**INTRODUCTION**

The importance of spatial memory in locating food by animals is well documented (Bailey et al., 1987; Howery et al., 1999; Kovalcick, 1984; Laca, 1995; Olton et al., 1977). In a grazing context, understanding such memory may help prevent uneven grazing distribution. Spatial memory is the ability of organisms to orient their behaviour on the basis of previous experience with a specific spatial pattern of external stimuli (Staddon and Ettinger, 1989). Howery et al. (1999) defined spatial memory in a grazing behaviour context as “the ability of an animal to remember where it has foraged and use the information to determine where it will travel and forage”. Spatial memory could either be long-term (reference memory) or short-term (working memory). Reference memory is used to complete successive tasks, while working memory is used for a particular task, after which the information becomes unnecessary (Howery et al., 1999). It is spatial memory that allows animals to orient behaviour with respect to a location or object that provides no immediate stimulus whatsoever (e.g., it is out of sight). The orientation is based on a map-like representation of the position of the object in relation to other stimuli, and on the recognition of the organism’s current position in relation to the same stimuli. Spatial memory can be important to increase the efficiency of locating preferred food patches. When using spatial memory, livestock can spend less time searching for feed and more time foraging.

The core of the present study was to test the duration of spatial memory using an 8 row by 8 column-grid of plastic containers. In traditional mazes, animals return to the same decision area before making a choice for a particular arm. All arms have the same chance of being chosen at any given time. In real environments, animals search for food in 2 or 3 dimensions and do not need to return to any decision areas. The protocol we use is similar to the one used by Edwards et al. (1997) and Laca (1995). The present protocol uses a more realistic testing area for long-term spatial memory. Steers would enter the paddock where the plastic containers were located and try to find a specific set of containers with feed.

The purpose of this experiment was to test the ability of the steers to use their spatial memory to remember the location of food. While previous studies (Bailey et al., 1989; Willson and Wilkie, 1993) focused on short-term memory, this experiment deals with long-term or reference memory. This study emphasised the duration of spatial memory of steers. The hypothesis was that steers would learn and then forget the location of food as time since last experience passes.

**MATERIALS AND METHODS**

**Experimental arena**

The experimental arena consists of two 55 by 55 meter paddocks. Each paddock contained an 8 row by 8 column grid of plastic containers 5 meters apart. The use of 2 paddocks was only to minimise testing time. The area was dominated by Old-World bluestems (Bothriochloa spp.). This experiment was conducted at the Texas Tech Experimental Ranch, Justiceburg, Texas USA, from 7 June
to 19 October 1994.

Animals

Six steers were used to conduct this experiment. The average weight was about 400 kilograms. The steers were grazing an Old-World-bluestem pasture when not tested. They were grazing with 4 other steers in the herd. Water was available *ad libitum*. The steers were fed 25 kg of supplemental feed every other day. The experimental protocol and animal handling and use were approved by the Texas Tech University Animal Care and Use Committee.

Treatments

In order to test our hypothesis, steers were trained to find containers with feed (loaded containers) in 4 constant locations. An initial training was performed before applying treatments to each steer. Five treatments were tested. The first treatment was a control. Animals in this treatment were tested immediately after the initial training. The other 4 treatments tested 5, 10, 20 and 48 days since last experience. Each of the steers was used for all five combinations. First, all six possible combinations of the 5 day, 10 day, and 20 day treatments were observed. For instance, steer no. 1 was tested for the 5 day, 10 day and then 20 day treatments, respectively; steer no. 2 was tested for 5 day, 20 day and 10 day treatments, respectively and so on. Consequently six steers were needed to observe all six combinations. The 48 day treatment was added at a later stage for all six steers.

Training

All steers were trained initially before starting the experiment. These steers were very familiar with this protocol and were previously used in the same arena in similar trials. They were trained 11 times each, over a 3 day period. Training was also done after the first testing session on each testing day. The purpose of these training sessions was to make the steers remember well the location of the four loaded containers. Each steer had a different combination of four loaded containers out of the 64 container-grid. The combination for each steer was kept the same for the whole experiment. Steers were allowed to locate their combination of 4 loaded containers until they found them all. At that time, the training session was terminated and the animal was let out of the experimental paddock. A Hand full of feed pellets was placed under each of the 64 containers to prevent the animals from finding food on the basis of odour. These feed pellets could not be seen nor eaten, they were out of reach of animals.

