Influence of social rank on habitat use and performance of free-ranging cattle
by B Ross Macdonald

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal and Range Sciences
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Abstract:
Social dominance amongst cattle may influence their distribution and performance. However, this has not been quantified on a large scale. To examine the existence of a social dominance hierarchy among free-ranging cattle, over 600 hours of observation time were logged from April through June in 1998 and 1999. Approximately 155 cows from one herd in southwestern Montana were observed. One on one confrontations were recorded with one cow being recorded as winner and the other, loser. The observations were used to construct a social dominance hierarchy for the cow herd. The stability of the hierarchy between the two years was tested using Spearman's Rank Correlation. The social rank was significantly correlated between years ($P < 0.05$). A global positioning system (GPS) receiver was used to record each cow's position in the summer pasture once daily. Habitat and environmental variables were documented at each cow position. Variables included vegetation type, temperature, relative humidity, wind speed, distance to water and shade, topography, aspect, slope and insect density. Forage quantity and quality were measured within each vegetation type. Daily weight gains of the calves were calculated for the summer grazing period as a measure of cow performance. Each year the top and bottom 30 cows from the social hierarchy were selected for analysis (n=60). The experiment was completely randomized in a factorial arrangement. Analysis of covariance was used for the habitat use and animal performance data. Cow social rank (high vs. low) and study year were factors. Cow age was the covariable. Analysis of variance was used for forage quantity and quality data. Vegetation type and study year were the factors. Of the two years, 1998 was relatively warm and dry as evidenced by higher NDF and ADF percentages in the forage that year ($P \leq 0.10$). Between the two years, high-ranked cows were found in riparian areas equally while low-ranked cows were found in riparian areas less in 1998. The high-ranked cows excluded low-ranked cows from riparian areas in the warm, dry year. High-ranked cows had calves with higher gains than low-ranked cows. Social rank had a significant influence on free-ranging cattle distribution and performance.

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B. Ross Macdonald

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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STATEMENT OF PERMISSION TO USE

Signature [signature]

Date 11/28/00

This thesis is dedicated to my family and friends. May all of you have years filled with your equivalent of good horses, pretty loops and fat cattle.

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ABSTRACT

Social dominance amongst cattle may influence their distribution and performance. However, this has not been quantified on a large scale. To examine the existence of a social dominance hierarchy among free-ranging cattle, over 600 hours of observation time were logged from April through June in 1998 and 1999. Approximately 155 cows from one herd in southwestern Montana were observed. One on one confrontations were recorded with one cow being recorded as winner and the other, loser. The observations were used to construct a social dominance hierarchy for the cow herd. The stability of the hierarchy between the two years was tested using Spearman's Rank Correlation. The social rank was significantly correlated between years ($P < 0.05$). A global positioning system (GPS) receiver was used to record each cow's position in the summer pasture once daily. Habitat and environmental variables were documented at each cow position. Variables included vegetation type, temperature, relative humidity, wind speed, distance to water and shade, topography, aspect, slope and insect density. Forage quantity and quality were measured within each vegetation type. Daily weight gains of the calves were calculated for the summer grazing period as a measure of cow performance. Each year the top and bottom 30 cows from the social hierarchy were selected for analysis (n=60). The experiment was completely randomized in a factorial arrangement. Analysis of covariance was used for the habitat use and animal performance data. Cow social rank (high vs. low) and study year were factors. Cow age was the covariable. Analysis of variance was used for forage quantity and quality data. Vegetation type and study year were the factors. Of the two years, 1998 was relatively warm and dry as evidenced by higher NDF and ADF percentages in the forage that year ($P \leq 0.10$). Between the two years, high-ranked cows were found in riparian areas equally while low-ranked cows were found in riparian areas less in 1998. The high-ranked cows excluded low-ranked cows from riparian areas in the warm, dry year. High-ranked cows had calves with higher gains than low-ranked cows. Social rank had a significant influence on free-ranging cattle distribution and performance.

