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BEHAVIORAL CHARACTERISTICS AFFECT HABITAT
SELECTION OF DOMESTIC RUMINANTS

by

Cody B. Scott

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1995

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ABSTRACT

Behavioral Characteristics Affect Habitat

Selection of Domestic Ruminants

by

Cody B. Scott, Doctor of Philosophy

Utah State University, 1995

Major Professor: Dr. Roger E. Banner
Department: Rangeland Resources

I evaluated some of the factors affecting livestock distribution by conducting experimental (Chapters II and III) and observational (Chapter IV) studies. In Chapter II, I described the effect of locations of familiar foods and social interactions on choice of feeding location by lambs. Lambs were exposed to a pasture as subgroups of strangers and companions with different dietary habits (i.e., three lambs that preferred milo with three lambs that preferred wheat). Milo was placed on one end and wheat on the other, about 100 m apart. Strangers typically fed in different locations, reflecting dietary preferences. Conversely, companions fed in both single subgroups and in separate subgroups because both social interactions and dietary preferences affected choice of feeding location.

The objective of Chapter III was to evaluate the effect of experience with a pasture on choice of feeding location. Lambs with different levels of familiarity with

the pasture were exposed as subgroups with different dietary habits. Lambs familiar with the pasture typically fed in separate locations, reflecting dietary preferences. Lambs naive to the pasture always fed in one subgroup and consumed both foods because social interactions overrode dietary preferences.

Results in Chapter IV describe cattle observations on a 1,030-ha grazing allotment. Cattle home ranges were similar in location (i.e., site fidelity) between 1990 and 1991, even though home ranges increased in size and (or) shifted in location in response to water availability. Moreover, forage availability did not account for changes in home range size or location. Site fidelity probably developed because of experiences early in life while foraging with mother and (or) peers.

Managers may be able to improve distribution by manipulating foraging experiences. Placing familiar foods/supplements in underutilized areas, controlling the amount of experience livestock have with different habitat types, and culling animals that spend a disproportionate amount of time in riparian zones may improve distribution. Herding could also improve distribution. Herding integrates social interactions and experience with foods by controlling the exposure of social groups to particular foods and habitats. Nevertheless, livestock may still spend considerable time in riparian zones unless other watering points are available.

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CHAPTER I

INTRODUCTION

Recently, the public has become more aware of environmental issues such as the loss of endangered species, wildlife habitat, and biodiversity as well as riparian degradation and water pollution (Drew, 1994; Mitchell, 1994a, b). Environmental degradation is often attributed to livestock grazing. As a result, environmentalists often support the complete removal of livestock grazing and the establishment of wildlife preserves. Nevertheless, removal of grazing may not necessarily restore plant communities to their "pristine" composition, especially on arid and semiarid rangelands (Laycock, 1991, 1994). Current theories suggest that any successional state can change in several ways, some of which may be less desirable to humans than others (Westoby et al., 1989; Friedel, 1991). In several national parks and wildlife refuges, management techniques have resulted in dramatic shifts in animal and plant composition, often causing the regional extinction of some species and the propagation of others (Chase, 1987, 1995). Environments also vary in their resistance to change, and it can take significant disturbances to shift them into different stages (Taush et al., 1993; Laycock, 1994).

Disturbances such as grazing can be beneficial in controlling the rate and direction of successional change to meet management goals (Allen and Hoekstra, 1994). For instance, livestock grazing can improve wildlife habitat through altering vegetation composition, increasing productivity of desirable species, and increasing nutritive quality (Severson and Urness, 1994). Urness (1990) showed that mule deer (*Odocoileus hemionus*) winter ranges can deteriorate without cattle grazing. Plots

excluded from cattle grazing shifted from a shrub-bunchgrass mix to a dominance by bunchgrasses, apparently due to a reduction in the shrubs' ability to compete with bunchgrasses. Conversely, shrubs dominated on areas grazed by cattle during spring and summer. Considering that shrubs are a significant portion of mule deer diets in winter, cattle grazing actually enhanced habitat suitability for mule deer. Importantly, however, Severson and Urness (1994) suggested that overgrazing may override any beneficial effects of grazing and cause range degradation.

Grazing may also improve biodiversity (Johnson and Mayeux, 1992; West, 1993). Livestock grazing causes a mosaic of vegetation, especially when food preferences vary between herbivore species (Archer and Smeins, 1991). Plant populations are also disproportionately distributed across the landscape, and vary in their nutrient content, growth stage, and secondary metabolite concentrations, all of which affect plant acceptability to animals. Moreover, grazing can increase the rate of nutrient cycling, and further increase ecosystem integrity and stability (Shariff et al., 1994). Once again, however, most warn that light to moderate grazing may enhance ecosystem health, whereas excessive use can cause successional retrogression.

Controlling the distribution of livestock is essential for insuring moderate utilization across all plant communities (Vallentine, 1990). Consequently, range managers have suggested several approaches to improve distribution. These include herding (Skovlin, 1957; Cook, 1967), grazing systems (Taylor et al., 1993a, b), repellents (Engle and Schimmel, 1984), fencing, water development, and salt placement (Cook, 1967). However, most of these approaches are inadequate because

they either do not improve grazing distribution or have unjustifiably high costs (Workman and Hooper, 1968; Vallentine 1990). The reasons many of these methods fail to improve distribution are unclear, but may reflect our lack of knowledge of the causal mechanisms affecting habitat selection. This is not surprising because most of the knowledge was generated from observations of habitat selection, which can provide useful information for describing particular situations, but they do not provide experimental evidence of the causal factors affecting behavior (Romesburg, 1981; Provenza, 1991).

The purpose of this dissertation is to explore some of the mechanisms that may affect habitat selection. There are correlations between habitat use and forage availability (Senft et al., 1985, 1987), distance from water (Squires, 1981), and topography (Mueggler, 1965; Cook, 1966; Bryant, 1982). Nevertheless, animals occasionally feed in locations with low forage availability and steep topography, so other factors must also influence habitat selection.

I believe food preferences and social interactions warrant further investigation for their role in habitat selection. Herbivores are faced with the challenge of locating nutritious foods that are distributed across a landscape in patches that vary in their size and location (Stephens and Krebs, 1986). Consequently, factors such as social interactions and food preferences, which influence the probability of selecting nutritious foods within a patch (Provenza, 1994, 1995), may also affect habitat selection. Accordingly, I designed a set of experiments to determine the role of social interactions and food preferences on choice of feeding locations within the

environment.

I conducted the first experiments in 1992-1993. These experiments assessed how experience with particular foods and their locations affected choice of feeding location by lambs. Lambs were reared together for 4 mo to insure a familiarity among members. I also exposed half of the animals to one grain and half of the animals to another grain. I then exposed subgroups of animals with different dietary preferences to areas with the two foods in different locations to test the relative importance of dietary preferences and social interactions on choice of feeding location.

The second experiments were conducted in 1994 and examined the role of experience with the environment on social interactions and initial food preferences. For these experiments, I varied the amount of exposure to an experimental pasture, a similar pasture with similar forage species, or no exposure to a grazing environment. Animals were reared in social groups with half of the animals receiving one grain and half receiving another grain. This allowed me to test the role of experience with the environment on dietary preferences and social interactions.

Finally, I used data collected from an observational study of cattle grazing in south-central Idaho. The study was conducted from 1990 through 1991 and recorded the location and activity of individual cows daily throughout a grazing season. These data provide some evidence to the role of experience early in life on choice of foraging locations in a natural setting.

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CHAPTER II
DIETARY HABITS AND SOCIAL INTERACTIONS AFFECT
CHOICE OF FEEDING LOCATION BY SHEEP

Abstract

Individuals often occur in subgroups that differ in their choice of food and habitat, even within the same environment. Different foods occur in disparate locations and thus differences in dietary habits could provide one explanation for the formation of subgroups and their use of the environment. In addition, subgroups may form as a result of social interactions. I conducted experiments to study the effects of food preference and social interactions on choice of feeding location by lambs. In 1992, 12 lambs that had been reared together were separated into two groups of six lambs. Groups were conditioned to prefer one of two grains, either milo (*Sorghum bicolor*) or wheat (*Triticum aestivum*) by feeding milo or wheat for 14 d. Lambs were conditioned to avoid the other grain by following its ingestion with a mild dose of the toxin lithium chloride on three consecutive days. During testing, milo and wheat were placed at opposite ends of a 0.25-ha pasture. Lambs were first allowed to feed as groups consisting of three lambs that preferred milo and three lambs that preferred wheat, and then allowed to feed as groups in which one lamb preferred milo with three lambs that preferred wheat, and vice versa. Under both conditions lambs always fed on their preferred food. Lambs also fed on their preferred food when the locations of the foods were switched. In 1993, I repeated the study from 1992 in a larger pasture (1 ha) and without the use of LiCl. Lambs were reared in three different

groups and fed either milo (group 1), wheat (group 2), or half of the lambs were fed milo and the other half were fed wheat (group 3) for 4 mo to condition a preference for either milo or wheat. When I combined lambs that preferred milo from group 1 with lambs that preferred wheat from group 2 to form subgroups of strangers, lambs fed in different locations. Conversely, social interactions and food preferences both affected choice of feeding location when lambs were reared together (companions). For instance, some lambs that preferred wheat grazed in the vicinity while peers ate milo, whereas lambs that preferred milo grazed in the vicinity while peers ate wheat. In other cases, one or two lambs separated from the rest of the group and ate their preferred grain. I conclude that food preference had a primary influence on choice of foraging location when lambs were reared separately (strangers) and preferred different foods. Food preferences and social interactions both influenced choice of foraging location for companions unless animals were made averse to one of the foods with LiCl, in which case dietary preferences overrode social influences.

1. Introduction

Individuals within species often occur in subgroups that differ in their choice of food and habitat, even within the same environment (Roath and Krueger, 1982; Howery et al., 1995). For instance, sheep and cattle often aggregate when they rest but disperse as subgroups to different locations when they forage (Hunter and Milner, 1963; Hewson and Wilson, 1979; Squires, 1981). We reasoned that food preferences and social interactions could cause the formation of subgroups. When preferred foods occur in disparate locations in the environment, dietary preferences may provide one

explanation for the organization of subgroups. Subgroups might also arise as a result of social interactions.

Experience affects food selection. Dietary habits are formed through experiences early in life (Provenza, 1994). For instance, lambs consume more of foods they had been exposed to early in life (Nolte et al., 1990; Nolte and Provenza, 1992). Ruminants also acquire preferences for the flavors of foods that are nutritious based on positive postingestive consequences, and avoid foods that are toxic and cause postingestive malaise (Provenza, 1995). Postingestive feedback can override social influences. For instance, when a lamb eats a food with its mother, and subsequently receives a mild dose of the toxin lithium chloride, the lamb subsequently avoids eating the food (Provenza et al., 1993).