Testing

A calendar was established to plan the testing dates for each steer. At each testing day, a steer was allowed to locate its combination of 4 loaded containers. A testing session was stopped when the steer found all four loaded containers. At each testing day, except for the 48 day treatment, steers were allowed to locate the loaded containers 5 times. The first time was considered testing and the other 4 times were considered training. Again, feed pellets were placed under each container to control for smell.

Measured variables

All training and testing sessions were entirely observed. At each training and testing day, a map of the paddocks was used to record data. The maps represented the location of all containers including the loaded ones. Every time a steer was tested, the path followed was drawn and containers visited were marked. At the side of the map, a table was used to record time at start of each session, time spent at each loaded container and time at end of each session.

Calculated variables

Number of containers visited was referred to as NC, loaded containers visited was referred to as LC, and total visits (including revisits) is referred to as TV. Two ratios were calculated to test working and reference memory. Working memory was tested using the ratio of NC over TV (NCTV). Reference memory was tested using the ratio of LC over NC (LCNC). A Z test was performed to test if searching for food by animals can was at random or based on behavioural mechanisms (Tillié et al., 1996). Distance walked was digitally estimated after paths followed by steers during testing were scanned.

Experimental design and analysis

The experiment allows two means of assessing the duration of spatial memory. First, compared the performance of steers in relation to their maximum performance achieved immediately before they started the treatment period of no exposure to the food distribution was compared. This comparison uses each animal as its own control and removes potential differences due to differences in prior experience of individual animals. The test focuses on whether any decline in performance can be detected as the decay period between training and testing increases. Second, the average performance of each steer against the performance expected if steers visited food containers in a random order, ignoring containers already visited within each session (no replacement) was compared. This test aims at detecting the length of time necessary for memory to decay until performance cannot be distinguished from random chance. Although this test does not use each animal as its own control, we were statistically conservative in extrapolating to other steers. By using animals as replicate and ignoring the different sequence of treatments to which animals were exposed, effects of sequence of total number of exposure (table 1) appear as error and prevent inflation of
the power of the test. In any case, the average (across steers) number of exposures was the same for the 3 intermediate treatments (table 1) and very similar to that for the 48 day treatment.

A completely randomised design was used to analyse the data (SAS 1985). A test for normality and homogeneous variances was performed to assess the validity of using an F-test to compare treatments. Dunnett’s t test (SAS 1985) was performed to compare the control treatment to each of the other four treatments.

RESULTS AND DISCUSSION

Steers remembered the location of food containers for up to 48 days post training (table 2). The analysis is discussed for each variable separately.

Total visits or TV was transformed to its logarithm base 10 (LTV). Treatments did not affect LTV p>0.05 (table 2). The 48 day treatment had the highest value of 0.80. However, the control treatment was not significantly different when compared to each of the other four treatments p>0.05. The number of days since last experience did not alter the number of visits made to locate the loaded containers.

The variable NC was also transformed to its logarithm base 10 (LNC) because it did not have homogeneous variances. Treatment did not affect LNC at p>0.05 (table 2). Steers in all treatments visited the same number of containers as the control.

The ratio NC/TV did not have homogeneous variances. For that reason, it was transformed to its square root (SNCTV). There was no treatment effect on the SNCTV p>0.05 (table 2). A perfect score was observed for the 10 day and 48 day treatments (1.0 for each of the treatments). Steers in these two treatments did not revisit any of the previously located containers. The ratio gives us an idea about their working memory. Because of the absence of treatment effect, all treatments did well in avoiding previously visited locations. This is a mechanism that can be used by grazing animals in rangelands. Grazing animals could use their working memory to save the energy of visiting recently depleted areas. Avoiding the depleted areas increases their chances of encountering non-depleted food patches, and therefore increases their foraging efficiency.

A Z test was used to test if NC/TV was better than expected by chance. The Z test was not different between the control and each of the other treatments p>0.05 (table 2). However, animals in all treatments did better than expected by chance (Tillié et al., 1996). The average Z value for each treatment was compared to a Z table of 1.64 (figure 1). The value of 1.64 is the limit under which a performance can be expected by chance assuming a random search without replacement. The lowest Z value was observed for the 48 day treatment (6.42), and the highest was observed for both the 10 and the 20 day treatments (7.64 for each treatment).

