AN ABSTRACT OF THE THESIS OF

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Title: Ecology and behavior of bison in the Henry Mountains, Utah.

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Bruce E. Coblentz

Aspects of bison ecology and behavior were studied in the Henry Mountains, Utah during summer 1977 and summer 1978. Foraging distributions of bison and of cattle were compared to elevation, slope, horizontal distance from water, vertical distance from water, aspect, and availability of preferred forage. The effect of bison-cattle interactions on distribution of the 2 species was evaluated. Patterns in geographical and altitudinal distribution of the bison herd during summer were described. The sizes of bison cow groups were determined and compared to habitat structure. The stability of bison cow groups was evaluated.

Distribution of foraging bison was positively related to availability of preferred forage. Distribution of foraging cattle was negatively related to slope and vertical distance from water, but was not related to availability of preferred forage. Slope and vertical distance from water showed little or no relationship to bison distribution. Elevation, horizontal distance from water, and aspect showed little or no relationship to distribution of either species.

Geographical and altitudinal distribution of bison was characterized by both similarities and differences between summer 1977 and summer 1978. Differences possibly were because of decreased forage production during a drought in 1977.

Bison cow groups typically totalled 15 animals. Group size was closely related to habitat structure; larger groups were found in more open habitats. Bison cow groups possessed little stability, and changed composition frequently. Groups that persisted did so in part through a lack of contact with other bison. Stable subgroups, if they existed at all, comprised only a few animals.

Ecology and Behavior of Bison in the Henry Mountains, Utah

by

Dirk Van Vuren

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Ecology and Behavior of Bison in the Henry Mountains, Utah

INTRODUCTION

Research on the American bison (Bison bison) began only about 25 years ago (McHugh 1958, Fuller 1960, 1962), despite the importance of bison in North American history and literature. Several areas of bison biology have had little study, including ecology and certain aspects of behavior.

Bison originally occupied a variety of habitats throughout much of North America, ranging from prairie to mountain peak (McHugh 1972:24). Following the extirpation of bison in the last century, domestic cattle were introduced and replaced bison as the dominant herbivore in many areas. Bison and cattle appear similar ecologically; they are closely related species, and both eat primarily grasses and grass-likes (Stephens 1966, Mackie 1970, Meagher 1973, Peden et al. 1974, Peden 1976, Cook and Harris 1977, Reynolds et al. 1978). In the only published study in which habitat use by bison was evaluated, Peden et al. (1974) compared foraging behavior of bison and cattle on the shortgrass plains of Colorado. Differences in habitat selection were found; cattle preferred swales and shallow depressions, whereas bison primarily grazed surrounding upland areas. Ecological differences between the 2 species may exist elsewhere; Fryxell (1928) and Nelson (1965) stated that bison in mountain areas frequented steeper slopes than did cattle. Although these statements were unsubstantiated, they were consistent with the observations of Julander and Robinette (1950), Julander (1955), Julander and Jeffery (1964), Mueggler (1965) and Cook (1966) that cattle distribution in mountain habitats was negatively affected by slope, distance from water, or both. Data are not available regarding the effects of environmental factors on the distribution of bison in mountain habitats.

Certain aspects of bison behavior, including group size and stability, are not well documented. McHugh (1958) described 2 kinds of groups in bison social organization, "bull groups" and "cow groups". Bull groups consisted of a few bulls and an occasional cow. Cow groups included a mixture of calves, yearlings, and mature animals of both sexes, although mature bulls were uncommon. Other researchers found that cow group size was variable; groups in open grasslands typically numbered 50 or more (Shackleton 1968, Shult 1972), whereas bison groups in forested habitats usually totalled less than 30 animals (Fuller 1960, Egerton 1962, Shackleton 1968). The difference in group size appeared related to habitat structure; larger groups occurred in more open areas. A more thorough evaluation of the relationship between habitat structure and size of bison cow groups is important to understanding bison social structure.