Social factors also influence dietary habits. Young sheep and goats can learn which foods to eat from their mothers and generally acquire a preference for those foods (Mirza and Provenza, 1990, 1994; Biquand and Biquand-Guyot, 1992). As young animals age, young companions influence one another's dietary habits (Stolba et al., 1990; Lynch et al., 1992; Biquand and Biquand-Guyot, 1992), grazing behavior (Lawrence, 1990; Howery, 1993), and use of supplemental foodblocks (Lawrence and Wood-Gush, 1988). This is exemplified when heifers and lambs made averse to a particular food consume more of that food when grazing with animals that eat the food (Lane et al., 1990; Ralphs and Olsen, 1990; Thorhallsdottir et al., 1990; Provenza and Burritt, 1991; Ralphs et al., 1994).

Social factors can also influence habitat selection. Archeological evidence suggests that the migratory behavior of a moose population in Norway follows a traditional pattern that has been unchanged for the last 5,000 years, apparently because of transgenerational learning between mother and offspring (Anderson, 1991). Mother's influence on her offspring declines after weaning, when peers begin exerting influence on food and habitat selection, but as adults, offspring again show a high degree of fidelity to the home range of their mother (Lawrence and Wood-Gush, 1988; Lawrence, 1990; Howery, 1993). Social interactions vary in importance depending on familiarity of the individuals. For instance, sheep released in an established herd in southeastern Norway did not join other members of the herd and they strayed as far away as 14 km from the herd's normal range (Warren and Mysterud, 1993).

It is evident that acquired food preferences and social interactions influence food and habitat selection, but it is not known how these factors interact to influence use of the environment. I designed experiments to determine how preferences for particular foods influenced use of the environment by subgroups of sheep, and if social factors could override acquired preferences and aversions.

2. Animals, materials, and methods

I conducted four experiments at the Green Canyon Ecology Center, Utah State University, Logan, Utah, USA. Each experiment was designed to assess how the location of a preferred food affected use of the environment by subgroups of animals with different dietary habits. The experiments were conducted in two different pastures. For Experiment 1, I used a 0.25-ha pasture dominated by the grass *Bromus*

tectorum and shrubs of the genus *Caragania*. For Experiments 2 through 4, I used a 1-ha pasture dominated by two grass species, *Bromus inermis* and *Dactylis glomerata*. Lambs used in Experiment 1 were different from those used in Experiments 2 through 4. Lambs received a basal diet of alfalfa pellets ad libitum, soybean meal, and one of two grains along with salt and water ad libitum. In all cases, lambs had no prior experience with the foods used in the experiments.

2.1. Experiment 1

The objective of the first experiment was to assess the effects of food preference on choice of foraging locations by lambs. I separated lambs that had been reared together into two groups of six animals each. Lambs in one group were exposed to milo whereas lambs in the other group were exposed to wheat. Following a 14-d exposure, lambs that received milo were given wheat for 3 d. For each day that animals consumed wheat, they received a mild dose ($150 \text{ mg kg}^{-1} \text{ BW}$) of lithium chloride (LiCl) to condition an aversion to the novel food (du Toit et al., 1991). Lambs that had received wheat were given milo for 3 d and dosed with LiCl. Two separate groups of six lambs that preferred milo (M) or wheat (W) then were exposed to the 0.25-ha pasture for 4 d to familiarize them with the environment and with the locations of the two foods, which were placed at opposite ends of the pasture.

To determine the degree to which food preferences affected choice of foraging locations, three lambs were randomly chosen from each group to form two subgroups of six lambs, three that preferred milo and three that preferred wheat (M + W). Each subgroup was then exposed for 30 min to the pasture over 3 d. Milo (3150 g) was

placed on one end and wheat (3150 g) on the other end. After each 30-min interval, lambs were returned to their original groups. Lambs had access to alfalfa pellets and water ad libitum in the pens, and water was placed in the center of the pasture during testing.

To further assess the degree to which food preference affected choice of foraging location, I formed subgroups consisting of all combinations of 1M + 3W and 1W + 3M. When a lamb that preferred milo was exposed with three lambs that preferred wheat, I placed 700 g of milo at one end and 2100 g of wheat at the other end and vice versa when one lamb that preferred wheat was exposed with three lambs that preferred milo. I recorded the location (i.e., which half of the pasture) and the activity (i.e., eating wheat or milo, grazing) of each animal at 1-min intervals for 30 min on 3 d.

As a final test to assess the degree to which preference for food affected foraging location, I switched locations of milo and wheat in the pasture. Lambs were exposed to the pasture as a group of six animals that either preferred milo or wheat. I placed 2100 g of each grain at both ends of the pasture, and recorded the location and the activity of each animal at 1-min intervals for 30 min on 3 d.

2.2. *Experiment 2*

The objective of this study was similar to Experiment 1 in that I examined the effects of food preferences on choice of foraging locations by lambs, but in Experiment 2 LiCl was not initially used to condition an aversion and we used a larger pasture and more treatments. Eighteen 1-mo-old crossbred lambs were reared

separately in each of three treatment groups. Lambs in treatment 1 ate milo, those in treatment 2 ate wheat, and half of the lambs in treatment 3 ate milo while half ate wheat. Lambs were offered either milo or wheat daily for 4 mo to condition a preference for the food (Nolte et al., 1990). Groups of lambs were allowed to forage in the pasture daily for 4 mo prior to the study. During this time neither milo nor wheat was in the pasture.

During testing, milo and wheat were placed at opposite ends of the pasture, about 100 m apart. Three groups of lambs (n=6 lambs/group) from each treatment were allowed to forage separately in the pasture. For Treatments 1 and 2, lambs (6/group) had a preference for either milo (Treatment 1) or wheat (Treatment 2), but for Treatment 3, three lambs preferred milo and three lambs preferred wheat. Locations (i.e., which half of the pasture) and activities (i.e., eating milo or wheat, grazing) of individuals were recorded at 1-min intervals for 30 min for 4 d.

I also assessed the effect of amount of grain offered on use of the environment. I offered 2400 g/group on days 1 and 2 and 4800 g/group on days 3 and 4. After each observation period, grains (orts) were weighed to determine intake for the respective groups.

During Experiment 2, I observed that social interactions and dietary preferences had differing influences on choice of feeding location by lambs. I hypothesized that preexisting foraging patterns may have influenced the response of lambs to milo and wheat in the pasture. To assess this hypothesis, I observed how the pasture was used by lambs when the grains were not present. Each group was exposed for 30 min for 2

d. Locations were recorded every minute for individual lambs.

2.3. Experiment 3

I conducted a third study to determine if an aversion to one of the two foods would further influence use of the environment by the lambs used in Experiment 2. Lambs from all three treatments were exposed to the alternate food, either milo or wheat, for 2 d and given a mild dose ($150 \text{ mg kg}^{-1} \text{ BW}$) of LiCl if they ate the food. I used the same protocol for sampling as in Experiment 2.

2.4. Experiment 4

This experiment assessed the effects of rearing (companions vs. strangers) and food preference on choice of foraging location by lambs. Three lambs reared in a group that preferred milo and three lambs reared in a group that preferred wheat from Experiments 2 and 3 were combined to form subgroups with different dietary habits. Combining lambs that preferred milo from one treatment with lambs that preferred wheat from another treatment enabled us to indirectly compare the results when lambs were reared together (Experiments 2 and 3) or separately (Experiment 4). The sampling protocol was the same as that used in Experiments 1 to 3.

2.5. Statistical analyses

In Experiment 1, there were only two replications of each treatment (M + W) with three animals/replication, so I calculated means with 95% confidence intervals. Means were considered different when the intervals did not overlap. When I compared $3\text{M} + 1\text{W}$ or $3\text{W} + 1\text{M}$, there was sufficient replication to conduct an analysis of

variance. For Experiments 2 to 4, the design for the analysis of variance was a repeated measures (Hicks, 1993). There were three replications/treatment with six animals/replication. For Experiment 4, five subgroups were formed by combining three animals from treatment 1 with three animals from treatment 2. One lamb died between Experiments 3 and 4, which reduced the number of subgroups from six to five. Differences among means were tested by least significance difference (LSD) when F-values were significant at $P=0.05$ (Gomez and Gomez, 1984). Data were analyzed using the statistical computer package Rummage (Bryce, 1980).

3. Results

3.1. Experiment 1

Lambs with different food preferences foraged in different locations. Lambs that preferred milo spent more time eating milo during the first 20 min when 3 M fed with 3 W. Conversely, lambs that preferred wheat spent more time eating wheat (Table 1). The average intake of milo was 2980 g (95% CI \pm 686), whereas the average intake of wheat was 2643 g (95% CI \pm 651). Lambs that preferred milo spent more time in the milo area during all three periods while animals that preferred wheat spent more time in the wheat area during period 1 (Table 1).

When one M or one W lamb was exposed to the pasture with three lambs with different dietary preferences, the lamb with different dietary habits always foraged alone on its preferred food during the first 10 min (F-value_(2,20)=43.56 for milo, 19.59

Table 1

Time spent eating and in different locations for groups (n=6 lambs/group) comprised of lambs that preferred either milo (n=3 lambs) or wheat (n=3 lambs) in Experiment 1

Period ¹	Food/Location	
	Milo	Wheat
<u>Percent of Time Eating</u>		
Preferred Milo		
1	63±22 ²	0.4±2 ²
2	16±10	1.3±2
3	5±6	4.0±8
Preferred Wheat		
1	0	68±27
2	0.4±2	12±10
3	0	18±20
<u>Percent of Time in Location</u>		
Preferred Milo		
1	92±16	8±16
2	80±18	20±18
3	74±22	26±22
Preferred Wheat		
1	30±15	70±15
2	60±10	40±10
3	45±14	55±14

¹Each period was 10 min.

²Values are means and the 95% confidence interval.

for wheat, 7.34 for area use, $P < 0.05$; Table 2). After the initial 10-min period, all lambs grazed together.

When I switched locations of foods, lambs switched foraging locations. Lambs that preferred milo spent more time consuming milo while lambs that preferred wheat spent more time consuming wheat during the first period (Table 3).

3.2. Experiment 2

Lambs foraging in homogeneous groups that preferred milo (M) spent more time eating milo (F-value_(4,12)=5.34, $P < 0.05$), whereas lambs that preferred wheat (W) spent more time eating wheat (F-value_(4,12)=4.97, $P < 0.05$). But mixed groups, in which lambs preferred either milo or wheat (M + W), spent time eating both milo and wheat (Table 4). Lambs ate more grain (F-value_(6,18)=5.46 for milo, 6.53 for wheat, $P < 0.05$) when offered 4800 g/group on days 3 and 4 than when offered 2400 g/group on days 1 and 2, but amount of grain offered had no effect on time spent eating or use of the area. The time spent grazing increased (F-value_(2,12)=51.44, $P < 0.05$) as the 30-min interval progressed for all treatments. After the initial 10-min period, lambs did not differ (F-value_(4,12)=7.25, $P > 0.05$) in their use of the two areas.