The ratio LC/NC did not have homogeneous variances and therefore was transformed to its square root (SLCNC). Again, treatments did not affect SLCNC p>0.05 (table 2). The highest value was observed in the 10 day and 20 day treatments with an average of 0.96. Each of the treatments when compared to the control had similar SLCNC.

Table 1. Number of times steers were exposed to feed containers for each treatment: right after training (treatment 0), 5, 10, 20 and 48 days since last encounter

| Treatment | Steer ID | 2R | 25R | 53R | 61W | 61R | 74R | Avg. |
|-----------|---------|----|-----|-----|-----|-----|-----|------|
| 0 (Control) |         | 11 | 11  | 11  | 11  | 11  | 11  | 11   |
| 5         |         | 21 | 16  | 16  | 26  | 26  | 21  | 21   |
| 10        |         | 26 | 21  | 26  | 16  | 21  | 16  | 21   |
| 20        |         | 16 | 26  | 21  | 21  | 16  | 26  | 21   |
| 48        |         | 28 | 28  | 28  | 28  | 28  | 28  | 28   |
| Total     |         | 102| 102 | 102 | 102 | 102 | 102 | 102  |

Table 2. The performance of steers (N=6) right after training (treatment 0), 5, 10, 20 and 48 days since last encounter

| Treatment | LTV | LNC | Z Value | SNCTV | SLCNC | LTD |
|-----------|-----|-----|---------|-------|-------|-----|
| 0 (Control) | 0.74 | 0.70 | 7.09 | 0.96 | 0.90 | 1.60 |
| 5         | 0.78 | 0.73 | 6.85 | 0.94 | 0.87 | 1.72 |
| 10        | 0.63 | 0.63 | 7.64 | 1.00 | 0.96 | 1.55 |
| 20        | 0.66 | 0.63 | 7.64 | 0.97 | 0.96 | 1.49 |
| 48        | 0.80 | 0.80 | 6.42 | 1.00 | 0.83 | 1.60 |

1 LTV: Logarithm base 10 of Total Visits; LNC: Logarithm base 10 of New Containers; Z value: a Z test for randomness of ratio of New Containers per Total Visits; SNCTV: Square Root of ratio New Containers per Total Visits; SLCNC: Ratio of Loaded Containers per New Containers.

Figure 1. The effect of days since last experience on randomness of finding food by steers using a Z test. A Z value below 1.64 (solid line) indicates a random search. Vertical lines indicate standard error.
treatments were similar to the control in their efficiency of finding the loaded food containers. Their success of encountering loaded containers per container visited was the same. Length of delay since last experience did not affect their success rate.

The distance walked was transformed to its base 10 logarithm (LTD) because the original data did not meet the analysis of variance assumption of homogeneous variance. To locate the loaded containers, steers travelled the most in the 5 day treatment (table 2). However, the control was not significantly different from any of the other four treatments p>0.05. Steers walked the same distance to locate the food containers despite the length of period since last experience. In other words, grazing animals would walk similar distances to locate preferred food patches, regardless of delay since last experience.

The present study showed that cattle can remember the location of preferred food for long periods (up to 48 days). This agrees with a study done by Kovalcick and Kovalcick (1986), where 77% of cows and 46% of heifers performed well, after six weeks of interruption. However, these results are different from the findings by Bailey et al. (1989). The authors studied the length of periods that cattle remembered food locations. They found that cattle remembered the location of food for 8 h. It is important to state that this study and that of Bailey et al. (1989) tested two distinct aspects of spatial memory. The present study investigated long-term spatial memory and Bailey and his colleagues studied short-term spatial memory. Memory decay has also been studied for rats by Beatty and Shavalia (1980). Their findings agree with those reported here in the sense that animals have efficient spatial memory. Moreover, Shettleworth and Krebs (1982) reported the efficiency of seed recovery from recently visited locations. Short-term spatial memory, however, was tested in their protocol.

