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Sequential Analysis of Cattle Location: Day-to-Day Movement Patterns*

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ABSTRACT

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Studies were conducted in Texas and Colorado to determine if there were consistent movement patterns of grazing cattle. Based on optimal foraging theory, we hypothesized that cattle would select the same area of a pasture to graze for several days in a row. In the Colorado study, the location of cattle was observed each morning for 6 weeks. The 50-ha pasture was separated into 10 sections. The calculated number of cattle that moved from one section to another was analyzed using a transition matrix. Cattle were rarely observed in the same section of the pasture on two successive mornings. In the Texas study, the location of cattle after they began grazing was observed each morning for eight seasonal trials lasting 6-15 days. The 248-ha pasture was divided into 63 units based on plant community, slope, aspect, elevation and distance from water. Cluster analysis was used to group these units into five separate areas. Clusters were based on the amount of grazing in each unit during the trials. The number of cattle that moved from one area to another during successive mornings (calculated from expected values) was analyzed using a transition matrix. Separate analyses were made for spring, summer and winter periods. There was no consistent movement pattern across all seasons. Cattle seldom grazed in the same area for more than two successive mornings. The transitions on successive mornings from areas separated by the greatest distance generally occurred less often than expected by chance. The hypothesis that cattle would select the same area to graze for several successive mornings was rejected. In both studies, cattle appeared to graze nearby areas on the following morning.

INTRODUCTION

The intensity of utilization by grazing livestock usually varies among plant communities (Hunter, 1962; Low et al., 1981; Senft et al., 1985). Large herbi-

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vores apparently match the time spent grazing in a plant community to the forage resources that are found there (Senft et al., 1987). Although the overall spatial distribution pattern has been described, the mechanisms or behaviors that result in this pattern must be determined to develop accurate models of animal distribution. Multiple regression models using forage quantity, forage quality, distance to water, topography, etc. have often explained $<50\%$ of the variation in utilization of pastures by livestock (Cook, 1966; Gillen et al., 1984; Senft et al., 1985).

Bailey (1988) suggested a mechanism that should result in a matching pattern between time spent in a habitat and the forage resources found there. Cattle would return to productive areas of a pasture more often than less productive areas. This hypothesis assumes that cattle have the ability to remember where they have foraged. Cattle appear to have an accurate spatial memory (Bailey et al., 1987). Cattle also appear to be able to associate relative food quantity to spatial locations and order their choices from higher to lower reward (Bailey et al., 1989). We assume that cattle select productive areas before selecting less productive areas (after initial exploration). However in many situations, foraging alternatives (plant communities or patches) are similar. Optimal foraging theory would predict that cattle should remain in the same patch until the instantaneous energy intake rate dropped to a level equal to the average energy intake rate of the entire pasture (Charnov, 1976). An alternation among foraging alternatives would be predicted by the win–switch strategy suggested by Olton (1978) and Olton et al. (1981). Two studies were conducted to determine day-to-day movement patterns of cattle in pastures where variation among foraging alternatives was relatively low.

MATERIALS AND METHODS

Behavior studied

The diet selection process involves a hierarchy of grazing decisions at various temporal and spatial scales (Senft et al., 1987). Bout-to-bout and day-to-day temporal scales are identifiable and correspond to distinct changes in behavior. Although cattle move throughout the day (grazing, watering, locating loafing sites), they must select where to begin intensive grazing bouts. The movement pattern within a grazing bout (grazing path) results from a different set of processes than the day-to-day grazing pattern.

Sequential analysis of cattle location during the early morning grazing bout was used as an indication of the patch selection process at a day-to-day temporal scale. There were three major reasons for using these observations. (1) The early morning grazing bout is well defined by the shift from night resting behavior to intensive grazing activity (Low et al., 1981; Goodman et al., 1989). In both studies, there were few cattle engaged in activities other than grazing during the early morning period. (2) Since there is a distinct shift in behavior, cattle must select where to begin the morning grazing bout (stay near the resting site or move to another location). Later in the day, cattle travel to water and loafing sites, and much of the grazing occurs near these sites (Goodman et al., 1989; Walker et al., 1989). (3) In large pastures, the location of cattle near sunrise was found to be a good indication of where a cow did most of its grazing during a 24-h period (Low et al., 1981).

