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Spatial–temporal arrangements of supplementation to modify selection of feeding sites by sheep

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Abstract

Undesirable grazing distribution results in land degradation and inefficient forage utilization. Rewards like food supplements have been commonly provided at predictable times and locations in the less preferred areas in order to improve grazing distribution. The problem with this approach is the generation of search patterns that are concentrated at certain times and locations, causing either overgrazing of new areas or the rapid return of the animals to the most preferred areas. Our model of spatial–temporal schedule of reinforcement proposes that rewards that are unpredictable in space and time should promote search patterns that are extended in space and time. In order to test predictions from the model, we studied how the spatial–temporal arrangement of supplementation influenced selection of feeding sites by sheep on a grass-legume pasture. Each experimental plot had a fertilized and an unfertilized side (8 m × 16 m each) either adjacent (Trial 1) or separated by an alley (1 m × 32 m) (Trial 2). In both trials groups of three ewes were randomly assigned to each of four treatments resulting from the combination of two spatial and two temporal arrangements of supplementation in the unfertilized side of the pasture. All treatments received the same amount and type of supplement (500 g alfalfa/corn pellets per ewe per day). There were two repetitions per treatment. Animal positions were recorded every 2 min during 2 h daily grazing sessions for 12 (Trial 1) or eight (Trial 2) consecutive days. The response variable was the proportion of time spent on the unfertilized side of the pasture. In Trial 1 neither treatment effects nor the interaction treatment by day was significant ($P > 0.05$). In Trial 2, the random spatial and/or temporal arrangements of supplementation tended to increase the occupation of the unfertilized side of the pasture by sheep. The differences among treatments were larger at the beginning of the trial, when the availability of forage was relatively higher than towards the end of the trial, when the availability of forage was relatively lower. In both trials the proportion of time spent on the unfertilized side of the pasture decreased

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($P < 0.01$) as the daily grazing session progressed from the first half hour to the second half hour to the last hour. Our results raise some interesting possibilities that warrant future tests of the model of spatial–temporal schedule of reinforcement to modify selection of feeding sites by free grazing animals.

Keywords: Sheep; Grazing behavior; Spatial distribution; Conditioning techniques; Feeding and nutrition; Supplementation

1. Introduction

Domestic and wild animals select feeding sites based on their abiotic and biotic characteristics (Senft et al., 1987). Factors, such as slope, distance to water, and forage quantity and quality can affect selection of feeding sites. Animals frequently concentrate grazing near water sources and in areas with the highest nutrient abundance. The resulting uneven grazing distribution causes undesirables effects on grasslands, such as species loss, species replacement, soil erosion, water pollution, and inefficient forage utilization. Management practices like water development, fencing, placement of salt and supplements, herding, and riding have been implemented to improve grazing distribution (Vallentine, 1990). When food supplements are used as attractants, they are commonly provided at predictable times and locations in the less preferred areas. The problem with this approach is the generation of search patterns that are concentrated at certain times and locations, causing either overgrazing of new areas or the rapid return of the animals to the most preferred areas (Laca, 1998, 2000).

It has long been established that animal behavior changes as a result of its consequences (Skinner, 1938, 1981). It is also known that the pattern of the conditioned response depends on the temporal schedule of reinforcement. Fixed time intervals between rewards result in concentrated responses just prior to the expiration of the fixed time, whereas random time intervals between rewards result in more constant responses over time (Staddon and Ettinger, 1989). Laca (2000) proposed a parallel spatial dimension in schedule of reinforcement for free grazing animals. He hypothesized that rewards provided at fixed locations result in concentrated searching behavior, whereas rewards provided at random locations result in a more widespread searching behavior. Therefore, search behavior should respond to the interaction between temporal and spatial distribution of rewards. Rewards that are predictable in space and time should generate search patterns that are concentrated at certain times and locations, whereas rewards that are unpredictable in space and time should promote search patterns that are extended in time and space.

In order to test predictions from the model of spatial–temporal schedule of reinforcement, we did a study to determine how spatial–temporal arrangements of supplementation influenced selection of feeding sites by sheep on a grass-legume pasture. In the context of our study, a feeding site was either a fertilized or an unfertilized area, 8 m wide × 16 m long. The rationale of the experiment was to create a pasture with a site (fertilized half) that was strongly preferred by sheep. Then, we would study the reversal of the preference by manipulation of the spatial–temporal distribution of a supplement on the unfertilized half.