Days since last experience did not alter the number of visits made to locate the loaded containers. Animals did not locate food at random. They used some mechanism to be efficient. Spatial memory was assumed to have played a prominent role. The initial intention was to use these results to manipulate the length of resting periods in grazing methods. Such information would have been incorporated as a decision tool on the length of non-use of plant communities. Animals would forget where preferred food was, and therefore start a new searching pattern, leading to a more uniform grazing distribution.

**IMPLICATIONS**

Animals learn preferred food locations based on past experience, among other factors (Valentine, 1990). Limiting the ability of the animal to learn spatial characteristics of areas grazed may be efficient in improving the distribution pattern. Laca (1995) suggested to frequently move the animals among grazing units. A grazing method that includes shorter utilisation periods may be a practical scheme. Cost involved could be a major disadvantage. Long non-use periods, however, cannot be incorporated into most grazing methods. Nevertheless, the duration of spatial memory may be much longer than the 48 day-period tested. Our field observations suggest that cattle may remember the location of food for months. Besides limiting the learning process of herbivores, we suggest using rewards as a tool to promote uniform grazing.

It is believed that the reward of visiting a food location may affect the learning abilities of animals. Hosoi et al. (1995) reported that it may be more important for cattle to remember how they failed than to remember how they succeeded. Training livestock to expect high rewards can be used to promote grazing distribution (Laca, 1995). It was also suggested by Laca (1995) to place supplemental feed in different locations. This would increase the evenness of the distribution of the animals and help increase their reward expectations. Not having a definite duration of spatial memory in cattle is an important outcome of the present study. Future research should therefore shift the focus to other fields of grazing behaviour, in order to promote uniform grazing distribution.

**REFERENCES**

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

Bailey, D. W., L. R. Rittenhouse, R. H. Hart and R. W. Richards. 1989. Characteristics of spatial memory in cattle. Appl. Anim. Behav. Sci. 23:331-341.

Beatty, W. M. and D. A. Shavalia. 1980. Spatial memory in rats: time course of working memory and effects of anesthetics. Behav. Neural Biol. 28:454-462.

Edwards, G. R., J. A. Newman, A. J. Parsons and J. R. Krebs. 1997. Use of cues by grazing animals to locate food patches: an example with sheep. Appl. Anim. Behav. Sci. 51:59-68.

Hosoi, E., D. M. Swift, L. R. Rittenhouse and R. W. Richards. 1995. Comparative foraging strategies of sheep and goats in a T-maze apparatus. Appl. Anim. Behav. Sci. 44:37-45.

Howery, L. D., D. W. Bailey and E. A. Laca. 1999. Impact of Spatial Memory on Habitat Use. In: Grazing Behaviour of Livestock and Wildlife (Ed. K. L. Launchbaugh, K. D. Sanders and J. C. Mosley). Idaho Forest, Wildlife and Range Exp. Sta. Bull. #70. pp. 91-100.

Kovalcick, K. and M. Kovalcick. 1986. Learning ability and memory testing in cattle of different ages. Appl. Anim. Behav. Sci. 15:27-29.

Laca, E. A. 1995. Spatial memory and foraging efficiency of cattle. Abstr., 48th Annual meeting. Soc. Range Manage., 1995, Phoenix, AZ.

Olton, D. S., C. Collison and M. A. Werz. 1977. Spatial memory and radial arm maze performance of rats. Learn. Motiv. 8:289-
SAS Institute Inc. 1985. SAS user’s guide: Statistics. Cary, NC 27511-8000. p. 956.

Shettleworth, S. J. and J. R. Krebs J.R. 1982. How marsh tits find their hoards: The roles of site preference and spatial memory. J. Exp. Psy. 4:354-375.

Staddon, J. E. R. and R. H. Ettinger. 1989. Learning: An Introduction to the Principles of Adaptive Behaviour. Harcourt Brace Jovanovich, San Diego, p. 436.

Tillé, Y., J. A. Newman and S. D. Healy. 1996. New tests for departures from random behaviour in spatial memory experiments. Anim. Learn. Behav. 24:327-340.

Valentine, J. F. 1990. Grazing Management. Academic Press, Inc. San Diego, p. 533.

Willson, R. J. and D. M. Wilkie. 1993. Pigeons remember briefly trained spatial location-food associations over extended time periods. J. Exp. Psychol. 19:373-379.