When both grains were removed from the pasture, use of the area did not differ during period 1. All lambs spent more time in the milo area during period 2, and more time in the wheat area during period 3 (F-value_(2,12)=6.16, $P < 0.05$).

3.3. Experiment 3

Administering LiCl after lambs ate the alternate food did not strengthen their

Table 2

Time spent eating and in different locations for groups (n=4 lambs/group) comprised of 1 lamb whose food preferences differed from those of the other 3 lambs in Experiment 1

Period ¹	Food/Location	
	Milo	Wheat
<u>Percent of Time Eating</u>		
Preferred Milo		
1	42 ^{a*}	0 ^{c*}
2	3 ^b	0 ^c
3	5 ^b	1 ^c
Preferred Wheat		
1	0 ^b	59 ^a
2	0 ^b	15 ^b
3	0 ^b	9 ^{bc}
<u>Percent of Time in Location</u>		
Preferred Milo		
1	88 ^{a*}	12 ^{c*}
2	70 ^{ab}	30 ^{bc}
3	58 ^b	42 ^b
Preferred Wheat		
1	15 ^c	85 ^a
2	48 ^b	52 ^b
3	50 ^b	50 ^b

¹Each period was 10 min.

*Means within columns with differing superscripts are different ($P < 0.05$).

Table 3

Effect of switching food locations on time spent eating for homogeneous groups (n=6 lambs/group) comprised of lambs that preferred either milo (n=6 lambs) or wheat (n=6 lambs) in Experiment 1

Period ¹	Food	
	Milo	Wheat
Preferred Milo		
1	50±20 ²	7±3 ²
2	3±4	7±2
3	13±22	2±2
Preferred Wheat		
1	0	74±4
2	0	4±4
3	0	2±2

¹Each period was 10 min.

²Values are means and the 95% confidence interval.

affinity for the area that contained their preferred food. Instead, lambs in M + W continued to eat both milo and wheat, while lambs in homogeneous groups continued eating their preferred grains (F-value_(4,12)=15.44 for milo, 29.82 for wheat, $P<0.05$; Table 5), which is similar to the outcome of Experiment 2. The time spent eating (from 7 to 13%) and intake (from 1440 to 2688 g) of grain increased as the amount of grain offered increased from 2400 g/group to 4800 g/group. This response was accompanied by a decrease in grazing time during the first period. Grazing time increased as each period progressed (F-value_(4,12)=4.08, $P<0.05$).

3.4. Experiment 4

Lambs reared separately, and with different food preferences, fed on different foods (Table 6). This is in contrast to Experiments 2 and 3, where lambs reared

Table 4

Time spent eating and in different locations for groups comprised of lambs that preferred either milo (n=6 lambs/group) or wheat (n=6 lambs/group), or for groups (n=6 lambs/group) where some lambs preferred milo (n=3 lambs/group) and others preferred wheat (n=3 lambs/group) (M + W) in Experiment 2

Period ¹	Food/Location	
	Milo	Wheat
<u>Percent of Time Eating</u>		
Preferred Milo		
1	46 ^{a*}	0 ^{c*}
2	7 ^c	0 ^c
3	9 ^c	1 ^c
Preferred Wheat		
1	10 ^c	59 ^a
2	8 ^c	15 ^b
3	9 ^c	9 ^{bc}
M + W		
1	30 ^{ab}	29 ^{ab}
2	11 ^{bc}	25 ^{ab}
3	8 ^c	10 ^{bc}
<u>Percent of Time in Location</u>		
Preferred Milo		
1	86 ^{a*}	14 ^{b*}
2	39 ^b	61 ^a
3	32 ^b	68 ^a
Preferred Wheat		
1	36 ^b	64 ^a
2	32 ^b	68 ^a
3	49 ^b	51 ^a
M + W		
1	37 ^b	63 ^a
2	51 ^b	49 ^a
3	39 ^b	61 ^a

¹ Each period was 10 min.

*Means within columns with differing superscripts are different (P<0.05).

Table 5

Time spent eating and in different locations, after receiving lithium chloride, for groups comprised of lambs that preferred either milo (n=6 lambs/group) or wheat (n=6 lambs/group), or for groups (n=6 lambs/group) where some lambs preferred milo (n=3 lambs/group) and others preferred wheat (n=3 lambs/group) (M + W) in Experiment 3

Period	Food/Location	
	Milo	Wheat
<u>Percent of Time Eating</u>		
Preferred Milo		
1	49 ^{a*}	0 ^{c*}
2	3 ^c	0 ^c
3	1 ^c	0.4 ^c
Preferred Wheat		
1	1 ^c	58 ^a
2	0.3 ^c	1 ^c
3	0.4 ^c	1 ^c
M + W		
1	33 ^b	12 ^b
2	5 ^c	6 ^{bc}
3	8 ^c	1 ^c
<u>Percent of Time in Location</u>		
Preferred Milo		
1	76 ^{ab*}	24 ^{de*}
2	42 ^d	58 ^b
3	45 ^{cb}	54 ^{bc}
Preferred Wheat		
1	19 ^e	81 ^a
2	53 ^{bcd}	47 ^{bcd}
3	56 ^{abcd}	44 ^{bcde}
M + W		
1	67 ^{abc}	33 ^{cde}
2	61 ^{abcd}	39 ^{bcde}
3	77 ^a	23 ^e

¹ Each period was 10 min.

*Means within columns with differing superscripts are different ($P < 0.05$).

Table 6

Time spent eating for groups (n=6 lambs/group) comprised of lambs that were reared separately (strangers) and that preferred either milo (n=3 lambs) or wheat (n=3 lambs) in Experiment 4

Period ¹	Food	
	Milo	Wheat
	Preferred Milo	
1	63 ^{a*}	0 ^{b*}
2	8 ^b	0 ^b
3	5 ^b	0 ^b
	Preferred Wheat	
1	0 ^b	55 ^a
2	0 ^b	8 ^b
3	0 ^b	1 ^b

¹ Each period was 10 min.

*Means within columns with differing superscripts are different ($P < 0.05$).

together, but with different dietary experiences, often fed together. After the initial 10-min segment, lambs grazed as a group and there were no differences (F -value_(2,16)=2,58, $P > 0.05$) in area of use.

4. Discussion

My results are consistent with the notion that locations of preferred foods influence choice of foraging location (Razmi, 1978; Senft et al., 1985; Lawrence and Wood-Gush, 1988), and that social interactions affect grazing distribution (Lynch et al., 1992; Howery, 1993). In essence, my findings suggest the relative importance of the location of preferred foods and social interactions vary depending on prior experience of individuals with forages and with other members of the flock.

4.1. Location of foods

In every experiment, lambs spent more time in the area containing their preferred food when that food was available (Tables 1 to 6). This occurred whether or not lambs were made averse to one of the foods using LiCl, suggesting that exposure to a food early in life can condition strong preferences for familiar foods and avoidance of novel foods (Mirza and Provenza, 1994; Provenza, 1994). Furthermore, when grain was absent, there was no difference in use of any particular area in the pasture, which is consistent with the importance of food preference in choice of foraging locations (Roath and Krueger, 1982; Senft et al., 1985; Stuth, 1991). Other studies have shown that manipulation of feed locations (Razmi, 1978), forage quality (Samuel et al., 1980), and location of supplemental feeds (Lawrence and Wood-Gush, 1988) all affect choice of foraging location.

Switching the location of a preferred food caused lambs to switch foraging locations. On the first day when the foods were moved, lambs initially walked to the location where milo (wheat) had been located, and within 5 min began walking in the opposite direction. Within 20 min, lambs were at the other end of the pasture eating their preferred grain. On the second day, lambs returned again to the location where their preferred food was originally, and then travelled quickly to the new location. On the third day, lambs went directly to the new location. These results are consistent with the idea that animals change foraging locations in response to changes in availability of preferred foods (Bailey et al., 1989a, b).

4.2. *Social interactions*

Food preference had a greater effect on choice of foraging location when sheep fed with strangers (Experiment 4) than when they fed with companions (Experiments 2 and 3). These results are consistent with the idea that social relationships within a herd affect the degree to which animals influence one another's choice of foraging location (Howery et al., in press), and with observations that lambs placed in an unfamiliar herd remained separate from the rest of the herd and foraged in different locations (Warren and Mysterud, 1993). Others have reported that different foraging experiences cause disparate dietary habits (Mirza and Provenza, 1990, 1994; Biquand and Biquand-Guyot, 1992), which can affect preference for foraging locations, as illustrated in a cross-fostering study with ewes and lambs (Key and MacIver, 1980).

Food preference also had a primary effect on choice of foraging location in Experiment 1, but not in Experiments 2 and 3. In Experiment 1, lambs in mixed groups always fed independently on their preferred food, but in Experiments 2 and 3 their response varied. In some groups, lambs that preferred wheat grazed in the vicinity while peers ate milo, and then lambs that preferred milo grazed in the vicinity while peers ate wheat. In other groups, one or two lambs travelled to the opposite end of the pasture to eat their preferred grain. In yet another group, three lambs foraged on milo and three lambs foraged on wheat. Finally, in one case lambs that preferred milo foraged on milo until the majority was consumed, and then all lambs in the group grazed throughout the pasture showing no propensity to eat wheat.

There are several reasons why the results of Experiment 1 may have differed from those of Experiments 2 and 3. The smaller pasture used in Experiment 1 may have allowed lambs to forage on different foods without being far enough apart to affect the outcome. And some lambs remained in holding pens, at the east side at both ends of the pasture, which may have affected the response. Moreover, in Experiment 1, animals that preferred milo were exposed separately from animals that preferred wheat for 4 d before testing lambs as mixed subgroups; this previous experience with the food and pasture may have strengthened the response of the lambs. In Experiment 1, I conditioned an aversion to the novel food by exposing lambs as homogeneous groups that preferred either milo or wheat for 3 d. Individual lambs were dosed on each day they consumed the novel food. Conversely, in Experiment 3, I attempted to condition an aversion to a food the lambs had eaten, and I exposed lambs to the "novel" food for only 2 d. Lambs from the mixed subgroups (M + W) consumed small amounts of the "novel" food when foraging on the pasture during Experiment 2, and as a result the strength of the food aversion was likely weaker for Experiment 3 (Burritt and Provenza, 1991, in press). Finally, during Experiment 3, lambs fed in mixed groups during exposure to the "novel" foods, which likely diminished the strength of the aversion (Provenza and Burritt, 1991).