2. Materials and methods

2.1. Pasture

The study was conducted during the period January–March 2003, on a grass-legume pasture located at the University of California campus in Davis, California. An area of 64 m × 64 m was subdivided into eight experimental plots (8 m wide × 64 m long each) and fenced with 1.2 m height polyethylene mesh. On January 15 half of each plot was fertilized (273 kg ha^{-1}; 16% N, 16 % P_2O_5, 16% K_2O, 7% S). We fertilized the side of the pasture closest (approximately 50 m) to the sheep barn to enhance its natural attractiveness to the sheep, which were born, raised and fed at the barn.

Total and green biomass, pasture height, and species cover were estimated in each experimental plot a month after fertilization. Observations were taken on 32.5 cm × 32.5 cm quadrats placed every 2 m along 30 m long transects. There were four transects per plot, two in the fertilized side, and two in the unfertilized side. Total and green biomass and the percentage of species cover were visually estimated. Biomass estimations were further adjusted by clipping five quadrats on each side (fertilized, unfertilized) of each experimental plot. The harvested material was oven dried, weighed, and sorted into green and dead biomass. The green fraction was analyzed for neutral and acid detergent fiber (Goering and Van Soest, 1970), and nitrogen (mass spectrometry). Total aerial biomass in each side of each experimental plot was also estimated by the disk technique (Bransby et al., 1977), five times during each trial.

Before starting Trial 1, both the fertilized side and the unfertilized side of each experimental plot were subdivided into two equal areas (8 m wide × 16 m long each). Trial 1 was run on the central adjacent fertilized and unfertilized areas (Fig. 1). Trial 2 was run on the extreme distant fertilized and unfertilized areas, which were connected by an alley (1 m wide × 32 m long)(Fig. 1).

2.2. Animals

Twenty-four ewes (Rambouillet–Targhee–Dorset–Finn–Polypay crossbreeds; 2–4-year-old; average weight 80 kg) born at the sheep facilities of the University of California—Davis were used in the experiment. The same ewes were used in both trials. Ewes were accustomed to eating alfalfa-hay and alfalfa-corn pellets in winter, and fresh grass-legume pastures the rest of the year. Animals were weighed at the beginning and at the end of Trials 1 and 2.

2.3. Pre-trials

During 3–19 February 2003 ewes grazed on a grass-legume pasture near the study area from 10:00 to 17:00 h. The rest of the time they were held at the sheep barn, where they

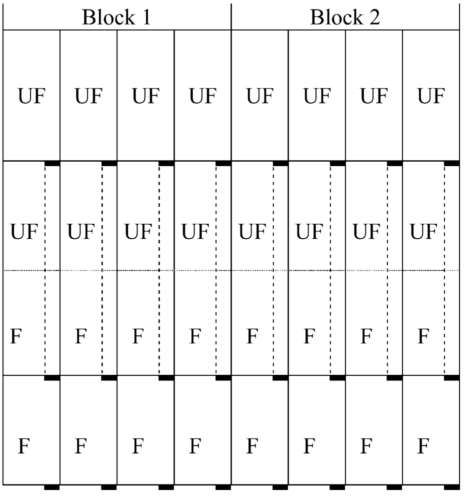

Fig. 1. Diagram of the study area. Fertilized (F) and unfertilized (UF) sites were 8 m wide × 16 m long. Trial 1 was run on the central adjacent F and UF sites. Trial 2 was run on the extreme distant F and UF sites, which were connected by an alley (1 m wide × 32 m long). Continuous lines were permanent fences, short engrossed lines were gates, whereas broken lines were temporary fences used to construct the alley in Trial 2. The central dotted line was the delimitation between F and UF sites.

had free access to water and salt. The objective was to get ewes used to grazing on fresh pasture, since they had been on hay and pellets since November of 2002.

