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Characteristics of Spatial Memory in Cattle*

D.W. BAILEY[1], L.R. RITTENHOUSE[1**], R.H. HART[2] and R.W. RICHARDS[3]

[1]*Department of Range Science, Colorado State University, Fort Collins, CO 80523 (U.S.A.),*
[2]*High Plains Research Center, USDA-ARS, Cheyenne, WY 82009 (U.S.A.),*
[3]*Department of Psychology, Colorado State University, Fort Collins, CO 80523 (U.S.A.)*

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ABSTRACT

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Two studies were conducted to examine spatial memory of cattle. In Study 1, six heifers were trained and observed in a radial- and parallel-arm maze at two levels of complexity. Grain was placed at the end of each arm, and heifers were released individually and allowed to choose arms freely until all grain was consumed. Incorrect choices occurred when heifers entered a previously entered arm. At the 4-arm level, the mean number of correct choices in the first four entrances was 3.83 and 3.60 for the radial and parallel mazes, respectively. At the 8-arm level, the number of correct choices in the first eight entrances was 7.78 and 7.36, respectively. Heifers were slightly more efficient ($P<0.05$) in the radial maze in which directional and distal cues were more pronounced.

In Study 2, two sets of monozygous twin steers were trained in a radial-arm maze using similar procedures as Study 1. The mean number of correct choices in the first eight entrances was 7.68. A variable delay interval was then imposed between Choices 4 and 5. Steers rarely made errors after delay intervals from 5 min to 4 h. Performance appeared to decline ($P<0.1$) after an 8-h delay interval. Accuracy declined dramatically ($P<0.001$) after a 12-h delay interval. The mean number of correct choices in the first eight entrances was 7.63, 7.29 and 5.80 for delay intervals of 4, 8 and 12 h, respectively. Cattle appear to have the ability to associate several locations with food resources and to remember the locations for periods of up to 8 h.

INTRODUCTION

Cattle prefer to graze in areas of high forage quantity and quality. Senft et al. (1985) found that the relative preference of cattle for short-grass plant communities was proportional to the biomass and nitrogen content of preferred plant species. Large herbivores appear to match the time spent in a plant

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**Author to whom correspondence should be addressed.

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community to the food resources found there (Senft et al., 1987). Factors such as topography and distance from water, salt and fences can modify livestock distribution (Mueggler, 1965; Cook, 1966; Senft et al.,1985).

Although the patterns in which livestock utilize habitats have been described, the mechanisms or individual behaviours that result in these patterns are not understood. Senft et al. (1987) suggested several hypotheses that might result in the matching pattern. Herbivores might turn more frequently and travel slower in more productive and nutrient-rich plant communities. Another possibility is that large herbivores remember where they grazed in the previous grazing bout, and simply return to areas of high resources and avoid areas of low resources. This hypothesis requires that herbivores have the ability to remember locations (spatial memory) and the resources found there.

Spatial memory of rats has been studied in radial-arm mazes (Olton, 1977, 1978). Rats perform very efficiently and little training is required (Olton and Samuelson, 1976). The spatial memory of rats was accurate after delays of up to 8 h (Beatty and Shavalia, 1980). Spatial memory of pigeons in radial mazes is comparable to that of rats (Roberts and Van Veldhuizen, 1985). Cattle can solve simple spatial discriminations. Heifers quickly learned which side of a modified T maze contained grain (Kovalcik and Kovalcik, 1986). Under range conditions, foraging decisions are likely to involve several choices. There is little literature on the ability of livestock to solve complex spatial tasks.

Two studies were conducted to examine the spatial memory of cattle. In Study 1, the performance of heifers was evaluated in radial- and parallel-arm mazes at two levels of complexity. In Study 2, the time course of spatial memory was examined in a radial-arm maze.

MATERIALS AND METHODS

Study 1

Six Hereford×Holstein crossbred heifers were trained and observed in a radial-arm maze and later in a parallel-arm maze. Heifer performance was compared between two types of mazes. Mazes were constructed from electric fence, and were located in a pasture composed of crested wheatgrass (*Agropyron desertorum*), bindweed (*Convolvulus arvensis*) and rabbitbrush (*Chrysothamnus nauseosus*).