5. Implications

Studies of cattle foraging on a 1,030-ha allotment during the summer clearly show that (1) individual animals have distinctly different home ranges, (2) the home ranges of cows vary from 70 to 327 ha, (3) foraging bouts generally last from 2 to 3

h, and (4) cattle typically move 1 to 2 km from loafing areas to foraging areas (Howery, 1993). These data suggest that cattle meet their needs with a relatively small part (7-33%) of the total area of the allotment. My results suggest that both food preferences and social interactions influence choice of feeding location. A synthesis of these findings suggests that the distribution of livestock is a function of foraging with peers in the nearest habitats that contain preferred foods.

I believe my results offer opportunities to manipulate use of environment by livestock. For example, early exposure to foods or supplements, followed by strategic placement of those foods or supplements, may improve animal distribution. Similarly, social models (i.e., mother or peers) may aid in improving distribution. Field studies have shown that both mother and peers influence spatial distribution, which is in agreement with my findings that social interactions influence choice of feeding locations. Exposing social groups to underutilized habitat types early in life may increase their use when animals are faced with a choice, for instance, between upland and riparian habitats. Finally, some rangeland managers report that livestock can learn to avoid riparian habitats when herding is practiced on a regular basis and water and forage are available in upland locations. Herding integrates the importance of social interactions and experience with foods by controlling the exposure of social groups to particular foods and habitats, and thus probably offers the best opportunity to improve grazing distribution.

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CHAPTER III
FAMILIARITY WITH A PASTURE INFLUENCES CHOICE
OF FEEDING LOCATION BY SHEEP

Abstract

The objective of this study was to determine if lack of familiarity with an environment increased the importance of social interactions in the choice of foods and feeding locations by lambs with different dietary habits. Three groups of crossbred lambs (18/group) were reared separately for 2 mo. One group was exposed daily for 6 h to the 1-ha experimental pasture, a second group was exposed daily for 6 h to a different 0.5-ha pasture with similar forage species, and a third group was held in confinement and not allowed to graze. Half of the lambs within each treatment were fed milo (*Sorghum bicolor*) and half were fed wheat (*Triticum aestivum*), to condition preferences for milo and wheat, respectively. To determine the effect of social influences on food selection, three lambs that preferred milo and three that preferred wheat were exposed as a group to the 1-ha experimental pasture, with milo and wheat placed at opposite ends, about 100 m apart. I found that subgroups familiar with the pasture typically fed in separate locations, whereas lambs naive to the environment foraged together. When I exposed subgroups to the pasture without either grain present, they did not differ in location of use, which indicates that preference for grain influenced choice of feeding location. Finally, preferences for either milo or wheat persisted for animals familiar with the experimental pasture, but lambs naive to the pasture acquired a preference for both foods. Collectively, these results suggest that

social factors may override food preferences in novel environments, while food preferences may be more influential in determining feeding locations in familiar environments.

1. Introduction

When lambs are in a familiar environment, preference for particular foods plays an important role in their choice of foraging locations. For example, subgroups of lambs that acquired preferences for different foods and foraging locations, as a result of experiences early in life, generally fed in different locations (Chapter II). Moreover, their preference for foods was typically stronger than their preference for the companionship of other lambs, especially when the lambs were strangers (i.e., they had not been reared together). Thus, familiarity with the physical and social environment caused lambs to restrict their foraging to particular foods and locations in the environment.

This may not be true when lambs are introduced into an unfamiliar area because they lack information about the physical environment (e.g., locations of foods, concentrations of nutrient and toxins in different foods) (Provenza and Balph, 1987; Provenza and Cincotta, 1993). In such cases, being with familiar companions may be more important than preferences for foods in a lamb's choice of foraging location (Winfield et al., 1981). As a result, preferences for foods and foraging locations may come to represent the collective preferences of the group, which may cause animals to use a greater portion of the environment. For instance, when sheep were released onto an unfamiliar range in Norway, they ranged over 150 km² (Warren and Mysterud,

1993).

My objective was to determine if lack of experience with the physical environment increased the importance of social interactions in the choice of foods and foraging locations by lambs. I hypothesized that social interactions would have more influence than dietary preferences in choice of foraging locations by lambs in an unfamiliar environment.

2. Animals, materials, and methods

I conducted the experiment, consisting of three trials, at the Green Canyon Ecology Center, Utah State University, Logan, Utah, USA. The first two trials assessed how diet preferences and social interactions affected choice of foraging location in a 1-ha pasture dominated by *Bromus inermis* and *Dactylis glomerata*. For the third trial, food preferences of lambs were determined in individual pens. During all trials, lambs received a basal diet of alfalfa pellets (ad libitum), soybean meal, and one of two grains along with salt and water ad libitum.

Fifty-four Suffolk-Polypay-Columbia-Targee crossbred lambs were randomly allocated to each of three treatments (18/treatment), and lambs in each treatment were reared separately. In each treatment, half of the lambs were fed milo while half were fed wheat daily for 2 mo to condition a preference for the food (Nolte et al., 1990). Lambs from Treatment 1 were allowed to forage in the experimental pasture daily for 6 h during the 2 mo prior to the study. Lambs from Treatment 2 were allowed to forage in a 0.5-ha pasture with similar forage species. During this time neither milo nor wheat was in the pastures. Lambs from Treatment 3 were held in confinement

and not allowed to graze prior to the study.

2.1. Trial 1

Before assessing the influence of experience with the environment on choice of feeding location, I exposed lambs that preferred either milo (n=9) or wheat (n=9) from each treatment to the experimental pasture for 4 d. Milo (3600 g) and wheat (3600 g) were placed at opposite ends of the pasture, about 100 m apart. Activities (i.e., eating milo or wheat) of individuals were recorded at 1-min intervals for 30 min for 4 d. Lambs were herded from one food location to the other daily to insure they were familiar with the locations of both grains.

To determine how experience with the experimental pasture influenced food selection and social interactions, three subgroups of lambs (n=6 lambs/group) from each treatment were allowed to forage in the pasture. Three lambs in each subgroup initially preferred milo and three preferred wheat. Milo (2400 g) and wheat (2400 g) were placed in the same locations used during in the initial exposures. Locations (i.e., which half of the pasture) and activities (i.e., eating milo or wheat, grazing) of individuals were recorded at 1-min intervals for 30 min for 4 d. Orts of milo and wheat were weighed to determine group intake.

2.2. Trial 2

In Trial 2, I observed how the pasture was used by sheep when grains were not present. I hypothesized if location of preferred grain affected location of use, then treatments should not differ in use of the pasture when the grains were removed. Each

group was exposed for 30 min for 2 d. Locations and activities were recorded for individual lambs every minute.

2.3. Trial 3

To determine if lambs maintained their initial food preferences throughout the study, I penned lambs individually and offered each animal a choice between 700 g of milo and 700 g of wheat for 5 min for 2 d. Orts of each food were weighed to determine intake.

2.4. Statistical analyses

During the initial 4 d of Trial 1, two groups of nine lambs from each treatment were exposed to the pasture. Because treatments were not replicated, I analyzed behavioral responses and intake data using repeated measures analysis of variance for nonreplicated studies, and used the highest interaction term as the residual error term (Hicks, 1993). For the remainder of Trial 1 and for Trial 2, there were three replications/treatment with six animals/replication. Consequently, traditional repeated measures analysis of variance was used to determine significant effects (Hicks, 1993). For Trial 3, there were three treatments and lambs were nested within treatments. Because data were collected for 2 d, repeated measures analysis of variance was used. Differences among means were tested by least significance difference when $P \leq 0.05$ (Gomez and Gomez, 1984). Data were analyzed using the statistical computer package JMP (SAS, 1989).

3. Results

3.1. Trial 1

For the initial 4 d, lambs ($n=9/\text{group}$) that preferred milo spent more time consuming milo, while lambs that preferred wheat spent more time consuming wheat, regardless of treatment ($P<0.05$; Table 7). Lambs that preferred milo ate 4,754 g of milo and 1,714 g of wheat, whereas lambs that preferred wheat ingested 4,750 g of wheat and 1,700 g of milo.

When lambs were exposed in mixed subgroups of three that preferred milo and three that preferred wheat, their response depended on their experience with the environment. Subgroups familiar with the pasture and grazing (FF) typically fed in separate locations. Lambs that preferred milo spent more time consuming milo than wheat, whereas lambs that preferred wheat consumed both milo and wheat (F-value_(1,4)=17.97; Table 7). Nevertheless, one to three lambs often fed on wheat while the other lambs consumed milo. Lambs naive with the pasture and grazing (NN) and lambs naive to the pasture and familiar with grazing (NF) fed as single subgroups on both grains. As a result, there were no differences in the amount of time spent eating milo or wheat for NN lambs, regardless of initial food preference (F-value_(1,4)=4.4; Table 7). Lambs in the NF subgroups that preferred wheat spent more time consuming wheat, while lambs that initially preferred milo showed no preference for milo over wheat (F-value_(1,4)=9.1; Table 7). Lambs generally did not consume milo on day 1, they ate only small amounts on day 2, and they ate amounts similar to those consumed by F and NN subgroups on days 3 and 4.

Table 7

Percent of time spent eating milo and wheat for lambs familiar with the pasture and grazing (FF), naive with the pasture and grazing (NN), and naive with the pasture and familiar with grazing (NF). Lambs were exposed as subgroups of nine lambs that were reared together and preferred the same food during the initial 4 d. During Trial 1, lambs reared together were exposed in mixed subgroups of three lambs that preferred milo and three that preferred wheat

Treatment	Preference	Initial Exposure		Mixed Subgroups	
		Milo	Wheat	Milo	Wheat
FF	Milo	18 ^A	4 ^B	18 ^a	8 ^b
FF	Wheat	14 ^B	31 ^A	14	16
NN	Milo	20 ^A	15 ^B	9	13
NN	Wheat	5 ^B	28 ^A	6	14
NF	Milo	25 ^A	7 ^B	16	15
NF	Wheat	5 ^B	24 ^A	12 ^b	19 ^a

^{A-B}Means within rows for the initial exposure with different superscripts are different ($P < 0.05$).

^{a-b}Means within rows with different superscripts are different ($P < 0.05$) for mixed subgroups exposed to the pasture.

Lambs with different levels of familiarity with the environment responded differently in choice of feeding location. FF and NN subgroups spent similar amounts of time in the half of the pasture containing milo ($P>0.05$, $F\text{-value}_{(6,30)}=4.0$), even though FF lambs fed in separate subgroups and NN lambs fed in single subgroups (Table 8). Conversely, NF subgroups spent little time during days 1 and 2 in the milo half of the pasture (Table 8).

3.2. Trial 2

Foraging patterns of the groups were similar when preferred foods were removed from the pasture. All animals preferred the wheat area, but use differed across the 30-min observation period ($P<0.05$, $F\text{-value}_{(2,4)}=7.88$). Lambs spent somewhat less time in the wheat area during period 1 (61%) than during periods 2 (82%) and 3 (79%).