2.4. Trial 1

The 24 ewes were separated into eight groups of three individuals each and randomly assigned to two blocks and four treatments. Groups were of similar average age and weight. Blocking was based on the differences in pasture attributes. The four treatments (T) resulted from the combination of two spatial and two temporal arrangement of supplementation in the unfertilized side of the pasture. In T1 the supplement was offered (in a plastic feeder) at a constant location at the beginning of the daily grazing session. In T2 the supplement was offered (on the ground) at 12 constant locations (125 g per location) at the beginning of the daily grazing session. Feed locations were uniformly distributed on the unfertilized side of the pasture. In T3 the supplement was offered (in a plastic feeder) at a constant location at four times during the daily grazing session. Feeding times were separated by fixed intervals of 30 min each, starting at the beginning of the daily grazing session. The same amount of supplement (375 g) was offered each time. In T4 the supplement was offered (on the ground) at random locations within 8 m diameter circle at four times during the daily grazing session. Times and amount of supplement were as in T3. In T3 and T4, the supplement was delivered through automatic feeders (on time wildlife feeders—Lifetime Feeder # 11112; Ruston, LA, USA) that allowed the control of time, amount, and distance of delivery. The feeders were located at the center of the unfertilized side of the experimental plots, mounted on wood posts at 1.5 m above ground level. In T3 a plastic shroud surrounded the delivery system of the automatic feeder in order to redirect the supplement to a plastic feeder located under it. The amount of supplement totaled 500 g per ewe per day in all treatments. The supplement was alfalfa (70%)–corn (30%) pellets.

Trial 1 began on February 20 and continued for 19 consecutive days, until March 10. Daily grazing sessions lasted for 2 h, from 12:30 to 14:30 h or from 15:00 to 17:00 h. Ewes assigned to odd or even experimental plots grazed at different times of the day to reduce influences among animals in contiguous plots. Odd and even groups alternated daily between the early and late grazing sessions. The rest of the day ewes were held in a barn with free access to water and salt but without feed to ensure active feeding the next day in the experimental plots.

The ewes were given seven days to get used to the experimental conditions. Then the activity and the position of each animal were recorded every 2 min during each grazing session. Activity was categorized as eating or no eating, whereas position was categorized as fertilized or unfertilized side of the pasture. We did not differentiate in grazing or eating supplement because in T2 and T4 it was difficult to discriminate between both activities from the observation place. Ewes within groups had collars of different color to help in individual identification. Observations were made from towers (3 m height) located outside (10 m away) the experimental area. There were two observers per grazing session, each recording the activity and position of two groups of ewes. At the end of each grazing session, the unfertilized side of the pasture was inspected to assess the consumption of supplement.

2.5. Trial 2

The same animals used in Trial 1 assigned to the same experimental plots were used in Trial 2. This trial differed from Trial 1 in the spatial configuration of the fertilized and unfertilized side of the pasture and in the spatial or temporal arrangement of the supplement in T2, T3, and T4. In Trial 2 the fertilized and unfertilized sides of the experimental plots were 32 m apart and connected by an alley (1 m wide $\times$ 32 m long). In T2 the supplement was randomly spread all over the unfertilized side of the pasture at the beginning of the daily grazing session. In T3 the supplement was offered at a constant location at six random times during the daily grazing session. In T4 the supplement was offered at random locations within an 8 m diameter circle at six random times during the daily grazing session.

Trial 2 began on March 11 and continued for 17 consecutive days, until March 27. Ewes were allowed to get used to the experimental conditions during nine days. Then the activity and position of each individual were recorded as in Trial 1.

2.6. Statistical analyses

Data for Trials 1 and 2 were analyzed as a split-plot in time (Damon and Harvey, 1987) according to a random block design. Groups of ewes (3 individuals each) were considered as whole-plot units and groups of ewes at each particular day as sub-plot units. Factors were treatment, day, and period within the daily grazing session. Three periods were analyzed: first half hour, second half hour, and last hour. The error terms used to test for treatment, day, and period effects were the corresponding factor by replication interactions. In addition, treatment effects were also subjected to ANOVA after data transformation (arcsine square root), considering the entire 2 hour period and pooling the data across days. A dry matter (DM) ratio variable (DM in the unfertilized side/(DM in the unfertilized side + DM in the fertilized side)) was used as covariate in the analysis to account for pasture depletion along trials. Because eating (grazing or consumption of supplement) represented between 98 and 100% of the activity of ewes from all treatments in both trials, we decided to analyze the position of the animals only. The response variable was the proportion of time spent on the unfertilized side of the pasture (number of locations on the unfertilized side/(number of locations on the unfertilized side + number of locations on the fertilized side)). Repeated measure analysis and ANOVA were used to compare body weight of ewes and pasture attributes, respectively.