The radial-arm maze consisted of a center or decision area and 2–8 arms (Fig. 1). The decision area was 25.0 m in diameter and the arms were 37.5 m in length. Opaque feeders were placed at the end of each arm. On every trial, 0.2 kg of grain mix was placed in every feeder. A trial consisted of introducing one heifer into the decision area and allowing the animal to choose arms freely until all the grain was consumed or a time limit was exceeded. After all the grain was consumed, the heifer was herded out of the maze and the trial ended.

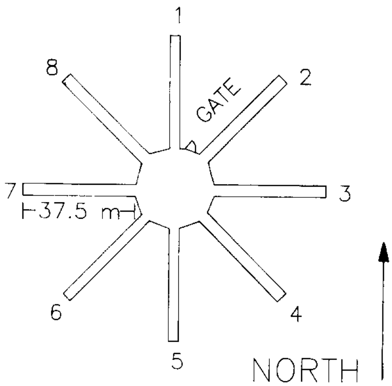

Fig. 1. Diagram of radial-arm maze.

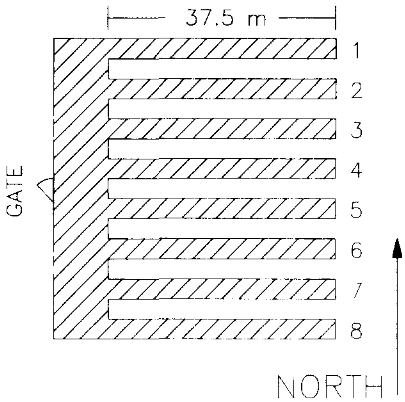

Fig. 2. Diagram of parallel-arm maze.

The other five heifers were kept in a holding pen near the maze during a trial. Each heifer was placed in the maze (one trial) 5–6 times per week. The order in which heifers entered the maze was randomized.

The time limit was based on the number of arms selected by the heifer and calculated by multiplying the number of choices by 5 min and adding an additional 5 min. When the time limit was exceeded, the observer herded the heifer into an arm still containing grain if she was stalled in the decision area. If the heifer was stalled in an arm, the observer started the heifer moving and avoided influencing her choice. Scoring under these circumstances is described below.

During initial training, only two arms were available. A new arm was added and performance evaluated at that level after a trial in which a heifer entered all available arms without assistance. When an animal had been trained to the 4-arm level, 5 trials per animal were performed and scored in the maze. Arms 1, 3, 5 and 7 were available at this level (Fig. 1). Training continued until the 8-arm level was reached and heifers were evaluated at this level until the end of the radial-arm maze portion of the study.

Responses used to evaluate performance were the number of correct choices within the first four or eight entrances (4- or 8-arm level, respectively), non-assisted choices, assisted choices, pushes and false starts. A correct choice occurred when an animal entered a previously unentered arm without assistance and consumed the grain. Heifers made mistakes when they entered an arm where the grain had been consumed. When the observer guided the heifer in the decision area toward an arm containing grain, the choice was recorded as assisted. If the observer started the heifer moving, but did not enter the decision area or guide it toward any arm, a push was recorded. Since every effort was made to avoid influencing the heifer's selection, the subsequent choice was termed non-assisted. A false start occurred when heifers freely entered, but traveled less than 1/3 the length of an arm before returning to the decision area. This was not considered as a choice or classified as an arm entrance.

When the evaluation of heifers in the radial-arm maze was completed, a parallel-arm maze was constructed (Fig. 2). The decision area was 6 m wide and 21, 33 or 45 m long for the 4-, 6- and 8-arm mazes, respectively. All arms were 37.5 m long and identical to those in the radial-arm maze.

The procedure on each trial and the variables recorded were identical to the radial-arm maze experiment. Only 4, 6 or 8 arms were used in the parallel-arm maze. Five trials per heifer were given for each size of maze. All six heifers were kept in each of the three levels of the maze for 4–6 h prior to any trials. The purpose was to familiarize the animals to new arms and to graze excess crested wheatgrass and bindweed. To minimize the chance of animals using grain odor as a cue for arm selection, additional grain was placed in an open container at the end of each arm behind the feeder and out of reach of the heifer.