3.3. Trial 3

Experience with the environment did not affect food preference of lambs familiar with the pasture, but changed food preferences of lambs naive to the pasture (Table 9). Preferences for milo and wheat persisted for lambs familiar with the experimental pasture ($P<0.05$, $F\text{-value}_{(1,32)}=21.4$), whereas naive lambs ate both foods ($P>0.05$, $F\text{-value}_{(1,32)}=1.5$ for NN lambs, 0.05 for NF lambs; Table 9).

4. Discussion

Lambs familiar with the experimental pasture typically foraged in separate locations, which agrees with my previous findings that experience influences choice of

Table 8

Percent of time spent in the milo area for lambs familiar with the pasture and grazing (FF), naive with the pasture and grazing (NN), and naive with the pasture and familiar with grazing (NF). Observations were recorded with milo and wheat in the pasture during Trial 1

Treatment	Day			
	1	2	3	4
FF	42	46	31	27
NN	51	52	53	44
NF	0*	7*	23	46

*Values are significantly ($P < 0.05$) lower than the remaining treatment values.

LSD_(0.05) = 22.44

Table 9

Average intake (g/lamb) of milo and wheat for lambs that were familiar with the experimental pasture and grazing (FF), naive with the experimental pasture and grazing (NN), and naive with the experimental pasture and familiar with grazing (NF) when given a choice between 700 g of milo and 700 g of wheat after Trials 1 and 2

Treatment	Preference	Milo	Wheat
FF	Milo	555 ^{a*}	160 ^b
FF	Wheat	240 ^b	456 ^a
NN	Milo	453	273
NN	Wheat	326	364
NF	Milo	317	298
NF	Wheat	339	314

*Means within rows with different subscripts are significantly ($P < 0.05$) different.

feeding location (Chapter II). In both studies, dietary preferences often overrode social interactions, as is evident from the fact that some lambs fed at one end of the pasture while the others fed at the opposite end. The location of preferred food influenced choice of feeding location in other studies as well (Razmi, 1978; Lawrence and Wood-Gush, 1988; Bailey et al., 1989a, b).

Lambs naive with the experimental pasture fed together at the same location. As a result, social interactions ameliorated preferences for milo and wheat, which is consistent with data that show social interactions affect food selection (Lane et al., 1990; Thorhallsdottir et al., 1990a, 1990b; Provenza and Burritt, 1991; Ralphs et al., 1994). Nevertheless, naive lambs still consumed both foods, which suggests that preference for grain influenced choice of feeding location. Others have also shown that locations of familiar foods influenced animal distribution in novel environments. Sheep increased their searching time for a familiar food (alfalfa) in new environments as the amount of alfalfa decreased (Gluesing and Balph, 1980). Deer also developed foraging patterns based on the location of a familiar food (apples) in a novel environment (Gillingham and Bunnell, 1989).

Social interactions may be crucial for animals in new locations because they lack knowledge of foods and food locations (Provenza and Balph, 1987; Galef, 1993; Provenza and Cincotta, 1993; Provenza, 1994). Naive livestock are often introduced to a new environment with other livestock that are familiar with the environment to facilitate efficient foraging. However, animals often avoid foraging with strangers (Winfield et al., 1981). For instance, sheep introduced to a new environment in

Norway did not join the existing herd and ranged as far as 150 km away from the herd's normal range (Warren and Mysterud, 1993). Similarly, results in Chapter II exhibited that lambs preferred to forage with companions and avoided feeding with strangers. Thus, strangers may have little effect on the foraging behavior of naive animals.

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CHAPTER IV
OBSERVATIONS OF CATTLE GRAZING BEHAVIOR IN THE
SAWTOOTH NATIONAL FOREST, IDAHO, USA:
IMPLICATIONS FOR MANAGEMENT

Abstract

This chapter describes cattle observations on a 1,030-ha allotment in the Sawtooth National Forest, Idaho, USA. Locations, habitats, and activities were recorded for individual cows during the summer grazing seasons (June-July) in 1990 and 1991. Home ranges of individual cows were calculated and compared among years. Home ranges shifted and (or) increased in size between years, apparently in response to lack of water. Cattle home range sizes were not affected by forage availability. Home ranges increased in size when forage and water were depleted but did not increase when only forage was depleted. Nevertheless, cows exhibited home range fidelity (35% overlap). Experiences early in life influence habitat use, and may explain why cows used the same areas each year, even though forage and water were depleted. Results also indicated that habitat use varied throughout the day. Cows fed in sagebrush-steppe and used riparian zones for drinking and loafing. Collectively, these results imply that distribution could be improved through (1) controlling the amount of experience livestock have with riparian zones, (2) providing familiar foods in underutilized areas, (3) culling animals that spend a disproportionate amount of time in riparian zones, (4) herding, and (5) providing alternate drinking and loafing sites.

1. Introduction

Experimental analyses of foraging behavior are often criticized because of their inability to account for the complexity of "natural" systems (Peters, 1991), but experimental studies can provide the conceptual basis for ecological thought (Romesburg, 1981). Nevertheless, before concepts can become an effective basis for management, they should be tested under natural systems without the influence of experimental manipulations. Observational studies allow herbivores to respond to environmental variables without experimental constraints, but they are limited to descriptions of what and when rather than an understanding of why and how natural phenomena occur (Provenza, 1991). Thus, both approaches to science are crucial for understanding and managing ecosystems. The objective of this chapter is to integrate habitat and home range data from a two-year study of cattle grazing a 1,030-ha allotment with the experimental evidence presented in Chapters II and III. In doing so, I hope to develop suggestions for improving livestock distribution and habitat use.

Howery (1993) originally used data from this study to determine (1) if individual cows exhibit unique home ranges and (2) the influence of mother on her offspring's home range and habitat use in subsequent years. Analyses showed that four distinct home ranges existed, Maxfield, Thompson, Intermediate Maxfield, and Intermediate Thompson (Howery et al., in press). Results also indicated that some home ranges shifted from one category to another between years, possibly in response to forage and water availability (Howery et al., in press). Home ranges may remain similar over time, even though their categorization changed. For instance, home ranges

may increase in size or shift in location to compensate for water and forage shortages. If so, home ranges should overlap between years but vary in size and absolute location as forage and water availability varies. I measured home range overlap and variations in size between years to assess the relationship between home ranges and forage and water availability. I also evaluated habitat use (sagebrush-steppe vs. riparian zones) over time.

2. Animals, materials, and methods

2.1. Study site

This study was conducted on the Maxfield-Thompson Grazing Allotment (1,030 ha) in the Sawtooth National Forest near Fairfield, Idaho, USA, during the summers of 1990 and 1991. The study site has two riparian zones, Maxfield and Thompson Creeks, both of which are dominated by an overstory of willows (*Salix* spp.) and an understory of sedges (*Carex* spp.) and rushes (*Juncus* spp.). The surrounding vegetation is dominated by sagebrush (*Artemisia tridentata*)-steppe with the herbaceous component consisting of a fescue/wheatgrass (*Festuca/Pseudoroegneria*) mix. Elevation ranges from 1,767 to 2,072 m. Topography is variable, with sagebrush-steppe and riparian habitats characterized by moderate slopes surrounded by steeper slopes covered with aspens (*Populus tremuloides*) and conifers (*Pseudotsuga menziesii*/*Pinus ponderosa*). Maxfield Creek differs from Thompson Creek in that it has fewer willows, more streambank damage, and some channel widening.

2.2. Animal collaring and sampling

Originally, 135 adult Angus-Hereford-Saler crossbred cows were randomly selected and collars were placed around each individual's neck. Each collar had a different combination of colored symbols (squares, triangles, and bars) for individual identification. One hundred and sixteen cows were observed in 1990 and 87 of those were observed in 1991. The number of cows decreased each year because some died, were culled, or were left on winter range. Stock density was approximately half as heavy in 1991 as in 1990 (0.14 vs. 0.29 head/ha) in response to drought.

Cows were monitored on the grazing allotment from June 22 to July 26 in 1990, and from June 21 to July 24 in 1991. Four observers were assigned to four different areas within the allotment. Each observer hiked and scanned an assigned area twice daily at random times (0530-2100 hrs). Collar identification, habitat type, and activity were recorded for each cow. Airphotos of the study site were carried by each observer. Airphotos were grided into 50 X 50 m pixels and assigned arbitrary coordinates. For each collared animal located, the observer recorded the appropriate map and coordinates of the pixel that represented the cow's location.

Observations were divided into four, 6-d periods. Each day was divided into three intervals, ranging from 0530-1100 hrs (morning), 1100-1500 hrs (midday), and 1500-2100 hrs (late-day).

2.3. Analysis of habitat and spatial use

The Map and Image Processing System (MIPSTM) was used to analyze habitat and home range data. All large-scale aerial photos and an orthophotoquad of the study

site were scanned into MIPS™. Aerial photos were georeferenced to the orthophotoquad so that animal locations and habitat use could be analyzed across the entire grazing allotment. A habitat map was created by digitizing around each habitat on the orthophotoquad.

Cow locations for each year were imported into MIPS™ and georeferenced to the orthophotoquad. Home range was calculated using the harmonic mean option. The harmonic mean method was used because it eliminates outliers that can erroneously inflate home range size (Dixon and Chapman, 1980). Home ranges were calculated using a 90% confidence level. I limited my analysis to the 87 cows that were present on the allotment both years. As a second constraint, I required each cow to be located at least 30 times based on the suggestion that 15 to 42 locations were required to adequately estimate home range (O'Brien, 1984). Finally, I combined Howery's (1993) classification of Maxfield and Intermediate Maxfield into group 1 (Maxfield) and Thompson and Intermediate Thompson into group 2 (Thompson) to compare home range size and overlap based on where each animal spent the majority of its time (i.e., 70% of its locations either on the Maxfield side or Thompson side of the allotment).

2.4. Quantitative analysis

Area size (ha) for each home range was calculated using MIPS™. An individual cow's home range from 1991 was overlaid with its 1990 home range. The total area of home range coverage was then calculated by combining home ranges for 1990 and 1991. I then used MIPS™ to calculate the area size (ha) of the polygon representing the amount of overlap between years. Percent (%) overlap was calculated

using the following equation:

$$\% \text{ overlap} = \frac{\text{ha of overlap}}{\text{total ha of both home ranges}} \times 100$$

I calculated means with confidence intervals for home range size and overlap. I assumed if confidence intervals did not overlap, means were different. For analysis of habitat use, I used analysis of variance for nonreplicated studies (Hicks, 1993), using the highest interaction as the error term. Means were separated using least significant difference (LSD) when $P \leq 0.05$ (Gomez and Gomez, 1984).

