those cues were absent during Phase 1 baseline ($M = 81.5$). This difference was significant [$F(1,5) = 22.2, p = .006$].

Comparison of free-choice accuracy during Phases 2 and 4 revealed that the intervening forced-choice procedure of Phase 3 had no overall facilitatory effect on correct choice (M Phase 2 = 85.8, M Phase 4 = 80.5).

If the addition of three brightness cues aided accurate performance by allowing the decomposition of the maze into smaller mazes (i.e., permitting "chucking" of arms into a "black," a "grey," and a "white" maze), the question arises as to whether the animals worked on one maze at a time or whether they simultaneously worked on several mazes. If they worked on one maze at a time, one would expect the gerbils to make sequences of choices of one level of brightness (e.g., six white choices in a row, six black choices in a row, etc.). Figure 6 shows that this was not the case, neither before nor after forced-choice training. This figure shows the number of times the gerbils chose the same brightness of arm in a row. On a large majority of cases one arm brightness was chosen only once before another arm brightness was chosen.

GENERAL DISCUSSION

The comparable performance of gerbils and rats, and their superiority to other species, may be used to evaluate the three general approaches, outlined in the introduction, that attempt to account for species differences in radial arm maze accuracy.

Although it is conceivable that rats and gerbils, like certain food-caching birds (Shettleworth, 1983) and unlike the other species tested in the maze, have good spatial memories that are adaptive specializations, there is no direct evidence that this is the case, nor is it by any means clear how such a specialization would have come about for these particular species.

At first glance the case appears stronger for an account based on phylogenetic scale. However, the poor performance of another member of the *Rodentia* order, the mouse, seems

Fig. 6. Percentage of times that each gerbil chose one, two, three, four, or five or more of the same type of arm in a row in Experiment 3.

troublesome for this interpretation. Nevertheless, caution must be exercised in concluding

that the CD-1 mouse is typical of the numerous strains of *Mus*.

Invocation of foraging ecology and strategies to account for maze performance also is not without problems. Although it is popular to classify species as food "generalists" or "specialists" in terms of breadth of diet (cf. Fleming, 1979), two other aspects of foraging ecology seem more relevant for predicting maze performance. The first is how food is spatially distributed in a niche and how the animal searches for it. One important distinction here is whether food is distributed in a uniform or patchy manner in the environment. The second distinction is whether the forager uses a "win-stay" strategy of returning to a patch in which food was recently found, or a "win-shift" strategy of avoiding such patches. Thus, it is believed that species that forage with a win-shift strategy in a patchy environment should do well in the maze relative to those species with "win-stay" strategies or those whose food is normally uniformly distributed in their niches. There are, however, several problems with this account of efficient maze performance.

The first problem concerns the notion of "patchiness." From the perspective of a human observer, the food supplies of all the species tested in the maze, and indeed of most species except perhaps of those like the baleen whales, are non-uniformly distributed. Neither the mosquito larvae preferred by the Siamese fighting fish (Roitblat et al., 1982), nor the seeds and fruits eaten by wild pigeons and doves (Goodwin, 1970), nor the various items of the omnivorous cosmopolitan pigeon (Goodwin, 1970) and omnivorous rodents (Landry, 1970) to our eye are uniformly available in these species' environments. However, patchiness is probably better approached from the perspective of the animal. Questions such as whether animals discriminate boundaries of patches as we do, whether patches are classified hierarchically (e.g., main patch, subpatch), and so forth seem in need of answers.

The picture is also complex when we consider search strategies. It seems unlikely that only a single foraging strategy would be available to a species. For example, for species whose food varies in a seasonal fashion, animals may return repeatedly to a large patch during early phases of harvesting but shift between patches as they become smaller and depleted. Also, if an animal categorizes a patch

hierarchically, the animal may be simultaneously both a win-stay forager, returning to the large patch, and a win-shift forager avoiding visited subpatches.

There are several further complications. Systematic, detailed observations of the foraging patterns of the wild forebears of the species studied in the radial arm maze are generally lacking. Even if such were available, several factors would complicate their extrapolation to the maze situation. The first is that foraging patterns in the wild are undoubtedly influenced by factors (e.g., presence of predators, territoriality, etc.) that are absent in the laboratory, and it is unknown how the relaxation of such influences might affect foraging. Members of several of the species studied in the maze have been domesticated for several generations and the influence of domestication (Boice, 1973) on the foraging strategies of these species is also largely unknown. However, Barnett, Dickson, Marples, and Radha (1978) found differences between wild and domesticated rats in patterns of visiting the four arms of a maze containing three types of food or nothing at the end of the arms.

Thus, we, like Gaffan and Davies (1981), have reservations about the utility of foraging concepts for models of spatial memory performance.