INTRODUCTION

Riparian areas are plant, animal and aquatic communities whose presence can be attributed to water (Kauffman and Krueger 1984). Thomas et al. (1979) classified riparian areas as having well defined habitat zones within much drier surrounding areas, comprising small percentages of the total area, with higher production in terms of biomass than the remaining area, and a critical source of diversity within rangelands. The greater diversity and production associated with riparian areas when compared to the surrounding uplands are the primary factors that create the importance of these areas as focal points for the management of livestock (Kauffman and Krueger 1984). Cattle tend to congregate on riparian areas and utilize the vegetation more intensively than surrounding uplands. This is attributed to availability of water, shade and quality and quantity of forage in the riparian areas.

Reduced stocking rates are often proposed as a solution to over-use of sensitive areas. However, the effect of changing stocking rate cannot be assumed to have a proportional difference in the stocking rate of the whole pasture (Hunter 1964). A decreased rate may empty the poorest area of the pasture first. Livestock may distribute themselves according to available resources, namely forage quantity and quality (Ganskopp and Vavra 1987, Pinchak et al. 1991). Methods such as water development, salting, fencing, burning, fertilizing and herding are used to control grazing livestock distribution (Vallentine 1990). While these methods may be effective, they also increase costs. As a result, lower cost methods to control livestock distribution have been suggested. Roath and Krueger (1982) and Howery et al. (1996, 1998) advocate culling cattle that spend a large amount of their time in riparian areas. If animals within a herd were consistently found in riparian areas, those animals would be culled and replaced with animals from other herds that prefer upland areas. This approach assumes cattle that spend excessive time in sensitive areas do so because of learned or genetic dispositions to use those areas. However, foraging choices by cattle may be influenced by other factors such as memory and social hierarchy (Bennett et al. 1985, Bailey et al. 1989, Mosley 1999, Sowell et al. 2000). If social hierarchy within a herd does influence foraging choices, selectively culling based on riparian use may not be effective. Social rank may affect distribution by forcing subordinate or less-dominant animals to graze less preferred areas (Lynch et al. 1985, Bennett et al. 1985, Mosley 1999). Culling cows from preferred grazing areas such as riparian areas would likely result in culling dominant animals. This may enable subordinate animals to fill the vacated areas (Hunter 1964).

No studies have identified a dominance hierarchy in a commercial sized, free-ranging cow herd or examined its association with habitat use. The existence of a stable social rank in a large herd may help to explain cattle distribution. My study was designed to identify the social rank of a large, free-ranging cow herd, test the stability of the social rank and evaluate the relationship between cow social rank, habitat use and weight gain of calves.

LITERATURE REVIEW

Cattle Distribution

Cattle distribution throughout an area or pasture has largely been associated with slope (Mueggler 1965, Roath and Krueger 1982, Ganskopp and Vavra 1987) and distance to water (Miller and Krueger 1976, Low et al. 1981, Brock and Owensby 2000). Climatic factors including ambient temperature, wind direction and speed, relative humidity, barometric pressure and precipitation have also been associated with cattle distribution (Arnold and Dudzinski 1978, Miller 1983).

Stocking rate, stock density, pasture size and length of grazing may be used to influence distribution (Kauffman and Krueger 1984). However, Hart et al. (1991) tested the impact of stocking rate on grazing cattle distribution and found that increased stocking rate did not have a major impact on distribution but usage of the different habitats increased proportionally with increased stocking rate. They suggested that in pastures containing widely different range sites, increased stocking rates may not provide the desired dispersion of cattle and over-use of some sites may occur.

Disproportionate use of sites may also be due to preference for specific forage species versus the availability of those species in different plant communities (Arnold and Dudzinski 1978). Pinchak et al. (1991) conducted a study on foothill range in Wyoming to identify the combined effects of physiographic diversity, spatial distribution of water and heterogeneity of plant communities on cattle distribution. They concluded that cattle distribution is constrained by spatial water distribution and physiographic complexity as well as by forage characteristics.

Models using forage quality and quantity values, topography and distance to water as predictors explain about fifty percent of grazing animal habitat selection (Cook 1966, Gillen et al. 1984). It is evident that these factors influence grazing animal distribution. Gillen et al. (1984) found that grazing distribution patterns are difficult to predict with useful precision because they are influenced by such a complex of physical and biological factors including animal social behavior. Brock and Owensby (2000) stated that difficulties in developing grazing distribution models arise from the large number of cofactors. The quantification of behavior as well as contributing environmental variables is necessary to improve distribution models (Senft et al. 1985).