3. Results

3.1. Pasture

Grass species were mainly represented by *Bromus* spp. and *Lolium perenne*, whereas legume species were mainly represented by *Trifolium repens*. Less abundant grass and legume species were *Dactylis glomerata*, *Festuca arundinacea*, *Medicago lupulina* and *Lotus corniculatus*. The two main weed species were *Plantago lanceolata* and *Stellaria media*.

Immediately before Trial 1, the total aerial biomass, green biomass, pasture height, and grass cover were greater ($P < 0.05$) in the fertilized than in the unfertilized side of the pasture, whereas legume cover was lower ($P < 0.05$) in the fertilized than in the unfertilized side of the pasture (Table 1). Blocks 1 and 2 did not differ ($P > 0.05$) in species cover, but total and green biomass and pasture height were higher ($P < 0.05$) in Block 1 than in Block 2 (Table 1). Nitrogen concentration was greater ($P < 0.05$) in the fertilized than in the unfertilized side of the pasture, whereas fiber concentration was similar ($P > 0.05$) in both sides (Table 2). Blocks 1 and 2 did not differ ($P > 0.05$) in fiber concentration, but nitrogen concentration was higher ($P < 0.05$) in Block 1 than in Block 2 (Table 2).

Fig. 2 shows average trends for total aerial biomass in the fertilized and unfertilized sides of the pasture along Trials 1 and 2. There was a marked reduction in the amount of forage in both the fertilized and the unfertilized sides of all experimental plots over time in both trials.

Table 1
Pasture structural attributes at the start of grazing trials

	Total biomass ($g\,m^{-2}$)	Green biomass ($g\,m^{-2}$)	Pasture height (cm)	Cover (%)		
				Grasses	Legumes	Weeds
Block 1						
Fertilized side	207.2 (6.4)	135.9 (4.0)	9.5 (0.4)	68.4 (1.8)	17.7 (1.5)	13.9 (1.3)
Unfertilized side	166.3 (6.4)	85.1(4.0)	7.0 (0.4)	59.5 (1.8)	20.9 (1.5)	19.3 (1.3)
Block 2						
Fertilized side	170.0 (6.4)	110.2 (4.0)	7.3 (0.4)	63.2 (1.8)	15.9 (1.5)	20.0 (1.3)
Unfertilized side	163.0 (6.4)	88.3 (4.0)	5.4 (0.4)	59.9 (1.8)	22.1(1.5)	17.6 (1.3)

Values are mean ($n = 8$) ± S.E.

Table 2
Pasture chemical attributes at the start of grazing trials

	Neutral detergent fiber (%)	Acid detergent fiber (%)	Nitrogen (%)
Block 1			
Fertilized side	47.9 (1.5)	21.9 (0.7)	23.3 (0.6)
Unfertilized side	43.4 (1.5)	23.2 (0.7)	17.9 (0.6)
Block 2			
Fertilized side	46.3 (1.5)	22.5 (0.7)	20.9 (0.6)
Unfertilized side	48.7 (1.5)	24.8 (0.7)	15.0 (0.6)

Values are mean ($n = 5$) ± S.E.

3.2. Trial 1

Eating (grazing or consumption of supplement) was the prevalent activity (98–100%) in animals from all treatments during the daily grazing sessions. Ewes consumed all the