Colorado study

The study was conducted in a 50-ha pasture located near Fort Collins, Colorado, that was subdivided into eight paddocks with a 4-wire fence (Fig. 1). The large paddock on the east was visually divided into 3 sections for a total of 10 sections (Fig. 1). Vegetation was composed primarily of crested wheatgrass (*Agropyron desertorum*) and bindweed (*Convolvulus arvensis*). The terrain was nearly level and should not have affected animal distribution. Five yearling heifers, 20 cow–calf pairs and 1 bull were released into the pasture on 6 June 1987. The number of yearling and adult cattle (no calves) in each section was recorded early each morning (05.30–06.30 h) until 19 July 1987. No observations were recorded on 5 July 1987.

Data were summarized so that the location of cattle each morning could be

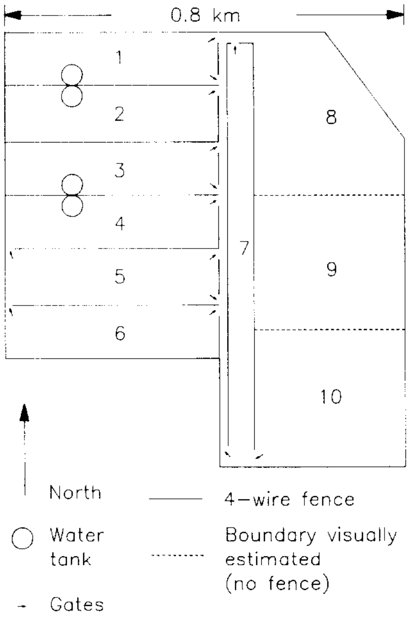

Fig. 1. Fifty-hectare Colorado study area. The eastern paddock was visually separated into 3 sections for a total of 10 sections.

organized in a sequence across the observation period and a Markov chain analysis could be conducted. Markov chains are sequences of behaviors in which it can be shown that the transitions between two or more behaviors are dependent on one another at some level of probability greater than chance (Lehner, 1979). Since cattle were not individually identified, the expected number of cattle in sections of the pasture on successive days was used in the analysis. For example, 16 head were observed in Section 1 on Day 1 and 10 head were observed in Section 2 on Day 1. On Day 2, 13 head were observed in both Sections 3 and 4. Assuming equal probabilities, the expected number of head that were in Section 1 on Day 1 and subsequently observed in Section 3 on Day 2 would be eight. Likewise, the expected number of head that were in Section 2 on Day 1 and subsequently observed in Section 3 on Day 2 would be five. Of the 13 head of cattle observed in Section 4 on Day 2, 8 head would be expected to have been in Section 1 on Day 1 and 5 head would be expected to have been in Section 2 on Day 1. Similar calculations were made for successive early-morning observations across the observation period.

The transformed data were then analyzed using a transition matrix (Lehner, 1979). Markov chains are often analyzed through the use of a transition matrix and a χ^2 test is used to compare the data with a random model. The transition matrix is not a true contingency table since the events included are not independent of each other (Lehner, 1979). Rejection of the null hypothesis implies that the sequence of locations is a first or higher order Markov chain. In other words, the location of an animal is dependent on its previous location. Matrix cells with χ^2 values that make large contributions to the overall χ^2 value indicate major deviations from the random model. In these studies, transition matrices were used as a descriptive tool. Since data from different individuals were pooled, the assumption of stationarity was violated (Lehner, 1979). Markov chain analysis can still provide a framework for studying patterns in the sequence of selected locations.

Texas study

The study was conducted at the Texas Experimental Ranch located on the eastern edge of the Rolling Plains resource region. The climate is continental, semiarid and variable. For a complete description of the study area see Heitschmidt et al. (1985).

The 248-ha pasture was stocked with crossbred cows at a moderate rate of 5.9 ha per cow per year. The pasture consisted of four plant communities (Fig. 2). Average above-ground net primary production for the plant communities ranged from 2500 to 3300 kg ha^{-1}. The pasture was divided into 63 units based on slope, aspect, elevation and distance from water. The number of cattle observed in each unit was recorded hourly during daylight hours for eight seasonal trials lasting 6–15 days.