Comparison of performance in the radial- and parallel-arm maze was confounded by two factors, i.e., experience in mazes and animal effects. In the 8-arm radial maze, most of the observations came from three heifers. To account for animal effects and to pool data from 4- and 8-arm levels, a sign test (Conover, 1980) was used to compare radial- and parallel-arm maze performance. Data were paired using animal, level and number of trials at a level.

The response pattern or sequence of arm choices in the radial maze was analyzed by examining the number of arms separating successive choices. This analysis is not appropriate for the parallel-arm maze because the possible number of arms separating successive choices depends on an animal's location within the maze. In the parallel maze, a Spearman's rank correlation coefficient was used to compare the sequence of arm selections in successive trials. Arm numbers were used as ranks and incorrect choices were ignored. This analysis gives some indication of the similarity of choice sequences. This analysis is not appropriate for the radial-arm maze because arm numbers do not represent distance of separation.

Study 2

Two sets of monozygous twin yearling steers were trained in a radial-arm maze. One set was Angus×Hereford and the other set was Barzona×Hereford. The maze was similar to the radial arm maze in Study 1, except that the gate was located between arms 3 and 4. This maze was constructed in a Russian wildrye (*Elymus junceus*) pasture without shrubs.

Initial training, variables observed and time limits were similar to Study 1. Initial training began with 4 arms and new arm were added two at a time. Performance was evaluated with 8 arms. Three steers were evaluated for 7 trials and Steer 15B was evaluated for 10 trials. Steer 15B did not adapt quickly to spending long periods of time in the maze. After this portion of the study, each steer was herded out of the maze between Choices 4 and 5 for a delay period. The delay interval was increased progressively from 5 min to 12 h. Three steers were evaluated for 2, 2, 3, 4, 4, 4, 5, 5 and 5 trials at delay intervals of 0.08, 0.17, 0.25, 0.5, 1, 2, 4, 8 and 12 h, respectively. Steer 15B was not evaluated at a delay interval of 12 h and only two trials were given for the 8-h delay. When the steers were herded out of the maze, 0.2 kg of grain was provided in the lane between the holding pen and maze. After the grain was consumed, steers were returned to the holding pen for the delay interval. When delays exceeded 15 min, arms were reloaded and other steers were released into the maze. Feeders were emptied or filled so that the configuration of empty and full feeders was exactly as the steer had left it. Visual barriers were established around the holding pen to prevent animals from observing feeders being filled or emptied.

Performance at delays of 0.5, 1, 2, 4, 8 and 12 h was compared to performance with no delay using a sign test (Conover, 1980). Data were paired using animal and number of trials at a delay period.

RESULTS

Study 1

The amount of initial training required varied among heifers. Three heifers required 6 trials before the number of arms in the radial maze was increased to three. One heifer required 9 trials and two heifers required 17 trials. The

TABLE 1

Mean and median performance of heifers in 4-arm radial and parallel mazes[a]

Item	4-arm level		8-arm level	
	Radial	Parallel	Radial	Parallel
Correct choices in first 4 or 8 entrances[b]	3.83	3.60	7.78	7.36
Total non-assisted incorrect choices	0.07	0.33	0.26	0.86
Assisted choices	0.10	0.10	0.04	0.11
Pushes	0.03	0.13	0.00	0.25
False starts	0.07	0.13	0.04	0.25

[a]Total of correct, incorrect and assisted choices may exceed 4 or 8 if multiple incorrect choices occurred in any trial.
[b]The number of arms that would be entered correctly by chance alone would be 3.1 (calculated using methods presented by Beatty and Shavalia, 1980) and 5.3 (Olton, 1978) for the 4- and 8-arm levels, respectively.