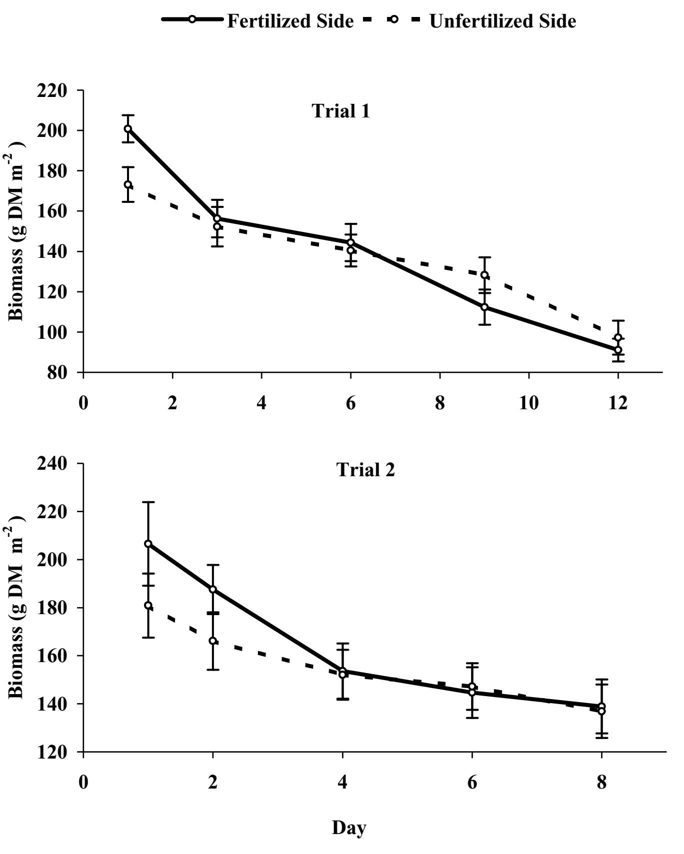

Fig. 2. Total aboveground biomass changes in the grass-legume pasture along Trials 1 and 2. Values are mean ($n = 8$) ± S.E.

Table 3
Body weight of sheep

Treatment (T)	Trial 1			Trial 2[a]		
	Start	End	S.E.	Start	End	S.E.
T1	80.7	80.6	3.0	75.6	76.1	3.6
T2	80.4	82.9	2.7	79.1	78.6	3.2
T3	78.1	78.9	2.7	73.5	71.8	3.2
T4	77.5	77.8	2.7	73.8	72.5	3.2

Values are mean ($n = 6$). In Trial 1 the supplement was offered either at one constant location (T1) or at 12 constant locations (T2) at the beginning of daily grazing sessions, or at four times separated by 30 min intervals either at one constant location (T3) or at random locations (T4). In Trial 2 the supplement was offered either at one constant location (T1) or random locations (T2) at the beginning of daily grazing sessions, or at six random times either at one constant location (T3) or at random locations (T4). All Trials 1 and 2 values are given in killogram.

[a] Sheep were sheared immediately before the start of Trial 2.

supplement regardless the spatial–temporal arrangement of supplementation. There were not significant ($P > 0.05$) changes in the body weight of ewes from any treatments during Trial 1 (Table 3).

Both the ANOVA and the split-plot in time analysis yielded a non-significant effect ($P > 0.05$) of the spatial–temporal arrangements of supplementation on the proportion of time spent by ewes on the unfertilized side of the pasture (Table 4). In the split-plot in time analysis the interaction treatment by day was not significant ($P > 0.05$) either, although the effect of day was significant ($P < 0.05$). On average, the proportion of time spent in the unfertilized side of the pasture increased from 0.36 in Day 1 to 0.56 in Day 12. There was also a significant interaction ($P < 0.05$) between treatments and period during the grazing session (first half hour, second half hour, last hour)(Fig. 3). The interaction was caused by the relatively lower proportion of time spent by ewes on the unfertilized side of the pasture in T2 during the first half hour and in T4 during the last hour of the grazing session, and by the relatively higher proportion of time spent by ewes in the unfertilized side of the pasture in T3 during the second half hour of the grazing session. The proportion of time in the

Table 4
Proportion of time spent by sheep on the unfertilized side of the pasture

Treatment (T)	Trial 1			Trial 2		
	Replicate 1	Replicate 2	Mean	Replicate 1	Replicate 2	Mean
T1	0.58	0.47	0.52 (0.08)	0.36	0.42	0.39 (0.03)
T2	0.43	0.53	0.48 (0.07)	0.38	0.53	0.45 (0.03)
T3	0.65	0.59	0.62 (0.15)	0.46	0.57	0.51 (0.03)
T4	0.34	0.68	0.51 (0.16)	0.41	0.61	0.51 (0.04)

Values are mean ($n = 12$, Trial 1; $n = 8$, Trial 2) ± S.E. In Trial 1 the supplement was offered either at one constant location (T1) or at 12 constant locations (T2) at the beginning of daily grazing sessions, or at four times separated by 30 min intervals either at one constant location (T3) or at random locations (T4). In Trial 2 the supplement was offered either at one constant location (T1) or random locations (T2) at the beginning of daily grazing sessions, or at six random times either at one constant location (T3) or at random locations (T4).