3. Results

3.1. Homogeneity in home ranges between years

Home ranges overlapped by 35% between years. Twenty-one cows exhibited substantial overlap (50-80%), while 13 exhibited moderate (40-50%) overlap. For 15 other cows, one year's home range was contained inside the other, indicating that one home range either increased from a central location or decreased toward a central location among years (Fig. 1). Cows with one home range contained inside of another were characterized by 27% (sem=4.1) overlap, while cows with home ranges that shifted in one direction or another accounted for 36% (sem=2.5) overlap. Only three cows did not have overlapping home ranges (Fig. 1).

3.2. Variations in home range size between years

From 1990 to 1991, 54% of the cows increased their home range size (\bar{x} =148

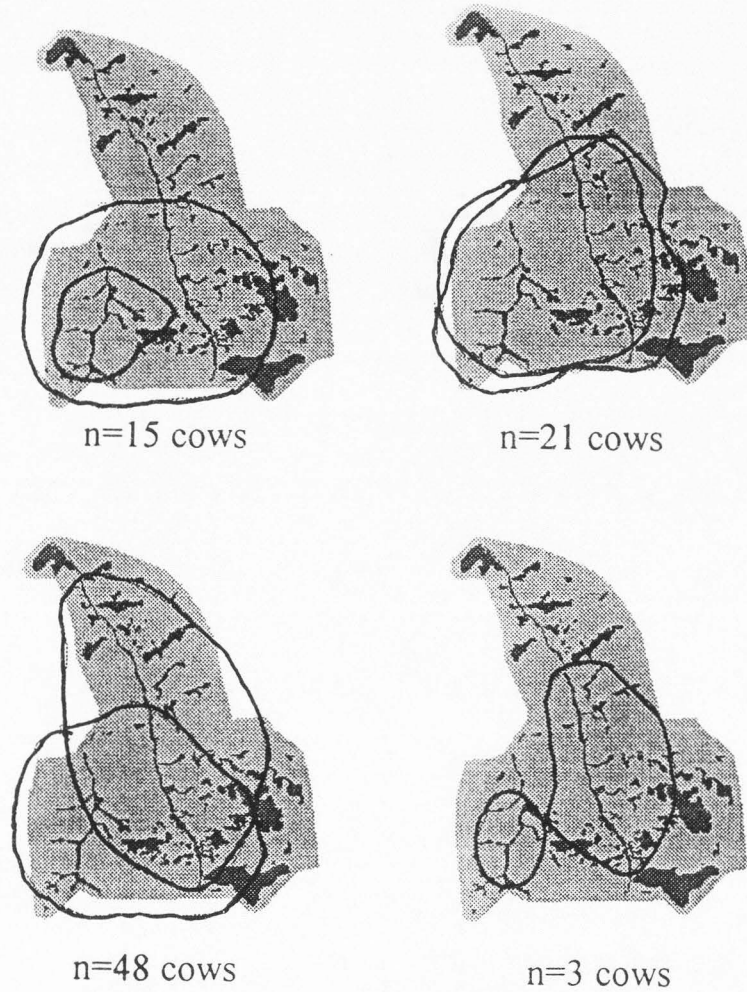


Fig. 1. Types of home range overlap between 1990 and 1991. One home range is completely contained within another in the top-left. Top-right corner illustrates home ranges that are almost equal in size and overlap. Bottom-left corner represents a home range that shifted from one year to the next. Bottom-right corner represents a home range that did not overlap.

ha, $sem=19.6$). Most cows that increased their home range size spent the majority of their time on the Maxfield side of the allotment during 1990. Conversely, cows on the Thompson drainage showed little change in home range size (Fig. 2). Home ranges were also larger if they contained water developments ($330 \text{ ha} \pm 28.4$ vs. $175 \text{ ha} \pm 20.7$) for both Maxfield and Thompson cows (Fig. 3) and in both years (Fig. 4).

3.3. *Habitat use*

Riparian and sagebrush-steppe habitats were preferred, but habitat use varied throughout the day. Cows spent the majority of their time in sagebrush-steppe during the early morning (0530-1100 hrs) regardless of time in the grazing season, whereas riparian zones were preferred during the rest of the day (1100-2100 hrs) (F-value_(2,6)=58.8 for sagebrush-steppe, 63.7 for riparian; Table 10).

3.4. *Activities associated with habitat use*

Activities varied with habitats. Cattle spent more time grazing (F-value_(2,6)=14.3) in sagebrush-steppe regardless of time of day (61% in sagebrush-steppe vs. 34% in riparian zones), while they typically loafed (F-value_(2,6)=5.6) in riparian zones regardless of time of the day (60% in riparian zones vs. 29% in sagebrush-steppe; Table 11). Time spent loafing in the riparian zones and time spent grazing in the sagebrush-steppe increased as the season progressed (Table 12).

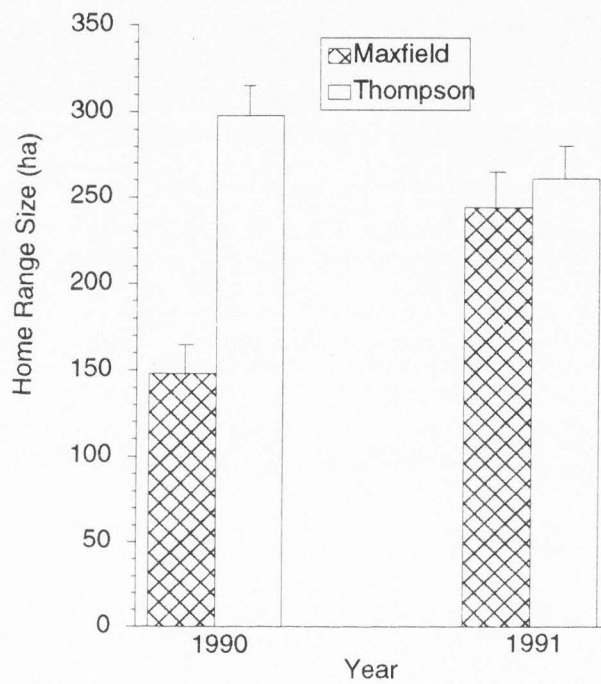


Fig. 2. Mean home range size and confidence interval for both Maxfield and Thompson cows during 1990 and 1991.

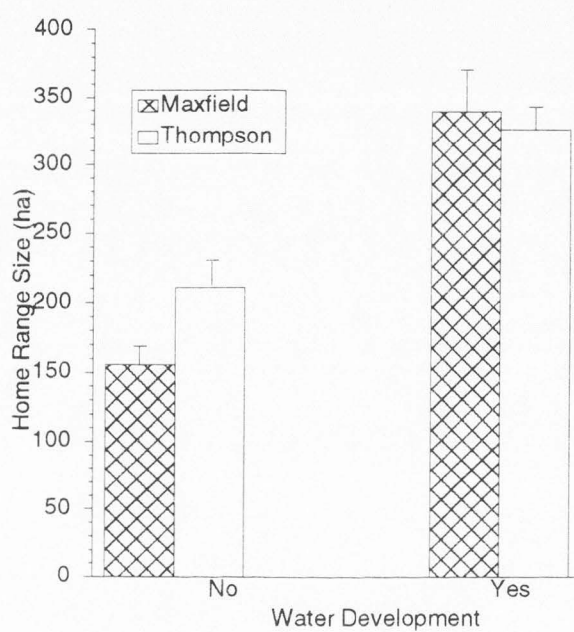


Fig. 3. Mean home range size and confidence interval for both Maxfield and Thompson cows with and without a water development within the home range boundary.

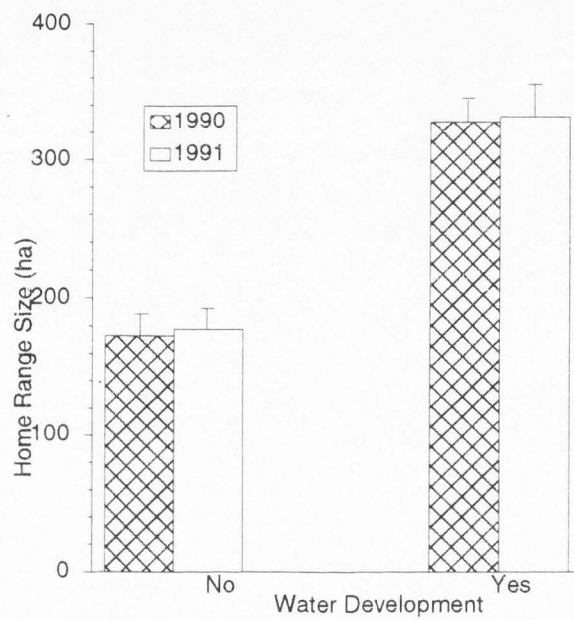


Fig. 4. Mean home range size and confidence interval for 1990 and 1991 with and without a water development inside the home range boundary.

Table 10
Percentage of cattle locations in each habitat type during 0530-1100, 1100-1600, and 1600-2100 hr

Habitat	Time of Day		
	0530-1100	1100-1600	1600-2100
Sagebrush-steppe	50 ^a	19 ^b	23 ^b
Riparian Zones	41 ^b	72 ^a	70 ^a

LSD_(0.05)=4 for sagebrush and for riparian zones.

Table 11
Percentage of activities in each habitat type during 0530-1100, 1100-1600, and 1600-2100 hr

Habitat	Time of Day		
	0530-1100	1100-1600	1600-2100

Grazing

Sagebrush-steppe	68 ^a	51 ^c	63 ^b
Riparian Zones	35 ^d	32 ^d	34 ^d

Loafing

Sagebrush-steppe	24 ^d	38 ^b	27 ^c
Riparian Zones	58 ^a	62 ^a	60 ^a

LSD_(0.05)=3 for grazing and 4 for loafing.

Table 12
Percentage of activities in each habitat type during periods 1 (June 21-June 27), 2 (June 30-July 6), 3 (July 9-July 15), and 4 (July 18-July 24)

Habitat	Period			
	1	2	3	4

Grazing

Sagebrush-steppe	52 ^b	65 ^a	62 ^a	63 ^a
Riparian Zones	37 ^{cd}	41 ^c	31 ^{de}	26 ^e

Loafing

Sagebrush-steppe	35 ^c	25 ^d	28 ^{cd}	30 ^{cd}
Riparian Zones	55 ^b	53 ^b	65 ^a	68 ^a

LSD_(0.05)=6 for grazing and 7 for loafing.