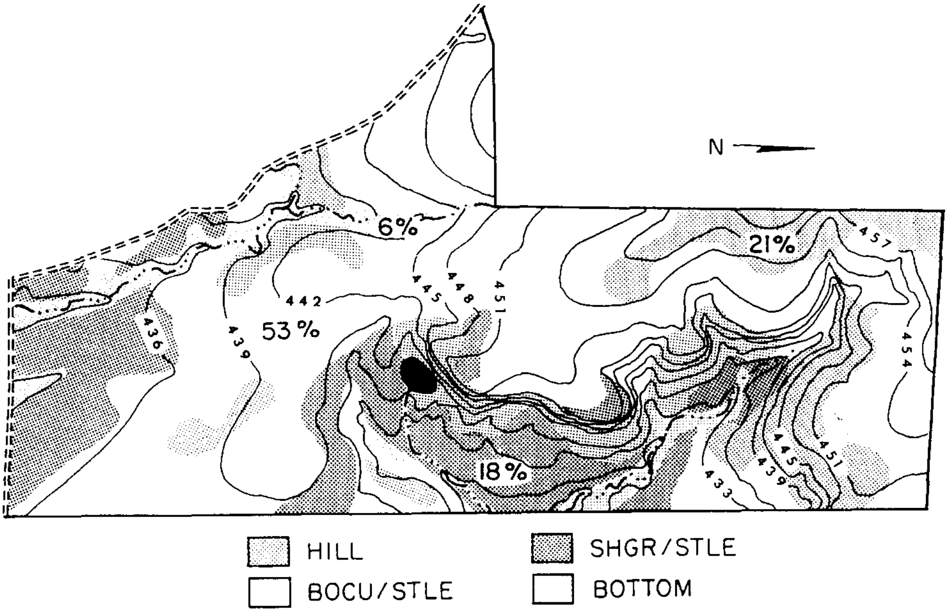

Fig. 2. Texas study area (248 ha). Three-meter contour intervals and delineation of plant communities are shown. There were four plant communities: Bottom, hill, Sideoats grama/Texas wintergrass (BOCU/STLE) and Shortgrass/Texas wintergrass (SHGR/STLE). See Walker et al. (1989) for a description of the plant communities. Numbers within a plant community represent the percent of the pasture that was in each plant community.

Accurate transition probabilities could not be estimated for the large number of units in the original data, therefore cluster analysis was used to pool units into larger areas. Each trial was analyzed separately. A single X and Y coordinate was assigned to each unit and used in cluster analyses. The number of times a coordinate was entered into the cluster analysis data set depended on the number of cattle observed grazing in that unit. Each record (X and Y value) represented 5–9 cows grazing in that unit. Values were entered for all hourly observations during a seasonal trial. For example, if 21 cows were observed at 08.00 h in Unit 20, the X and Y coordinate for Unit 20 would be entered in the data set 4 times. Units receiving more use had more influence in the cluster analysis. Thus the identified clusters represented contiguous units where grazing cattle were concentrated.

The final number of clusters was subjectively chosen based on the increase in explained variance over the previous stage. A maximum of eight clusters was considered. Five clusters explained 84–93% of the variance and appeared to be the most appropriate number for all trials. Results from all eight trials were pooled. Units were assigned to a cluster or area based on the most frequent designation from individual trial analyses (Fig. 3).