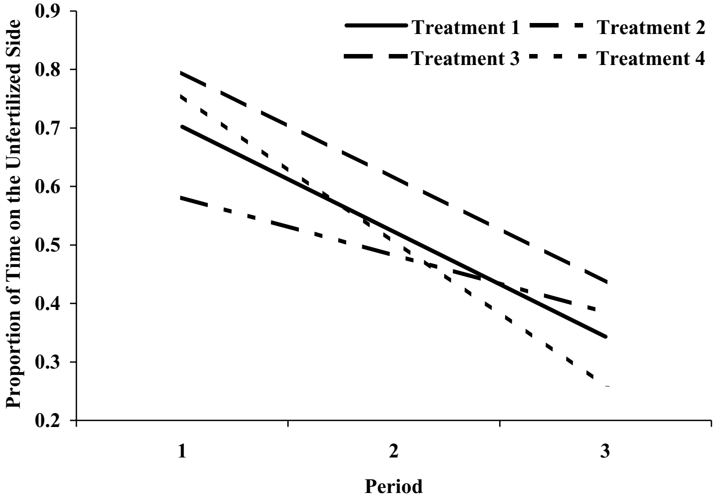

Fig. 3. Treatment by period interaction in the proportion of time spent by sheep on the unfertilized side of the pasture in Trial 1. In Trial 1 the supplement was offered either at one constant location (T1) or at 12 constant locations (T2) at the beginning of daily grazing sessions, or at four times separated by 30 min intervals either at one constant location (T3) or at random locations (T4). Periods 1, 2, and 3 correspond to the first half hour, the second half hour, and the last hour of the daily grazing sessions, respectively.

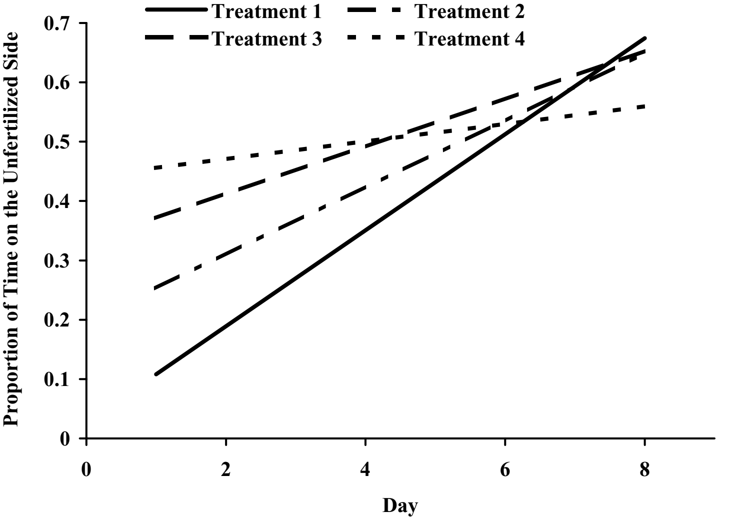

Fig. 4. Treatment by day interaction in the proportion of time spent by sheep on the unfertilized side of the pasture in Trial 2. In Trial 2 the supplement was offered either at one constant location (T1) or random locations (T2) at the beginning of daily grazing sessions, or at six random times either at one constant location (T3) or at random locations (T4).

unfertilized side of the pasture averaged 0.72, 0.51, and 0.36 for the first half hour, second half hour, and last hour of the daily grazing session, respectively.

3.3. Trial 2

Eating was also the prevalent activity (98–100%) of animals from all treatments during the daily grazing sessions in Trial 2. Ewes consumed all supplement regardless the spatial–temporal arrangement of supplementation. There were no significant ($P > 0.05$) changes in the body weight of ewes during Trial 2 (Table 3).