Habitat Selection

The manner in which free-roaming animals use space potentially affects diet selection, nutrient intake, efficiency of forage utilization as well as the impact of management strategies on the landscape or ecosystem level (Senft et al. 1983). Senft et al. (1987) suggested that grazing animals construct forage selection hierarchies. The grazing animal chooses a region in the pasture to graze. Within that region are landscape differences to chose from. Within each landscape are different plant communities and within each community are small patches of preferred plants to graze. The selection of certain plants and areas that contain those plants are based on a series of cognitive and affective processes resulting in positive or negative feedback responses (Provenza 1991). The chief factors affecting selection of plant communities and small patches (i.e., feeding stations) are the amount, quality and palatability of the forage (Brock and Owensby

2000). The memory of past grazing bouts may then be retained as well as memory of the area that contained the positive or negative grazing experiences, thus affecting future grazing behavior. The use of spatial memory to locate food patches has been documented in sheep (Edwards et al. 1996) and black-tailed deer (*Odocoileus hemionus*) (Gillingham and Bunnell 1989). Spatial memory may help sheep increase the rate at which they encounter preferred grazing areas and exploit spatial heterogeneity in food resources (Edwards et al. 1996). Bailey et al. (1989) demonstrated that cattle have the ability to associate locations with feed resources and to remember the locations for periods up to eight hours.

Bailey and Rittenhouse (1989) suggested that cattle develop a map-like mental image of the spatial relationships between plant communities. This map is developed and stored in the long-term memory of the grazing cattle as they explore a new pasture. The short-term memory is then used to select grazing patches from within their forage selection hierarchy. They also suggested that the initial map development may be constrained by diverse topography but spatial memory may still be useful to confine searching to a smaller area of the pasture (Edwards et al. 1996).

Accumulation of a spatial memory over time may be important. Cows grazing their traditional ranges may be more widely distributed than replacement animals and/or yearlings that lack familiarity with the area (Bryant 1982). Grazing experience gained from a variety of different pasture environments may also play a role in animal distribution. Arnold and Maller (1977) found that sheep with no previous experience in tall grass and shrub pasture stayed close to the fence and failed to find water in the center of the pasture. Yet, sheep raised in a tall grass/shrub pasture adjusted quickly to a new tall grass/shrub pasture.

Social Dynamics

Along with memory-based habitat selection, the social dominance hierarchy within a herd may be an important factor in determining habitat use. Few grazing management guidelines consider the effects of herd structure and social interactions on spatial behavior. For large herds the influence of social structure on dispersion may be as important as environmental influences (Senft et al. 1983). Syme and Syme (1979) suggested that complex social structures and interactions are possible in most wild and domestic species because most mammal species that form herds use their memory to recognize other individuals within the herd. Barroso et al. (2000) documented a clearly established, stable linear hierarchy in a small herd of goats.

The structure of the herd with respect to cow position may also have implications for dispersion. Association among animals in a herd is not random. Arnold and Pahl (1974) documented that the manner in which feral and wild sheep use an environment is determined in part by the social attachments between individuals and by social organization in the flocks or groups of animals. The social organization of bison (*Bison bison*) involves complex inter-individual associations (Green et al. 1989). The social organization of feral cattle has been described as a typical fusion-fission behavior (Lazo 1994). Small unstable groups or parties of animals change in size and composition depending on ecological factors. However, these parties are comprised of larger, socially stable subgroups. Thus a herd is the sum of the subgroups.

The social structure is determined and maintained by agonistic behavior to establish social dominance (Lazo 1994, 1995; Wilson 1975; Syme and Syme 1979; Mosley 1999; Sowell et al. 2000). Scott and Fredericson (1951) defined agonistic behavior as the group of behavioral adjustments associated with fighting which includes attack, escape, threat, defense and appeasement. It is composed of the continuum of behaviors from threat to aggression to submission. Dominance is an attribute of a relationship between two individuals (Barrette and Vandal 1986). McGlone (1986) stated that some of these behaviors are subtle to the human thus requiring more focused observation. Beilharz and Zeeb (1982) define dominance as the inhibition of an animal's behavior by the presence of another animal.