Data were transformed in a manner similar to the Colorado study so that

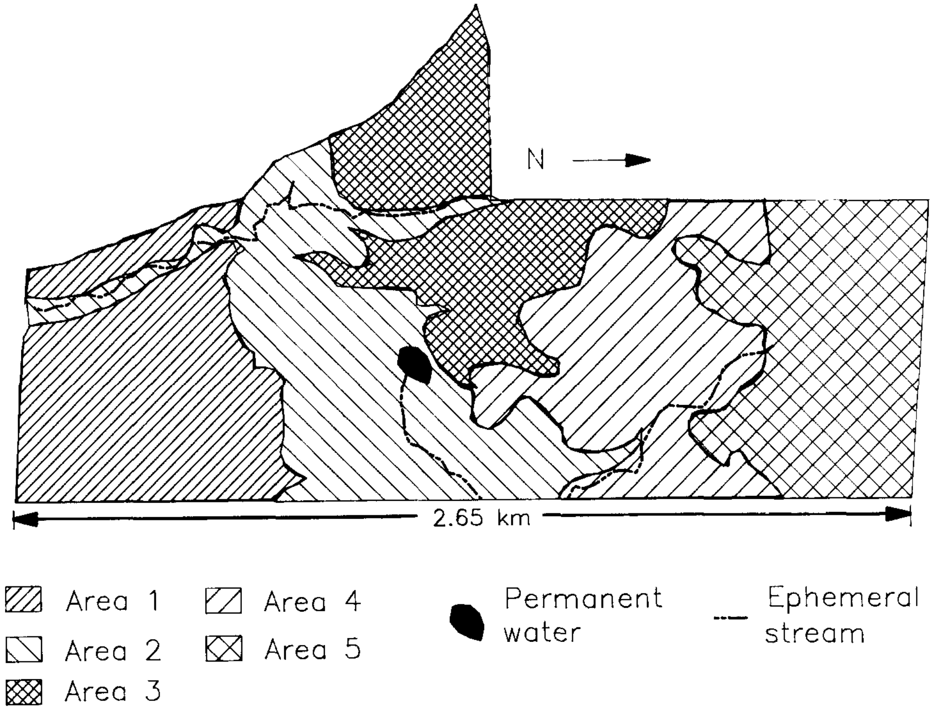

Fig. 3. Areas used in the transition matrix obtained from cluster analysis of Texas data.

the expected number of cattle observed in areas (clusters) of the pasture on successive mornings (after grazing had begun) could be analyzed using a transition matrix. Seasonal trials were pooled into spring, summer and winter periods. The spring period included trials from 12 to 20 March 1984 and 16–21 May 1984. The summer period included trials from 1 to 6 June 1983, 13–20 September 1983 and 17–25 August 1984. The winter period included trials from 26 October to 3 November 1982, 6–16 January 1983 and 5–18 January 1984.

RESULTS

Colorado study

The χ^2 test indicated that the location of cattle in the early morning was dependent on the location on the previous (early) morning (Tables 1 and 2). Animals seldom returned to the same section for two mornings in a row. In Sections 6, 8 and 10, the estimated (calculated) numbers of cattle observed in the same section on two successive mornings were 27, 24 and 26 head, respectively. Although the observations may have occurred throughout the 6-week

TABLE 1

Transitional matrix of the calculated number[a] of cattle observed on sections of the pasture (Fig. 1) during successive mornings in Colorado

Previous[b] section	Following section[c]									
	1	2	3	4	5	6	7	8	9	10
1	0	21	7	1	2	8	0	32	24	0
2	5	0	0	0	1	4	7	30	3	0
3	14	0	0	0	1	7	21	4	7	6
4	4	0	0	0	0	15	5	0	1	15
5	0	0	0	3	6	40	4	5	1	33
6	0	0	22	11	14	27	23	62	3	5
7	10	19	4	1	11	30	4	4	33	8
8	26	2	5	1	22	10	8	24	41	32
9	24	2	6	10	19	13	37	7	0	26
10	12	3	4	9	33	17	14	0	7	26

[a] Calculations described in the text.

[b] Location where cattle were observed during the previous early morning period (Day x).

[c] Location where cattle were observed during the following early morning period (Day $x+1$).