After pooling data across days the ANOVA yielded a non-significant effect ($P > 0.05$) of the spatial–temporal arrangements of supplementation on the proportion of time spent by ewes on the unfertilized side of the pasture (Table 4). However, the split-plot in time analysis yielded a significant ($P < 0.05$) positive trend in the occupation of the unfertilized side of the pasture from T1 to T4. The treatment by day interaction was also significant ($P < 0.05$) (Fig. 4). Except for Day 3, the differences among treatments were larger at the beginning of the trial than towards the end of the trial. The effects of day and of period within the grazing session were also significant ($P < 0.05$). On average the proportion of time spent on the unfertilized side of the pasture increased from Day 1 (0.29) to Day 8 (0.69), whereas it decreased from the first half hour (0.80) to the second half hour (0.46) to the last hour (0.14) of the daily grazing session.

4. Discussion

Our results did not agree (Trial 1) or agreed partially (Trial 2) with predictions derived from the model of spatial–temporal schedule of reinforcement. Specifically, the results from Trial 2 showed increased occupancy of the unfertilized side of the pasture as the supplement became less predictable in space and time at the beginning of the trial only. Collectively, the results from Trial 2 showed a tendency toward increasing the proportion of eating time on the unfertilized side of the pasture as the supplement became less predictable in space and time. Because of the fast consumption of the supplement, the prevalent activity of ewes on the unfertilized side of the pasture was grazing. The prevalence of grazing has been observed even when self-fed supplements were always available (Bailey and Welling, 1999).

The differences in spatial–temporal distribution of the supplement, in spatial configuration of the experimental plots and in conditioning to the supplement may explain the relative and absolute differences in ewe response to the spatial–temporal distribution of the supplement observed in Trials 1 and 2. In T2 of Trial 1 the supplement was offered at 12 locations that remained the same throughout the trial, whereas in T2 of Trial 2, the supplement was randomly spread over all the unfertilized side of the pasture. In T2 of Trial 1 ewes probably found and ate the supplement faster than in T2 of Trial 2. Animal search efficiency is higher when food locations are constant and clumped than when food locations are random (Laca, 1998). In T3 and T4 of Trial 1 the supplement was offered at four times separated by fixed time intervals, whereas in the same treatment of Trial 2, the supplement was offered at six random times during each grazing session. In T3 and T4 of Trial 1 it was observed that ewes searched more frequently for supplement (based on approaches to the automatic feeder) toward the end of the intervals between deliveries. Fixed time intervals between rewards results in a more concentrated search for the reward just prior to the end of the time interval (Staddon and Ettinger, 1989). In Trial 1, the fertilized and unfertilized sides were adjacent to each other, whereas in Trial 2 they were separated and connected by an alley (32 m long). Animals moved more readily from one side to the other in Trial 1 than in Trial 2. The shorter the distance among feeding sites the more readily sheep would move among them (Dumont et al., 1998). Finally, the level of conditioning to the supplement may also explain the different responses of ewes to the spatial–temporal arrangement of supplementation in Trials 1 and 2. For example, in Trial 1 the group of ewes from T4 Replicate 1 did not become conditioned to the supplement throughout the trial (Table 4). The lack of conditioning was clearly evident because these animals repeatedly failed to respond to food delivery by the automatic feeders. In Trial 2, the same animals were somewhat better conditioned to the supplement, although far behind the level of conditioning reached for animals from T4 Replicate 2 and T3 Replicates 1 and 2. Moreover, in T4 Replicate 1 the leading ewe (based on the follow response by the other ewes in the same group) exhibited the poorest response to the supplement (based on the response to pellet delivery by the automatic feeders). Conversely, the leading ewes from T4 Replicate 2 and T3 Replicates 1 and 2 were highly responsive to the supplement. Leadership is an important factor in animal movement (Arnold and Dudzinsky, 1978; Sato, 1982) and in selection of feeding sites (Greenwood and Rittenhouse, 1997).