The social dominance organization in a cattle herd is maintained by low-ranked animals avoiding high ranked animals, rather than by territorial behavior of the dominant animals (Beilharz and Zeeb 1982). Craig (1986) stated that social dominance hierarchies in female groups are generally stable. Oestrus cycles do not affect the social order as it is established and maintained in all periods of a cow's life in a herd (Schein and Forhman 1955). Sable (*Hippotragus niger*) proved to have a definite rank hierarchy based on age. The oldest cows were dominant, while yearling and two-year-old males were subordinate to all adult females (Estes 1971). The lowest ranking females remained at a slight distance from the herd. Their activity cycles appeared to be less synchronized than the others and their behavior was more alert and nervous; similar results were shown with wildebeest (*Connochaetes* spp.). Joubert (1971) observed that among roan antelope (*Hippotragus equinus*) cows the dominance/submission relationships gave rise to a dominance hierarchy. Sherwin and Johnson (1987) documented that sheep may remain in the sun because they will not approach more dominant animals occupying shade. Bennett et al. (1985) reported similar findings where subordinate cattle may be excluded from shade. In southwestern Germany, Beilharz and Zeeb (1982) found that high-ranked cattle from three dairy herds had more freedom in responding to stimuli than low-ranked cattle. Lazo (1994) with studies of feral cattle in southwestern Spain documented that social hierarchies were maintained primarily by avoidance and avoidance determined the distribution of feral cattle.

Social Dynamics and Animal Performance

A common assumption is that dominance confers priority of access to limited or highly localized resources (Craig 1986, Mosley 1999, Sowell et al. 2000). A level of basic dominance activity occurs even when resources are not limiting and increases as the resources decrease. The relationship appears to be one in which there may be a reward for the most dominant but little for the rest. Supporting evidence can be found in beef cattle, where the bottom third in terms of social rank were depressed in performance when compared to the top ranking animals (Schake and Riggs 1972). Ables and Ables (1987) demonstrated that social hierarchy regulates elk (*Cervus elaphus nelsoni*) populations and that dominant animals have greater opportunity to obtain food for survival and reproduction (Cole 1972). Hunter (1964) found that subgroups in a sheep flock occupied specific home ranges and that these subgroups occupied areas with better forage and had higher weight gains. Habitat selection by the roan antelope appears to be related to social dominance, with the higher-ranking animals having first choice of the resources (Joubert 1971). Sherwin and Johnson (1987) found that feed and shade use by sheep in western Australia were influenced by social forces. The lower ranking sheep had less access to resources because they avoided higher-ranking animals. According to Etkin (1964), there are strong evolutionary pressures in favor of dominance hierarchies as a principle of social organization. The advantages enjoyed by dominants in time of limited resources allow these animals and the species to survive.

Avoidance of high-ranked animals resulting in less access to resources such as food would likely translate into lower production from the subordinate animals. Hunter (1964) found that competition for resources may cause low-ranked sheep to graze on less preferred sites, thereby reducing production from the subordinate sheep. Wagnon et al. (1966) observed that dominant cattle prevented subordinate cattle from entering a feed-trough or accelerated the subordinates' activity at the trough. Sowell et al. (1997, 2000) reviewed the existence of social structure among cattle on pasture and confinement. They stress the importance of providing adequate resources to overcome the limited resources that lower ranking animals may face. At the Tropical Cattle Research Center in Australia, social rank within a grazing herd (n=17) of yearling steers was positively correlated with performance (Bennett and Holmes 1987). Lower ranked cattle had less access to resources than higher-ranked cattle. Barroso et al. (2000) found that goat production (milk and meat) was affected by dominance with the highest production in the mid-ranked animals.

MATERIALS AND METHODS

The study was conducted during 1998 and 1999, in the foothills of the Rocky Mountains in southwestern Montana on the Montana State University Red Bluff Research Ranch. The elevation of the site ranged from approximately 1400 - 1900 m in a 350 - 406 mm precipitation zone (Ross and Hunter 1976).

Dominant grasses include bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. and Smith), needleandthread (*Stipa comata* Trin. and Rupr.), Idaho fescue (*Festuca idahoensis* Elmer), Kentucky bluegrass (*Poa pratensis* L.), and basin wildrye (*Elymus cinereus* Scribin. and Merr.). Shallow sites surrounding rocky outcrops contained ponderosa pine (*Pinus ponderosa* Dougl.), limber pine (*Pinus flexilus* James) and Rocky Mountain juniper (*Juniperus scopularum* Sarg.).