TABLE 2

Arm choice sequences and the correlation coefficient between choice sequences of adjacent trials of Heifers 2 and 6 in the 8-arm parallel maze

Heifer	Trial	Arm choice sequence	Correlation coefficient[a]
Heifer 2	1	4 2 5 7 6 4 2 1 8 5 1 3	
	2	4 6 7 3 1 2 3 5 8	−0.14
	3	4 2 1 6 7 8 5 3	−0.88
	4	4 2 1 7 5 3 1 8 6	0.43
	5	4 1 2 7 5 3 8 6	0.98
Heifer 6	1	5 7 8 6 4 3 2 1	
	2	5 3 2 7 8 6 4 2 1	0.05
	3	5 3 1 8 6 7 8 4 2	0.90
	4	4 2 6 7 8 5 3 1	0.54
	5	5 7 3 1 2 4 8 6	−0.88

[a]Spearman's rank correlation between arm choice sequences from successive trials. Arm numbers (Fig. 2) were used as ranks and repeats (mistakes) were ignored.

TABLE 3

Correct choices in the first eight entrances by steers in an 8-arm radial maze with delay intervals of 0, 2, 4, 8 and 12 h between Choices 4 and 5[a]

Item	Delay interval (h)						
	0	0.5	1	2	4	8	12
Mean	7.68	7.81	7.75	7.68	7.63	7.29	5.80
Median	8	8	8	8	8	7[b]	6[c]
Range	4–8	6–8	7–8	6–8	6–8	6–8	5–7

[a]There were no incorrect responses by steers in Choices 1-4.
[b]The median value was different ($P = 0.008$) from the median value from the 0-h delay interval.
[c]The median value was different ($P < 0.001$) from the median value from the 0-h delay interval.

number of trials required before a new arm was added was similar among heifers after the 3-arm level (Bailey et al., 1987).

Heifers performed very efficiently in both the radial- and parallel-arm mazes at the 4-arm level (Table 1). The median number of correct choices in the first four entrances was 4 (range 3–4) for both the radial- and parallel-arm mazes. There were few assisted choices, pushes or false starts. The four heifers which reached the 8-arm level in the radial maze performed very efficiently (Table

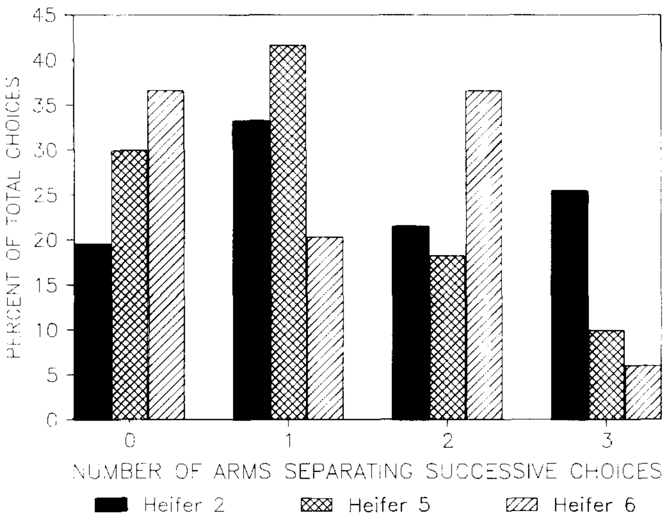

Fig. 3. Percent of successive choices by heifers in the 8-arm radial maze that were separated by 0, 1, 2 and 3 arms. If no arms separated successive choices, the heifer chose adjacent arms. If three arms separated successive choices, the heifer went directly across the maze on successive choices.

1). The median number of correct choices in the first eight entrances was 8 (range 7–8) and 7 (range 6–8) for the radial- and parallel-arm mazes, respectively. After pooling the results from the 4- and 8-arm levels, the number of correct choices in the first four and eight entrances was less ($P < 0.05$) in the parallel-arm than in the radial-arm maze. Heifers required more ($P < 0.05$) non-assisted choices to consume all the grain in the parallel-arm than in the radial-arm maze (4- and 8-arm levels pooled).

The response patterns in 8-arm radial and parallel mazes varied among heifers. In the radial-arm maze, 29, 31, 25 and 14% of successive choices were separated by 0, 1, 2 and 3 arms, respectively (Fig. 3). Correlation coefficients calculated on the sequence of arm choices on successive trials for each heifer in the parallel maze ranged from -0.88 to $+0.98$. Both extremes of the range were from Heifer 2 (Table 2).