The marked decrease in the occupancy of the unfertilized side of the pasture as the daily grazing session progressed (from the first half hour, to the second half hour, to the last hour), observed in Trials 1 and 2, may be explained by the spatial scale of the experiment and the nutritional status of the animals. The dimensions of the fertilized and unfertilized sides (16 m long × 8 m wide) were small enough for a group of three ewes to graze all the area before the end of a grazing session, and animals are reluctant to re-graze recently grazed areas (Bailey, 1995; Laca, 1998). Therefore, the reduced spatial scale of our study probably lead to an underestimation of the potential effect of providing spatially/temporally random rewards to modify selection of feeding sites by sheep. On the other hand, because the internal state of the animals presumably changed rapidly during the grazing session, it is possible that the value of the supplement to the sheep declined over time within sessions. Although ewes grazed for 2 h per day only, the consumption of forage plus the consumption of supplement was enough for them to maintain their body weight in both trials (Table 3). However, period within grazing session significantly interacted with treatment in Trial 1, which in part was explained by the relatively higher occupation of the unfertilized side of the pasture by animals from T3 during the second half hour of the grazing session (Fig. 3).

The positive daily trend in the occupation of the unfertilized side of the pasture observed in Trails 1 and 2 paralleled a negative daily trend in the amount of forage in the fertilized and unfertilized sides of the pasture in both trials (Fig. 2). This marked reduction in the amount of forage along trials may also explain the significant treatment by day interaction observed in Trial 2 (Fig. 4). The amount of forage may have been high enough for the expression of the differences among treatments at the beginning of the trial, whereas it may have been too low for their expression towards the end of the trial. Day 3 of Trial 2 was an exception since animals from all treatments were located in the fertilized side of the pasture (the closest to the sheep holding barn) most of the grazing session. This particular day was stormy and windy, which may explain the observed behavior. Weather conditions, including wind intensity and direction, can strongly influence animal movement (Arnold and Dudzinsky, 1978).

5. Conclusions

Our results raise some interesting possibilities that warrant future tests of the model of spatial–temporal schedule of reinforcement to modify selection of feeding sites by free grazing animals.

References

Arnold, G.W., Dudzinsky M.L., 1978. Ethology of Free-Ranging Domestic Animals. Elsevier, Amsterdam, p. 198.

Bailey, D.W., 1995. Daily selection of feeding areas by cattle in homogeneous and heterogeneous environments. Appl. Anim. Behav. Sci. 45, 183–200.

Bailey, D.W., Welling, G.R., 1999. Modification of cattle grazing distribution with dehydrated molasses supplement. J. Range Manage. 52, 575–582.

Bransby, D.I., Matches, A.G., Krause, G.F., 1977. Disk meter for rapid estimation of herbage yield in grazing trials. Agron. J. 69, 393–396.

Damon, R.A., Harvey, W.R., 1987. Experimental Design, ANOVA, and Regression. Harper & Row, New York, p. 320.

Dumont, B., Dutrone, A., Petit, M., 1998. How readily will sheep walk for a preferred forage? J. Anim. Sci. 76, 965–971.

Goering, H.K., Van Soest, P.J., 1970. Forage Fiber Analyses. Agronomy Handbook, vol. 379. ARS-USDA, Denver, 20 pp.

Greenwood, P.T., Rittenhouse, L.R., 1997. Feeding area selection: the leader–follower phenomena. Proc. West. Sec. Am. Soc. Anim. Sci. 48, 267–269.

Laca, E.A., 1998. Spatial memory and food searching mechanisms of cattle. J. Range Manage. 51, 370–378.

Laca, E.A., 2000. Modeling spatial aspects of plant–animal interactions. In: Lemaire, G., Hodgson, J., de Moraes, A., Nabinger, C., de F. Carvalho, P.C. (Eds.), Grassland Ecophysiology and Grazing Ecology, CABI Publishing, Wallingford, pp. 209–231.

Sato, S., 1982. Leadership during actual grazing in a small herd of cattle. Appl. Anim. Etho. 8, 53–65.

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

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. BioScience 37, 789–799.

Skinner, B.F., 1938. The Behavior of Organisms. Appleton-Century-Crofts, New York, 457 pp.

Skinner, B.F., 1981. Selection by consequences. Science 213, 501–504.

Vallentine, J.F., 1990. Grazing Management. Academic Press, San Diego, 533 pp.