The existing cattle herd on the ranch was used for the study . The herd consisted of about 155 Angus X Hereford cattle. The age of the cows ranged from 3 to 10 years of age, with female replacements being retained from the ranch herd. The cows calved from the end of February into April with the calves being weaned at the end of September. The breeding season was June through July. Cows were fed hay from February through May in various pastures and the calving lot. All hay was fed on the ground using round bales and a bale processor. Twenty percent of the cows were culled each fall based on pregnancy, age, and conformation. Traditional management for the herd was not changed for purposes of the study.

Social Rank

The social rank of the cows was determined from more than 300 hours of observation each year post-calving, from March through July. One observer made all observations. Observations were made on the winter and spring pastures and included periods when cattle were feeding, grazing, watering and using salt. The social rank was determined by recording the outcome of agonistic behaviors between two individuals. The result was tallied as a win or a loss for each cow. A winning animal was defined as an individual that displaced another animal from a location or one to which submissive behavior was directed. Behaviors observed were fights, butts, head thrusts and avoidances in accordance with Schein and Fohrman (1955). Mock fights (Reinhardt and Reinhardt 1982) were not recorded. Doubtful or indecisive outcomes were ignored.

All agonistic behavior observations were ordered into a linear dominance hierarchy for each year (Schein and Forhman 1955, Barrette and Vandal 1986). Age of the cattle was used as a secondary determinant in assigning the rank order. This was based on Schein and Fohrman (1955), where age was significantly correlated with social rank. No other determinants were used. Cattle without any social rank observations were excluded.

Habitat Use and Animal Performance

In both 1998 and 1999, habitat use was recorded for each cow in the summer pasture over 34 days from mid-August through September. Observations were made from horseback due to the diverse topography and size of the pasture (1078 ha). The pasture was classified and mapped into five vegetation types: coniferous forest, limber pine savanna, mountain grassland, riparian and sagebrush steppe (Figure 1).

Individual cow positions were recorded using a hand-held, Geo-explorer II, Global Positioning System (GPS) receiver that was accurate within 1 meter. All cows were observed while actively grazing from sunrise to early afternoon. The observer varied his travel route through the pasture so that the same route was not traveled two consecutive days. The observer rode next to each cow and recorded the cow ID (ear tag), GPS position, vegetation type and the environmental variables. In the event a cow was observed more than once in one day, only the first location of the day was recorded. The following environmental variables also were measured daily at each cow's position during the summer grazing period. Slope (%) and aspect (N, S, E, W) were measured using a clinometer and compass, respectively. A hand-held thermo-hygrometer was used to measure temperature (°C) and relative humidity (%), while an anemometer was used to measure wind speed (m/s). Distances to nearest water and shade (m) were estimated in the field. Insect density was classified as high, medium, or low.

Calf performance was measured by weighing each calf immediately before and after the summer grazing period. This occurred on 30 July, 1998/99 and 29 September, 1998/99, respectively.

Herbaceous standing crop was estimated at the beginning and end of each summer grazing period. Thirty 50 x 50-cm quadrats were sampled per vegetation type with three transects of ten quadrats spaced 10 meters apart. Quadrats were clipped to the soil surface. Forage quality was estimated from clipped samples. The samples were