4. Discussion

4.1. Homogeneity in home ranges between years

Cows used similar home ranges in 1990 and 1991, which is evident by the 35% overlap between years. These results coincide with Howery et al. (in press), who observed 78% of cows showed consistent home range fidelity with 33% (n=29) exhibiting total home range fidelity, 45% (n=39) showing slight variation, 18% (n=16) showing moderate variation, and only 3% (n=3) showing no fidelity between years. Thus, these results are consistent with the notion that livestock (Hunter and Milner, 1963; Key and MacIver, 1980; Roath and Krueger, 1982a) and wildlife (Festa-Bianchet, 1986a, b; Cederlund et al., 1987; Anderson, 1991; Dubois et al., 1994) return to the same areas each year.

Some suggest herbivores "evaluate" forage availability in habitats while searching for food and "decide" whether or not to forage in the habitat and how long to stay (Stephens and Krebs, 1986). Howery's (1993) evaluation of individual habitat and home range use showed that some cows continued to feed in habitats and areas after forage was depleted. Roath and Krueger (1982b) reported some cows remained in riparian zones even after forage availability limited intake (also see Kauffman and Krueger, 1984). Similarly, moose in Norway continue to use the same winter range even though mortality rates were high (Anderson, 1991). My results (Chapters II and III) showed that experiences with foods, the environment, and conspecifics shaped habitat selection. Thus, site fidelity probably occurs because of experiences early in life rather than forage availability, which would explain why animals stayed in the

same areas after forage depletion. Furthermore, herbivores are often reluctant to consume novel foods (Provenza et al., 1995) and forage in novel environments (Warren and Mysterud, 1993; Chapter III).

4.2. Home range size and the influence of water developments

Home range size varied between 1990 and 1991. Fifty-four percent of the cows increased their home range size, with most of these classified as Maxfield cows in 1990 (Fig. 2). The increase in home range size may be due to the lack of precipitation in 1991 (321 mm in 1990 vs. 189 mm in 1991), which caused Maxfield Creek to stop running by the third collection period. This caused cows to enlarge their home ranges to include either Thompson Creek or other watering points. Lack of forage may have caused cows to increase home range size, but this is not likely because only Maxfield cows increased their home range size (Fig. 2). In addition, home ranges with water developments were larger in both years for Maxfield and Thompson cows (Fig. 3 and Fig. 4). This suggests that water developments influenced home range size even when water was not in short supply in 1990.

4.3. Habitat use and activities

Sagebrush-steppe and riparian zones were the preferred habitats but for different reasons; cattle fed more in sagebrush and loafed more in riparian zones (Tables 10 and 11). Although this pattern occurred throughout the grazing season, cows fed more in the riparian zones during period 1 than the other three periods (Table 12). Afterwards, loafing was the predominant activity on both Maxfield and

Thompson Creeks, which agrees with other observations that riparian zones serve as feeding areas only during the first few days of the grazing season and then serve as loafing and drinking sites (Gillen et al., 1985; Senft et al., 1985). Sagebrush-steppe was the preferred habitat in early morning, which corresponds with feeding time; at midmorning, cows returned to the riparian zones, drank, and loafed until late afternoon when they dispersed to different regions and fed, as has been shown in other studies (Hewson and Wilson, 1979; Squires, 1981).

5. Implications

Home range size increased as water supply depleted to include alternate watering locations. Increases in home range size increase the distribution of livestock across the landscape. Nevertheless, site fidelity occurs, which influences the absolute location of home ranges. Several factors may be important in influencing home range size and location. These include (1) alternative watering points, (2) strategic placement of familiar foods and supplements, (3) learning from mother and peers, (4) experience with habitats, and (5) herding.

Installing water developments in upland sites may provide an opportunity to increase use of the environment, even when water is not in short supply. For instance, water developments were associated with larger home ranges in 1990, even though water was available throughout the year in both riparian zones (Fig. 4). Other observations also suggest that location of watering points influences distribution (Low et al., 1981). Furthermore, several cows continued to forage around water developments in 1991, even after they stopped producing water (Howery, 1993;

Howery et al., in press). In addition, the same subgroups of cows were often associated with particular water developments, which is consistent with the idea that similar experiences are the basis for subgroups (Chapters II and III).

Managers may improve distribution by strategic placement of familiar foods or supplements in the environment. Others have reported that feeding location (Razmi, 1978; Lawrence and Wood-Gush, 1988) and locations of preferred foods (Bailey et al., 1989a, 1989b; Chapters II and III) influence habitat use. When I exposed lambs to a pasture with milo on one end and wheat on the other as described in Chapters II and III, lambs travelled directly to their preferred grains as soon as they entered the pasture. After the grains were consumed, lambs grazed the entire pasture, which may be a function of the small size (1 ha and 0.25 ha) of the pastures. In a larger pasture (e.g., 1,030 ha grazing allotment described in this study), preferred foods or supplements could be placed far enough apart to change grazing patterns and decrease use of riparian zones. Alternatively, fertilization improves forage quality and livestock use (Samuel et al., 1980), but is not feasible in all cases because of terrain and costs (Vallentine, 1989). Patch quality can also be improved by burning (Angell et al., 1986; Svejcar, 1989), but improvements from burning are short-lived unless frequent regrazing or reburning occurs (Coppock and Detling, 1986).

The importance of social interactions in choice of feeding locations also offers management options. In Chapters II and III, I offered evidence that social interactions were influential in choice of feeding location. Others have also shown that mother and peers influence individuals' use of the environment (Hunter and Milner, 1963; Key and

MacIver, 1980; Roath and Krueger, 1982a; Lawrence, 1990; Stolba et al., 1990; Howery, 1993). Managers may be able to select individuals that utilize a wider array of the environment and cull those that limit their distribution to susceptible areas such as riparian zones (Roath and Krueger, 1982b; Howery et al., in press). Similarly, managers may be able to manipulate habitat use by limiting the amount of exposure to riparian zones when livestock are rearing offspring (Howery, 1993).

Herding is also an effective management technique for controlling the distribution of animals (Skovlin, 1957; Cook, 1966, 1967). Herding forces livestock to concentrate on ridgetops and other areas away from riparian zones. Herding is effective on a grazing allotment near the Maxfield/Thompson allotment, where cows are moved out of riparian zones every other day. Upland sites consist of adequate forage and alternate watering points, and cows are rarely seen in riparian zones.

6. Conclusion

This chapter demonstrates that controlled experiments, which suggest that experience (e.g., with foods, environment, conspecifics) affect habitat selection, are also applicable on large grazing allotments. Managers can improve distribution by developing management plans that include strategic placement of preferred foods/supplements, water developments, herding, selective culling, and limiting the amount of exposure to riparian zones. These suggestions can be implemented with any existing grazing management plan to improve livestock production, fish and wildlife habitat, and water quality.

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CHAPTER V

SUMMARY AND SYNTHESIS

1. Chapter II

The objective of research reported in Chapter II was to investigate the interactions between dietary habits and social interactions on choice of feeding location. I found that subgroups of strangers fed in different locations. Both dietary habits and social interactions affected choice of feeding locations for companions, which is evident from companions feeding in single subgroups. When lithium chloride was used to create an aversion to one of the two foods, dietary habits were strengthened, especially when lambs were exposed in a smaller pasture (0.25 ha vs 1 ha). Thus, both dietary experiences and social interactions influenced choice of feeding location, but the importance of dietary habits depended on familiarity with other individuals in the flock.

2. Chapter III

The objective of research described in Chapter III was to determine the effect of experience with the environment on dietary habits and social interactions. Experience influenced choice of feeding location. Lambs naive to the pasture fed in single subgroups and in locations that were often unrelated to their dietary habits. Conversely, subgroups of lambs familiar with the pasture fed in separate locations. Social interactions overrode dietary preferences for naive lambs, but not for lambs familiar with the pasture. I concluded that social interactions were more influential in

determining choice of feeding location in novel environments, whereas location of preferred food was more influential in familiar environments.

3. Chapter IV

The objective of Chapter IV was to integrate the experimental evidence from Chapters II and III with a cattle study conducted on a 1,030-ha grazing allotment. Comparisons of home ranges between 1990 and 1991 suggest that cattle returned to the same areas each year, even though home range size varied and (or) shifted in response to water availability. Experiences with foods, the environment, and peers offer the most plausible explanation for the cattle observations described in Chapter IV, especially considering that home ranges remained similar even though forage and water were depleted. Collectively, these chapters provide implications for controlling the distribution of animals. Managers may be able to influence distribution by (1) placing familiar foods or supplements in strategic locations, (2) increasing exposure to underused habitats through herding, (3) limiting exposure to riparian zones through herding, (4) culling animals that spend a disproportionate amount of time in riparian zones, and (5) developing alternate watering and loafing sites.

4. Synthesis

I used sheep and cattle as subjects for the experiments described in Chapters II through IV. Obviously, there are anatomical, physiological, and behavioral differences between these species, but dietary preferences and social interactions affect foraging behavior of both. For instance, most if not all ungulates have evolved physiological

and behavioral characteristics that generally match their food and habitat resources (Hofmann, 1988), but the physiological responses to nutrients and toxins are the same across species (e.g., acquired preferences, conditioned taste aversions) (Garcia, 1989; Zahorik et al., 1990; Provenza et al., 1992; Provenza, in press). Likewise, some species of sheep are more gregarious than some species of cattle, but social interactions affect foraging behavior of both species (Lawrence and Wood-Gush, 1988; Lynch et al., 1992; Howery, 1993).

Subgroups form within herds of cattle and flocks of sheep, and both species acquire fidelities to particular areas. For example, sheep (Hunter and Milner, 1963), cows (Roath and Krueger, 1982), moose (Cederlund et al., 1987; Anderson, 1991), bighorn sheep (Festa-Bianchet, 1986a), mountain sheep (Festa-Bianchet, 1986b), and mouflon sheep (Dubois et al., 1994) all return to the same areas year after year. Site fidelity is usually attributed to transgenerational learning while foraging with mother (Key and MacIver, 1980; Lawrence, 1990), but peers can also influence choice of feeding location for all species (Lawrence and Wood-Gush, 1988; Howery 1993).

Dietary preferences also influence food and habitat selection in all species. Criollo goats introduced to a new environment consumed foods they were familiar with from the environment where they were reared (Biquand and Biquand-Guyot, 1992). Likewise, sheep searched for familiar foods in new environments (Gluesing and Balph, 1980), as did deer (Gillingham and Bunnell, 1989). Finally, monkeys developed foraging patterns based on the locations of preferred foods (akebi fruit and chocolate) (Menzel, 1991).

Results in Chapters II and III suggested that both dietary habits and social interactions influence choice of feeding location. In reality, the development of dietary preferences from experiences early in life and social interactions cannot be separated. Mothers and peers play a crucial role in introducing animals to nutritious foods and habitats. Nevertheless, postingestive feedback can override social interactions from mother (Provenza et al., 1993a) and peers (Chapters II and III). Thus, social influences from mother or peers may facilitate experiences early in life, but ultimately, postingestive feedback allows preferences for habitats and their respective foods to develop.