Study 2

Three steers required 11 days of initial training. Steer 15B required 17 days of initial training. With no delay between Choices 4 and 5, the average number of correct choices in the first eight entrances was 7.68. The average numbers of unassisted choices, assisted choices, pushes and false starts were 8.19, 0.23, 0.87 and 0.1, respectively. Most of the required assistance was for Steer 15B. It required an average of 8.7 unassisted choices, 0.6 assisted choices and 2.4 pushes.

Steers performed accurately for delay intervals of up to 4 h (Table 3). Steers made no errors in Choices 1–4 for any of the delay intervals. When compared to performance with no delay, the number of correct choices in the first eight entrances was lower ($P=0.08$) after an 8-h delay and was dramatically lower ($P<0.001$) after a 12-h delay. There was no difference ($P>0.05$) between a 0-h delay and delays of 0.5, 1, 2, 4, 8 and 12 h for the median numbers of assisted choices and false starts. There were less ($P=0.032$) pushes with a 2-h delay than with no delay. There were no differences ($P>0.05$) in the number of pushes between a 0-h delay and the other delay intervals. Steer 15B accounted for most of the pushes with no delay and generally required less pushes as the study progressed.

As animals went through trials with increasing delays, their behavior appeared to change. Most of the change in behavior occurred during the pre-delay phase (Choices 1–4). By the time animals reached trials with delays of 4 h, three of the four steers appeared to adopt a strategy of choosing four adjacent arms during the pre-delay portion of a trial. Such a strategy would simplify the task during the post-delay phase. During Choices 1–4, adjacent arms accounted for 50 and 74% of successive choices for the 0- and 4-h delay trials, respectively. During subsequent choices (5+), adjacent arms accounted for 39 and 50% of the successive choices for the 0- and 4-h delay trials, respectively.

DISCUSSION

Both heifers and steers performed as efficiently as other species which have been tested in an 8-arm radial maze. Rats and pigeons made 7.6 and 7.1 correct choices in eight entrances, respectively (Olton and Samuelson, 1976; Roberts and Van Veldhuizen, 1985). Without a delay interval, a value of 5.3 correct choices in eight entrances would be expected by chance (Olton, 1978). Only in one trial, did a steer (15B) perform less than expected by chance.

Performance in the parallel maze was slightly less efficient, even though the heifers had more experience with maze tasks. Learning the parallel maze is generally more difficult for rats than is learning the radial maze (Staddon, 1983). The difficulty is attributed to the proximities and similar directions of the arms.

The efficient performance in the radial and parallel mazes indicates that cattle have an accurate spatial memory. However, there are alternative explanations that should be considered. Cattle could use olfactory cues such as grain odor or scent markings to determine which arm to enter. We attempted to control for any effect of grain odor by placing grain behind the feeder and out of reach of the animal. Performance remained high regardless of wind direction and speed. In Study 2, steers would have had to distinguish their scent mark from that of other steers in the maze during the delay interval. On one occasion, trials were conducted in the rain and 15 mm of precipitation fell during the delay interval. Performance of the steers remained well above expected chance levels. Cattle do not have interdigital scent glands (sinus interdigitalis) as do sheep (Dyce et al., 1987). Another possible explanation for success is the use of a simple rule such as choose the next arm to the left. The response patterns observed for both steers and heifers did not indicate any such rule. Each heifer in the radial maze was observed entering arms separated by 0, 1, 2 and 3 arms on successive choices. Steers tended to choose adjacent arms more frequently than did the heifers, but there was still variability in the number of arms separating successive choices. The size of the decision area can affect the sequence of arm choices. Yoerg and Kamil (1982) found that rats chose adjacent arms more frequently when the decision area was large, but accuracy was not affected. The sequence of choices by heifers in the parallel maze varied between trials. It is unlikely that any simple rule would result in such a variable response pattern.