TABLE 2

Contribution to the overall χ^2 of each cell in the transitional matrix[a] of the calculated number of cattle observed in sections during two successive early morning periods in Colorado (Table 1)

Previous section[b]	Following section[c]									
	1	2	3	4	5	6	7	8	9	10
1	8	68	2	2	6	3	11	19	17	13
2	0	2	2	2	3	2	0	62	1	7
3	14	3	3	2	4	1	29	3	0	1
4	0	2	2	1	4	11	0	6	3	15
5	8	4	4	0	1	43	4	6	8	31
6	15	7	28	5	0	0	1	49	13	15
7	0	34	0	2	0	5	7	12	26	5
8	8	4	1	4	1	11	7	0	25	3
9	10	3	0	5	1	4	25	11	16	2
10	0	1	0	5	32	0	0	20	4	4

Overall $\chi^2 = 880$ ($P < 0.001$)

[a] Values in this table were calculated from Table 1 using the following equation (Lehner, 1979)
$\chi^2 = (\text{observed} - \text{expected})^2/\text{expected}$
Calculated values in Table 1 were considered the observed values.

[b] Location where cattle were observed during the previous early morning period (Day x).

[c] Location where cattle were observed during the following early morning period (Day $x+1$).

observation period, these values are approximately equal to the entire herd (26 head) being observed in a section for two successive mornings. In all 10 sections, the calculated number of cattle observed in the same section for two successive mornings was less than expected by chance. Transitions from Sections 6 to 6 and 8 to 8 were close to levels expected by chance (the contribution to χ^2 was rounded to zero). Cattle often moved to nearby sections on the following morning (Table 1). Some of the more frequent transitions were from Section 6 to 8, Section 5 to 6 and Section 8 to 9. The contribution to the overall χ^2 for these transitions was high (Table 2).

Texas study

The χ^2 test indicated that the location of cattle in the early morning was dependent on the location on the previous morning for all three season periods

TABLE 3

Transition matrix and χ^2 analysis[a] of the calculated number [b] of cattle observed in areas of the pasture (Fig. 3) on successive mornings during the spring period in Texas

Previous area[c]		Following area[d]				
		1	2	3	4	5
1	Calculated	26	1	0	0	0
	Expected	4	4	7	5	7
	χ^2	139	2	7	5	7
2	Calculated	19	9	25	10	5
	Expected	9	10	19	14	17
	χ^2	11	0	2	1	8
3	Calculated	15	23	31	69	38
	Expected	23	25	49	35	43
	χ^2	3	0	6	31	1
4	Calculated	5	8	32	15	37
	Expected	13	14	27	20	24
	χ^2	5	3	1	1	7
5	Calculated	0	29	47	4	39
	Expected	16	17	33	24	29
	χ^2	16	8	6	16	3

Overall=292 ($P<0.001$)

[a] The expected value and the contribution to the overall χ^2 are listed below the calculated (observed) value.

[b] Based on observations; calculations are described in the text.

[c] Location where cattle were observed on the previous morning (Day x).

[d] Location where cattle were observed on the following morning (Day $x+1$).

TABLE 4

Transition matrix and χ^2 analysis[a] of the calculated number[b] of cattle observed in areas of the pasture (Fig. 3) on successive mornings during the summer period in Texas

Previous area[c]		Following area[d]				
		1	2	3	4	5
1	Calculated	34	12	87	48	47
	Expected	56	18	37	35	81
	χ^2	9	2	66	5	14
2	Calculated	15	2	18	23	11
	Expected	17	6	11	11	24
	χ^2	0	2	4	14	7
3	Calculated	101	16	4	0	39
	Expected	40	13	26	25	57
	χ^2	95	1	19	25	5
4	Calculated	17	8	27	6	67
	Expected	31	10	21	19	44
	χ^2	6	0	2	9	12
5	Calculated	53	33	10	61	151
	Expected	76	25	51	48	109
	χ^2	7	3	32	4	16

Overall $\chi^2 = 361$ ($P < 0.001$)

[a] The expected value and the contribution to the overall χ^2 are listed below the calculated (observed) value.
[b] Based on observations; calculations are described in the text.
[c] Location where cattle were observed on the previous morning (Day x).
[d] Location where cattle were observed on the following morning (Day $x+1$).

(Tables 3–5). Furthermore, the value of the χ^2 indicated that these deviations from randomness were greatest in the spring and summer as compared with the winter. Cattle often stayed in the same area for two successive mornings, but the majority of the cattle were only observed in the same area of the pasture for three successive mornings on two occasions (Fig. 4). The majority of the cattle were never observed in the same area for four or more successive mornings. Except in one case, animals were observed in the areas separated by the greatest distance (Areas 1 and 5) on successive mornings less than expected by chance (Tables 3–5). The calculated (observed) value for the transition between Area 1 to Area 5 was approximately equal to chance levels during the winter period (Table 5).