5. General Discussion

Improving livestock distribution has been the objective of numerous studies during the past 35 years. Recently, the importance of improving livestock distribution has taken a new precedent because of environmental concerns. Livestock are often targeted as the destroyers of biodiversity, riparian areas, and overall ecosystem health (Drew, 1994; Mitchell, 1994a, b). Paleoecological evidence suggest that livestock were not present on western rangelands prior to European man's arrival, and probably contributed significantly to the removal of "natural" vegetation types in many areas (Johnson and Mayeux, 1992; Tausch et al., 1993). Nevertheless, the probability of returning to "pristine" ecosystems is unlikely (Mack and Thompson, 1982; Westoby et al., 1989).

During the past 100 years, livestock grazing has become a major component of western rangelands and continues to influence today's vegetation dynamics. More

importantly, there is now evidence that livestock grazing can be used to maintain and improve rangeland condition (Archer and Smeins, 1991; Laycock, 1994), and to improve wildlife habitat (Urness, 1990; Severson and Urness, 1994). For successful grazing management, frequency and intensity of herbivory must be controlled, which is often difficult on large grazing allotments in the western United States. Most grazing allotments are characterized by several different vegetation types, with livestock preferring some habitats and avoiding others. I believe that increasing the understanding of the factors affecting habitat selection and building sound management practices on those principles are critical to the survival of livestock grazing on western rangelands.

Throughout the past few decades, managers have attempted to improve dispersion of livestock by developing grazing systems and building fences. Although both have improved our ability to manage rangelands, they do not address the problem of poor distribution of livestock. Site preferences occur because of experiences early in life with particular locations within the grazing environment, independent of pasture size. For instance, Hunter and Milner (1963) observed different home range groups even within a relatively small pasture (102 ha). Similarly, I observed sheep separating and feeding in separate locations in 1-ha and 0.25-ha pastures. Distribution could be improved by familiarizing livestock with the entire grazing environment, which would be easier in smaller pastures. Nevertheless, familiarizing livestock with larger pastures can be achieved using managerial creativity, which was one of the objectives described in Chapter IV.

I am not the first to suggest that herding, water developments, and placement of supplements/minerals can be used to improve distribution. In 1957, Skovlin described an allotment where herding, water developments, and strategic placement of salt were used to improve distribution. Similarly, Cook (1967) suggested the same factors could be used to improve distribution in northern Utah. A review of the literature suggests that these factors were commonly used to improve distribution throughout the western United States up until the last couple of decades (Ares, 1953; Cook, 1964; Skovlin, 1965; Workman and Hooper, 1968; Martin and Ward, 1973). Most ranchers still practice strategic placement of salt/minerals, and water developments can be found on most grazing allotments, even though some may be in poor condition, and a few ranchers still regularly herd livestock. Nevertheless, managers and researchers seem content to rely on grazing systems and fencing rather than herding to solve distribution problems. Skovlin (1957) described the daily activities of an experienced herder, Stanley "Bun" Anderson. Skovlin reported that experienced herders, like Anderson, are continuously developing watering points in underused areas, moving salting locations, and focusing herding efforts on animals that spend more time in riparian zones. Furthermore, Skovlin (1957) suggested that an experienced herder's knowledge of cows and grass were key to successful management of livestock distribution. It seems that researchers and managers have forgotten the benefits of using an experienced herder. Results of my dissertation offer some experimental validity to incorporating the suggestions of Skovlin (1957) and Cook (1967), but obviously other factors remain to be investigated.

6. Future research

6.1. *Varied diets and habitat selection*

Animals select a variety of foods when given a choice (Provenza et al., in press). Lambs given a choice between three foods that contained the same ingredients but different nutritional qualities consumed all three foods. Lambs initially ate the high-quality food (DE=2.68 Mcal/kg, DP=13.8%) followed by consumption of the medium- (DE=2.42 Mcal/kg, DP=11%) and low- (DE=2.21 Mcal/kg, DP=8.1%) quality foods. Others have observed sheep that given a choice between grass and clover consumed grass if they had recently fed on clover and vice versa (Illius et al., 1992), which affected patch choice (clover patch vs. grass patch) (Newman et al., 1992; Parsons et al., 1994). Similarly, steers preferred hay over silage if hay intake had been restricted (Ramos and Tennessen, 1993).

Although the mechanisms behind varied diets remain unclear, four possible explanations exist (Provenza, 1995, in press). Animals may select a variety of foods to increase the likelihood of ingesting required nutrients (Westoby, 1977), to limit the possibility of overingesting toxins (Freeland and Janzen, 1974), to rectify specific maladies or deficiencies (Richter, 1942), or because of a decrease in flavor preference for a food as it is eaten (Rolls, 1986, 1994). Evidence indicates that dietary habits vary in response to toxin levels (Wang and Provenza, unpublished data) and to varying nutrient loads (Villalba and Provenza, in press [a, b]). Lambs also select foods and fluids that rectify specific maladies (Phy and Provenza, unpublished data).

Herbivores can select a variety of foods in the environment because of the variety of habitat types found on most rangelands (Provenza and Balph, 1990). Habitat types are defined as "the collective area which one plant association occupies" (SRM, 1989, p.9). Habitat types result from the combination of climate, topography, grazing (vertebrate and invertebrate), fire, and initial species composition, which cause a mosaic of vegetation (Tausch et al., 1993). Thus, varied diets may affect habitat selection, but the issue has not been explored. Once we understand the effect of varied diets on habitat selection, managers may be able to manipulate vegetation stands in underused areas to meet the deficiencies/desires of foraging animals, thus improving distribution.

6.2. Experimental analysis of water, salt, and supplement placement

Results in Chapter IV suggested that locations of watering points influenced habitat use, as have others (Skovlin, 1957; Cook, 1966, 1967; Low et al., 1981). Nevertheless, an experimental analysis of water developments and distribution has not been conducted. Similarly, salt and mineral placement are used in attempts to improve distribution. Salt or mineral placements may be overemphasized as effective techniques to improve distribution. As salt intake increases, water intake must also increase to flush excess levels out of the animal's system (NRC, 1985; Squires, 1988), which forces animals to spend more time drinking in riparian zones. Salt is often placed away from riparian zones, on ridgetops and steep slopes. Unless water developments are nearby, cattle may be forced to travel to riparian zones to drink. If

so, travelling time would increase but grazing distribution would not.

Results in Chapter IV suggested that strategic placement of familiar supplements could improve distribution, but did not suggest the type of supplement. Supplementation is defined as supplying a limited nutrient to animals with unrestricted forage intake (Huston and Pinchak, 1991). Protein is often deficient on rangelands and is probably the most viable choice. However, the nutritional status of rangelands and herbivores varies with location, time and climatic conditions (Van Soest, 1994), and other alternatives may serve equally well. Nevertheless, an experimental analysis of supplement type could aid managers in choosing the correct supplement for improving distribution.

6.3. Predators and distribution of livestock

Optimal foraging theory predicts animals will select the optimal combination of prey items (e.g., forage) while minimizing the risk of predation (Stephens and Krebs, 1986; Werner and Hall, 1988; Abrahams and Dill, 1989). Savory (1988) suggested that man's domestication of livestock and control of predator densities has diminished the herding or flocking response in livestock. Others have shown that livestock still fearfully respond to predators by flocking together and fleeing when a predator approaches (Hulet et al., 1987; Anderson et al., 1988; Lynch et al., 1992). If so, the prevalence of predators may influence foraging behavior by increasing the importance of social interactions (i.e., flocking or herding) or cause livestock to avoid areas with high predator densities. Understanding the influence of predators on foraging behavior could change existing predator control paradigms. For instance, if predators have a

limited effect on distribution and livestock losses can be controlled, less emphasis may be placed on predator control. Conversely, if predators do influence distribution, managers may wish to direct more attention to controlling predator densities.

6.4. Energy costs and livestock distribution

Optimal foraging theory also predicts that animals will limit their energy expenditure for each prey unit captured (Stephens and Krebs, 1986; Belovsky et al., 1989). However, the interaction between dietary preferences and energy expenditure has not been investigated with livestock. For instance, steep topography would increase energy expenditure. Most suggest that cattle and sheep will not use areas with slopes greater than 35% (Mueggler, 1965; Cook, 1966; Bryant, 1982). Moreover, most range managers do not consider phytomass growing on steep slopes when calculating stocking rates. During the observations for Chapter IV, slope did not appear to restrict distribution. If slopes were avoided, it was because they were covered with dense conifer stands with little herbaceous vegetation. Thus, these areas were probably avoided because of lack of forage, not because of topography. Moreover, cows often grazed in areas with relatively steep slopes, even though forage was available in other areas.

Water location may also influence energy expenditure. Some evidence indicates that forage utilization dramatically decreases after 0.8 km from water, with 1.6 km as the outer limit of cattle and sheep grazing (Stuth, 1991). However, Squires (1981) reported that some subgroups of "walkers" travelled as far as 9 km away from water to feed while "nonwalkers" would graze in the vicinity of water. Thus, other variables

(e.g., forage preferences) may override the influence of energy expenditure. Results in Chapters II and III exhibited that experiences with foods influenced location preferences, which could be responsible for the different distribution patterns described by Squires (1981). For example, walkers and nonwalkers may consist of family groups in which transgenerational learning affects location of use. Future research efforts should address the effect of environmental constraints (distance to water, topography) on foraging behavior and determine if experience can override these constraints.

6.5. Training livestock to be "uplanders"

Range science is an applied science and is strongly influenced by management objectives and needs. One aspect that warrants further investigation is training livestock to avoid some habitats and to prefer others. Dietary habits can be shaped through experiences with social models (Lynch et al., 1983; Lynch and Bell, 1987; Thorhallsdottir et al., 1990a, b; Mirza and Provenza, 1990, 1992, 1994; Nolte and Provenza, 1991), through experiences early in life (Nolte et al., 1990; Distel and Provenza, 1991; Nolte and Provenza, 1992; Walker et al., 1992), by developing foraging skills (Flores et al., 1989a, b, c; Ortega-Reyes and Provenza, 1993a, b), and by developing conditioned food aversions (Burrill and Provenza, 1990, 1991; Provenza et al., 1993b). In Chapters II and III, I reported that experiences with foods, peers, and the environment influenced foraging behavior. Howery (1993) found that experiences with mother and peers influenced foraging locations, while Chapter IV provided other alternatives to control distribution. At some point, these variables should be applied in concert to attempt to train livestock to forage in certain areas and avoid others. In

doing so, livestock may become effective tools for maintaining and improving rangelands while maintaining production that is essential for rural communities.

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CURRICULUM VITAE

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Publications:

Scott, C.B., Provenza, F.D. and Banner, R.E., 1995. Dietary habits and social interactions affect choice of feeding location by sheep. *Appl. Anim. Behav. Sci.*, (submitted).

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