Visual stimuli were probably the primary cues for arm selection. Olton and Samuelson (1976) reported that rats did not use intramaze cues, and visual stimuli outside the maze were used to identify and remember visited arms. Accuracy was slightly higher in the radial maze where distal and directional cues were more pronounced.

The time course of spatial memory in steers was similar to that observed for rats (Beatty and Shavalia, 1980). Steers were very efficient during the initial delays of 5, 10 and 15 min, and no additional training was required. With a delay between Choices 4 and 5, 5.8 correct choices in eight entrances would be expected by chance (Beatty and Shavalia, 1980). Performance exceeded 5.8 for all trials with delay intervals of 5 min–8 h. The dramatic drop in performance for the 12-h delay interval may result from failure of memory or from confusion between trials. With long delays, steers may not have been able to distinguish whether they were beginning a new trial or completing a previous trial. Choices 5, 6 and 7 were often the same as Choices 1, 2 and 3 during trials with a 12-h delay interval. During the latter stages of Study 2, three steers may have been using a strategy of selecting adjacent arms for Choices 1–4 which would reduce the number of arms to be stored in memory and simplify the task. Such a strategy might be adaptive under natural conditions when the number of locations to be stored in memory would be large.

Cattle appear to have the ability to remember where they have foraged for periods of at least 8 h. Most grazing or resting bouts last <8 h (Low et al., 1981). Our studies suggest that cattle could either return to or avoid an area grazed during a previous bout by utilizing memory. Further studies are needed to test whether cattle are using memory for the selection of areas in which to graze.

REFERENCES

Bailey, D.W., Rittenhouse, L.R., Hart, R.H. and Richards, R.W., 1987. Spatial memory of heifers in radial- and parallel-arm mazes. Proc. West. Sec. Am. Soc. Anim. Sci., 38: 7–10.

Beatty, W.M. and Shavalia, D.A., 1980. Spatial memory in rats: time course of working memory and effects of anesthetics. Behav. Neural Biol., 28: 454-462.
Conover, W.J., 1980. Practical Nonparametric Statistics. 2nd Edn., Wiley, New York.
Cook, C.W., 1966. Factors affecting utilization of mountain slopes by cattle. J. Range Manage., 19: 200-204.
Dyce, K.M., Sack, W.O. and Wensing, C.J.G., 1987. Textbook of Veterinary Anatomy. Saunders, Philadelphia, PA, 820 pp.
Kovalcik, K. and Kovalcik, M., 1986. Learning ability and memory testing in cattle of different ages. Appl. Anim. Behav. Sci., 15: 27-29.
Low, W.A., Tweedie, R.L., Edwards, C.B.H., Hodder, R.M., Malafant, K.W.J. and Cunningham, R.B., 1981. The influence of environment on daily maintenance behaviour of free-ranging Shorthorn cows in central Australia. I. General Introduction and descriptive analysis of day-long activities. Appl. Anim. Ethol., 7: 11-26.
Mueggler, W.F., 1965. Cattle distribution on steep slopes. J. Range Manage., 18: 255-257.
Olton, D.S., 1977. Spatial memory. Sci. Am., 236: 82-98.
Olton, D.S., 1978. Characteristics of spatial memory. In: S.A. Hulse, H. Fowler and W.K. Honig (Editors), Cognitive Processes in Animal Behavior. Erlbaum, Hillsdale, NJ, pp. 341-373.
Olton, D.S. and Samuelson, R.J., 1976. Remembrance of places passed: spatial memory in rats. J. Exp. Psychol. Anim. Behav. Processes, 2: 97-116.
Roberts, W.A. and Van Veldhuizen, N., 1985. Spatial memory in pigeons on the radial maze. J. Exp. Psychol. Anim. Behav. Processes, 11: 241-260.
Senft, R.L., Rittenhouse, L.R. and Woodmansee, R.G., 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. J. Range Manage., 38: 82-87.
Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. BioScience, 37: 789-799.
Staddon, J.E.R., 1983. Adaptive Behavior and Learning. Cambridge University Press, New York, 555 pp.
Yoerg, S.I. and Kamil, A.C., 1982. Response strategies in the radial arm maze: Running around in circles. Anim. Learn. Behav., 10: 530-534.