REFERENCES

- Barnett, S. A., Dickson, R. G., Marples, T. G., & Radha, E. Sequences of feeding, sampling and exploration by wild and laboratory rats. *Behavioural Processes*, 1978, 3, 29-43.
- Bitterman, M. E. Phyletic differences in learning. *American Psychologist*, 1965, 20, 396-410.
- Boice, R. Domestication. *Psychological Bulletin*, 1973, 80, 215-230.
- Bond, A. B., Cook, R. G., & Lamb, M. R. Spatial memory and the performance of rats and pigeons in the radial-arm maze. *Animal Learning & Behavior*, 1981, 9, 575-580.
- Dember, W. N., & Kleinman, R. Cues for spontaneous alternation by gerbils. *Animal Learning & Behavior*, 1973, 1, 287-289.
- Dennis, W. Spontaneous alternation in rats as an indicator of the persistence of stimulus effects. *Journal of Comparative Psychology*, 1939, 28, 305-312.
- Fleming, T. H. Life-history strategies. In D. M. Stodart (Ed.), *Ecology of small mammals*. New York: Wiley, 1979.
- Gaffan, E. A., & Davies, J. The role of exploration in win-shift and win-stay performance on a radial maze. *Learning and Motivation*, 1981, 12, 282-299.

- Goodwin, D. *Pigeons and doves of the world* (2nd ed.). London: British Museum, 1970.
- Kamil, A. C. Systematic foraging by a nectar-feeding bird, the amakihi (*Loxops virens*). *Journal of Comparative and Physiological Psychology*, 1978, **92**, 388-396.
- Landau, B., Gleitman, H., & Spelke, E. Spatial knowledge and geometric representation in a child blind from birth. *Science*, 1981, **213**, 1275-1278.
- Landry, S. O., Jr. The rodentia as omnivores. *Quarterly Review of Biology*, 1970, **45**, 351-372.
- Miller, G. A. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, 1956, **63**, 81-97.
- Mizumori, S. J. Y., Rosenzweig, M. R., & Kermisch, M. G. Failure of mice to demonstrate spatial memory in the radial maze. *Behavioral and Neural Biology*, 1982, **35**, 33-45.
- Nauman, D. J. Open field behavior of the Mongolian gerbil. *Psychonomic Science*, 1968, **10**, 163-164.
- O'Keefe, J., & Nadel, L. *The hippocampus as a cognitive map*. New York: Oxford University Press, 1978.
- Olton, D. S. Characteristics of spatial memory. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, N.J.: Erlbaum, 1978.
- Olton, D. S. Mazes, maps, and memory. *American Psychologist*, 1979, **34**, 583-596.
- Olton, D. S., Becker, J. T., & Handelmann, G. E. Hippocampus, space, and memory. *The Behavioral and Brain Sciences*, 1979, **2**, 313-365.
- Olton, D. S., Collison, C., & Werz, M. Spatial memory and radial arm maze performance of rats. *Learning and Motivation*, 1977, **8**, 289-314.
- Olton, D. S., & Samuelson, R. J. Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 1976, **2**, 97-116.
- Olton, D. S., & Schlosberg, P. Food-searching strategies in young rats: Win-shift predominates over win-stay. *Journal of Comparative and Physiological Psychology*, 1978, **92**, 609-618.
- Reichman, O. J. Factors influencing foraging in desert rodents. In A. C. Kamil & T. D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches*. New York: Garland Press, 1981.
- Restle, F. Discrimination of cues in mazes: A resolution of the "place-vs.-response" question. *Psychological Review*, 1957, **64**, 217-228.
- Roberts, W. A., & Dale, R. H. I. Remembrance of places lasts: Proactive inhibition and patterns of choice in rat spatial memory. *Learning and Motivation*, 1981, **12**, 261-281.
- Roitblat, H. L., Tham, W., & Golub, L. Performance of *Betta splendens* in a radial arm maze. *Animal Learning & Behavior*, 1982, **10**, 108-114.
- Roper, T. J., & Polioudakis, E. The behaviour of Mongolian gerbils in a semi-natural environment, with special reference to ventral marking, dominance and sociability. *Behaviour*, 1977, **61**, 207-237.
- Shettleworth, S. J. Memory in food-hoarding birds. *Scientific American*, March 1983, **248**, 102-110.
- Shettleworth, S. J., & Krebs, J. R. How marsh tits find their hoards: The roles of site preference and spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes*, 1982, **8**, 354-375.
- Spetch, M. L., & Wilkie, D. M. A program that simulates random choice in radial arm mazes and similar choice situations. *Behavior Research Methods & Instrumentation*, 1980, **12**, 377-378.
- Suzuki, S., Augerinos, G., & Black, A. H. Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation*, 1980, **11**, 1-18.
- Tolman, E. C. Cognitive maps in rats and men. *Psychological Review*, 1948, **55**, 189-208.
- Thiessen, D., & Yahr, P. *The gerbil in behavioral investigations*. Austin: University of Texas Press, 1977.
- Wilkie, D. M., Spetch, M. L., & Chew, L. The ring dove's short-term memory capacity for spatial information. *Animal Behaviour*, 1981, **29**, 639-641.
- Zoladek, L., & Roberts, W. A. The sensory basis of spatial memory in the rat. *Animal Learning & Behavior*, 1978, **6**, 77-81.

Received September 27, 1982

Final acceptance June 2, 1983