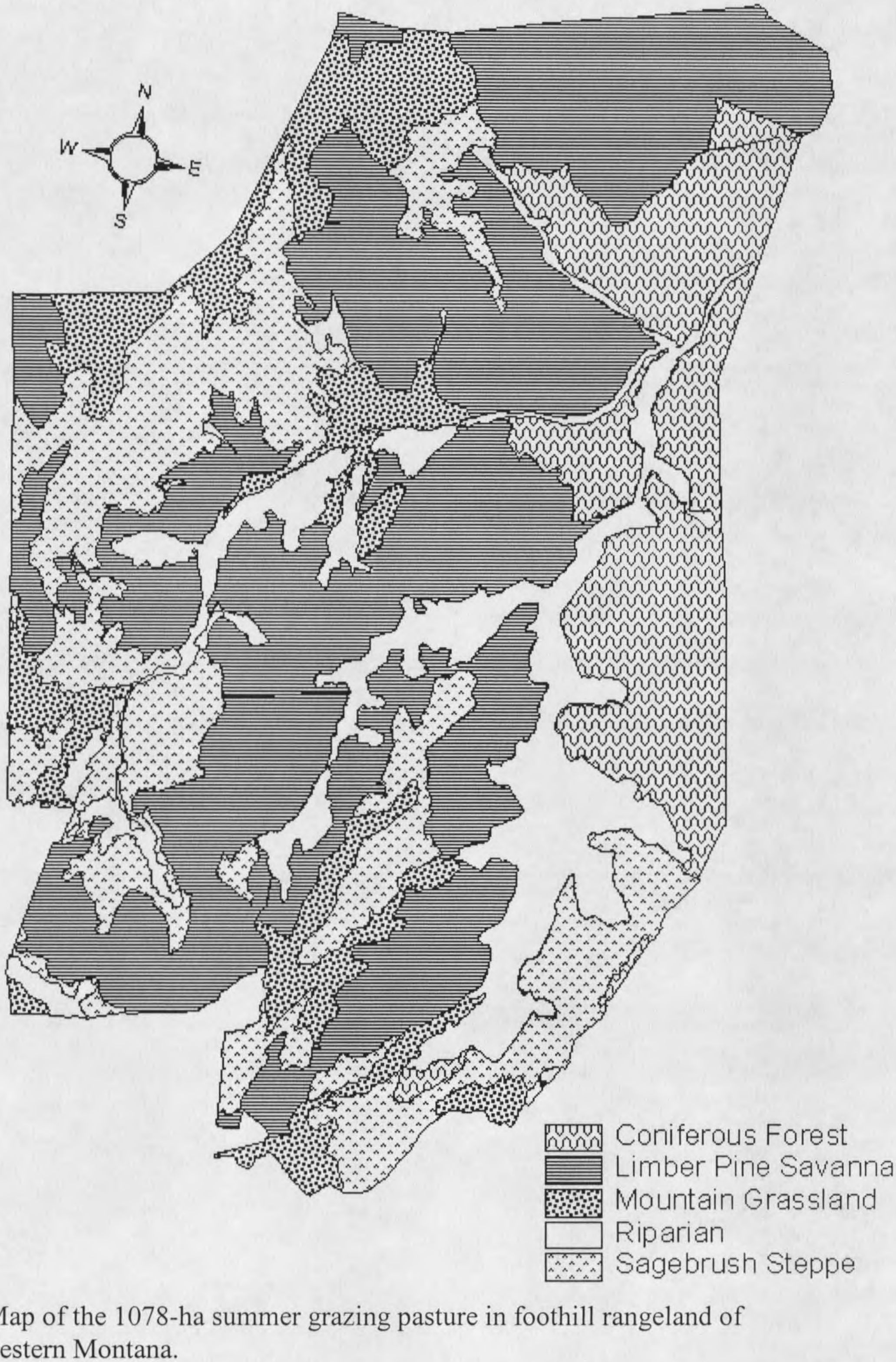

Figure 1. Map of the 1078-ha summer grazing pasture in foothill rangeland of southwestern Montana.

oven-dried at 58°C for 48 hours prior to weighing and analyses for CP (AOAC 1990), NDF and ADF (Van Soest et al. 1991).

Statistical Analyses

The 1998 social rank was compared to the 1999 social rank using Spearman's Coefficient of Rank Correlation (Steel and Torrie 1980). This was done to assess stability in the rank between years.

Each year, the 30 top ranking and 30 bottom ranking cows (n = 60) were selected for analysis to better compare high- and low-ranked cows. Altogether, the data analyzed were based upon 1,922 observations, averaging more than 16 observations per cow each year.

The study was completely randomized in design with a factorial arrangement. For the environmental variables and animal weight gain data, social rank (high and low) and year (1998 and 1999) were the factors. Data were analyzed with analysis of covariance. Cow age was the covariable because cow age is correlated with social rank (Schein and Forhman 1955, Estes 1971, Barroso et al. 2000) and cow habitat use and calf gains are correlated with cow age (Bryant 1982). For the forage quantity and quality data, vegetation type and year were the factors. Data were analyzed with analysis of variance. Pairwise comparisons among means were made with Fisher's Protected LSD test. All differences were declared significant at $P \leq 0.10$.