TABLE 5

Transition matrix and χ^2 analysis[a] of the calculated number[b] of cattle observed in areas of the pasture (Fig. 3) on successive mornings during the winter period in Texas

Previous area[c]		Following area[d]				
		1	2	3	4	5
1	Calculated	3	22	35	8	25
	Expected	9	20	28	12	23
	χ^2	4	0	2	1	0
2	Calculated	49	33	54	6	74
	Expected	22	46	66	28	55
	χ^2	33	3	2	18	7
3	Calculated	40	82	81	67	74
	Expected	34	72	105	45	87
	χ^2	1	1	5	11	2
4	Calculated	8	28	24	22	37
	Expected	12	25	36	16	30
	χ^2	1	0	4	3	2
5	Calculated	4	51	118	31	49
	Expected	26	53	77	33	64
	χ^2	18	0	22	0	3

Overall $\chi^2 = 145$ ($P < 0.001$)

[a] The expected value and the contribution to the overall χ^2 are listed below the calculated (observed) value.

[b] Based on observations; calculations are described in the text.

[c] Location where cattle were observed on the previous morning (Day x).

[d] Location where cattle were observed on the following morning (Day $x+1$).

Trial	Area where the majority of cattle were observed on successive mornings
Spring Period	
3/12-20/84	3 4 5 5 2 3 5 3 4
5/16-21/84	5 3 3 1 1
Summer Period	
6/1-6/83	5 4 5 5 5 1
9/13-20/83	5 5 4 3 1 3 1 3 5
8/17-25/84	1 5 5 2 3 1 1 1 4
Winter Period	
10/27/82-11/3/82	4 5 5 3 3 1 2 1
1/6-16/83	3 2 3 2 5 3 5 2 3 4 2
1/5-18/84	5 3 3 1 5 2 1 3 4 3 4 5 5 3

Fig. 4. The sequence of areas where the majority of the cattle were observed on successive mornings during the Texas study.

DISCUSSION

In the Colorado study, cattle were seldom observed in the same section of the pasture for two successive mornings while in the Texas study, cattle were observed in the same area of the pasture for two successive mornings 21% of the time averaged across the three seasons. This discrepancy is probably due to the larger scale of the Texas pasture and the smaller number of the subdivisions.

Optimal foraging theory would predict that animals would remain in the same patch until the marginal intake (energy) rate was equal to the average intake rate of all patches (Stevens and Krebs, 1986). Since the cattle were observed in the same section of the pasture for $\leqslant 2$ days, forage biomass in that area would not have been reduced appreciably. Therefore it is unlikely that cattle were using a "giving up" rule that would be predicted by marginal value theorem (Charnov, 1976).

Given similar foraging alternatives, cattle did not return to the same location for several days in a row. They appeared to alternate among areas of the pasture. This type of foraging pattern is similar to the win–switch strategy described by Olton (1978). Olton et al. (1981) speculated that foragers whose food resources were dispersed would not return to the same area for consecutive foraging bouts. Instead, they would alternate among patches in order to allow replenishment of food. Cattle may be using a win–switch foraging strategy to choose among similar patches. This would allow some plant regrowth between visits.

A systematic and predictable patch alternation pattern should not be expected. Heifers used variable, non-systematic response patterns when selecting arms in parallel- and radial-arm mazes (Bailey, 1988). Even though the response patterns varied, heifers were accurate in selecting arms.

Instead of remembering where to graze next, cattle may be using memory to avoid previously grazed areas. Over a period of time, this behavior would ensure that cattle grazed in most areas of the pasture. In relatively homogeneous habitats, animals that use a win–switch strategy should demonstrate a low plant community selectivity, which is in agreement with previous results (Walker et al., 1989). If the pastures used in these studies had been more heterogeneous, the results may not have been the same. Further studies are needed to determine the effect of forage quality and quantity on patch selection and movement patterns of grazing cattle.

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