RESULTS

The cow herd social rank was correlated between 1998 and 1999 ($P \leq 0.05$). Results from the habitat use, environmental conditions and calf performance data are given in Tables 1, 2, and 3, while the vegetation quality and quantity results are given in Table 4. Weather data were obtained from the Norris Madison Pump HS weather station adjacent to the summer grazing pasture (Western Regional Climate Center 2000). The 30-year average August-September temperature was 17.4 °C and total precipitation was 85.1 mm. The 1998 August-September temperature average was 20.0 °C and 46.5 mm of precipitation was received. The 1999 August-September temperature average was 17.0 °C and 100.3 mm of precipitation was received during these two months. Between the two study years, 1998 had higher temperatures and lower precipitation and 1999 had slightly lower temperatures and higher precipitation than the 30-year average.

Low-ranked cows spent more time on south-facing slopes than did high-ranked cows in 1998 ($P = 0.08$). I found that high-ranked cows were on north-facing slopes more in 1998 than 1999 ($P < 0.01$). Both high- and low-ranked cows were found on east-facing slopes more in 1999 than 1998 ($P < 0.01$ and $P < 0.01$, respectively). Cows spent more time on west-facing slopes in 1998 than 1999 ($P = 0.09$). The low percentage of observations on west aspects may in part be due to the topography of the pasture which yielded very few west slopes (Table 1).

Table 1. Mean (±SE) percentage of habitat use observations sorted by aspect and by vegetation type from cows of high and low social rank grazing foothill rangeland in southwestern Montana.

Habitat Variable	Year	Social Rank High	Social Rank Low	Mean
		(%)	(%)	
Aspect				
North	1998	41.8 ± 3.1 a[†]A[‡]	36.5 ± 3.0 aA	39.2 ± 2.1 A
	1999	25.8 ± 3.2 aB	30.2 ± 3.4 aA	27.8 ± 2.3 B
	Mean	33.9 ± 2.4 a	33.7 ± 2.2 a	
South	1998	31.6 ± 2.6 aA	37.8 ± 2.2 bA	34.7 ± 1.8 A
	1999	32.2 ± 3.2 aA	30.6 ± 2.4 aB	31.5 ± 2.0 A
	Mean	31.9± 2.0 a	34.6 ± 1.7 a	
East	1998	21.4 ± 1.5 aA	21.5 ± 2.4 aA	21.4 ± 1.4 A
	1999	38.9 ± 3.2 aB	36.1 ± 3.4 aB	37.6 ± 2.3 B
	Mean	30.0 ± 2.1 a	28.1 ± 2.2 a	
West	1998	5.0 ± 1.1 aA	4.1 ± 0.7 aA	4.5 ± 0.6 A
	1999	2.9 ± 1.0 aA	2.7 ± 1.0 aA	2.8 ± 0.7 B
	Mean	3.9 ± 0.8 a	3.4 ± 0.6 a	
Vegetation Type				
Limber Pine Savanna	1998	13.8 ± 1.5 aA	14.1 ± 1.5 aA	14.0 ± 1.0 A
	1999	20.2 ± 2.0 aB	19.6 ± 2.2 aA	19.9 ± 0.5 B
	Mean	17.0 ± 0.0 a	16.7 ± 1.3 a	
Mountain Grassland	1998	28.8 ± 2.0 aA	31.9 ± 1.8 aA	30.3 ± 1.3
	1999	25.6 ± 2.4 aA	20.0 ± 3.5 bB	23.0 ± 2.1
	Mean	27.2 ± 1.5	26.4 ± 2.0	
Riparian	1998	39.1 ± 1.7 aA	34.5 ± 1.9 bA	36.8 ± 1.3
	1999	36.2 ± 3.5 aA	41.3 ± 4.4 aB	38.6 ± 2.8
	Mean	37.7 ± 1.9	37.6 ± 2.3	
Sagebrush Steppe	1998	18.3 ± 1.8 aA	19.6 ± 1.4 aA	18.9 ± 1.2 A
	1999	17.2 ± 2.2 aA	19.3 ± 2.4 aA	18.2 ± 1.6 A
	Mean	17.8 ± 1.4 a	19.4 ± 1.3 a	

[†]Means within rows followed by the same lowercase letter are not different ($P > 0.10$).
[‡]Means within columns and within habitat variables followed by the same uppercase letter are not different ($P > 0.10$).