Published accounts of the composition and stability of bison cow groups are inconsistent. Several authors (Grinnell 1904:124, Seton 1929:693, Soper 1941) claimed that bison social structure was based on stable subgroups of related individuals, or clans. Garretson (1938:59) and McHugh (1958) disputed this claim; McHugh (1958) maintained that cow group composition was flexible and that a cow with calf was the only association based on genetic relatedness. Data were not offered in support of either argument. More recently, Fuller (1960:13) and Meagher (1978:127) postulated that social groupings were based on a "base unit" of 11-20 individuals. Larger groups resulted from temporary bunching of several base units. Again, few data were provided to substantiate the existence of base units. Clearly, the composition and stability of bison cow groups are poorly understood.

Opportunities for study of the ecology and behavior of free-ranging bison were limited; most bison in the United States were intensively managed on fenced ranges. The Henry Mountains of southern Utah supported 1 of the few herds of wild bison in the Unites States. The herd was begun in 1941-42 with the introduction of 23 bison obtained from Yellowstone National Park. The herd increased steadily in size, and during the present study numbered about 220 animals (Appendix A). Management since 1941 was limited primarily to annual public hunts, in which 10 bison usually were harvested. The herd provided an excellent object of study for 2 reasons. 1) Movements and distribution of the bison were not controlled; the herd roamed freely, and exhibited a seasonal pattern of altitudinal migration (Bureau of Land Management 1974). 2) The bison herd coexisted with several hundred range cattle.

The objectives of this study were: 1) to compare the distribution of foraging bison and cattle to elevation, slope, distance from water, aspect, and amount of preferred forage, and to evaluate the influence of interspecific interactions on distribution; 2) to determine patterns in geographical and altitudinal distribution of the bison herd during summer; 3) to evaluate the effect of habitat structure on size of bison cow groups; and 4) to evaluate the stability of bison cow groups.

STUDY AREA

The Henry Mountains are located in Garfield County, Utah, on public lands administered by the Bureau of Land Management (BLM). The mountain range is one of the youngest in North America, and was formed by an intrusion of granite into the sedimentary rock of the surrounding Colorado Plateau (Hunt et al. 1953). The terrain around the Henry Mountains is characterized by deserts, canyons and mesas, with an elevation of about 1000-1500 m. The Henry Mountains rise abruptly to over 3500 m.

The study area was located on Mount Ellen, the largest and northernmost peak in the Henry Mountains (Fig. 1). Bison were seen in this area frequently during recent years (BLM 1974). Most data were collected on the upper slopes of Mount Ellen, from about 2530 m elevation to the summit of Mount Ellen Peak at 3540 m, an area that totalled about 90 km^2. Several large areas on the south and southwest slopes of Mount Ellen, located at about 2130-2440 m elevation, were cleared of the pinyon pine (Pinus edulis) - juniper (Juniperus spp.) community during the 1960's, and seeded to introduced forages. Data on bison distribution were recorded on the seedings and on Cave Flat and surrounding areas, located about 20 km south-southwest of Mount Ellen, at 1770 m elevation.

Vegetation in the Henry Mountains varied with elevation. The lower elevation areas from about 1520 m to 2440 m were characterized by extensive stands of pinyon pine and juniper. Introduced forages were primarily crested wheatgrass (Agropyron desertorum), alfalfa (Medicago sativa) and clover (Trifolium spp.). Some browse species were becoming established in the seedings, particularly rabbitbrush (Chrysothamnus nauseosus, C. viscidiflorus), oak (Quercus gambelii), pinyon pine and juniper. A sparse belt of ponderosa pine (Pinus ponderosa) extended from about 2440 m to 2740 m. Vegetation above about 2740 m was characterized by stands of Douglas fir (Pseudotsuga menziesii), spruce (primarily Picea engelmannii) and quaking aspen (Populus tremuloides). The forest was discontinuous, with many openings dominated by sagebrush (Artemisia spp.) - grass communities. The

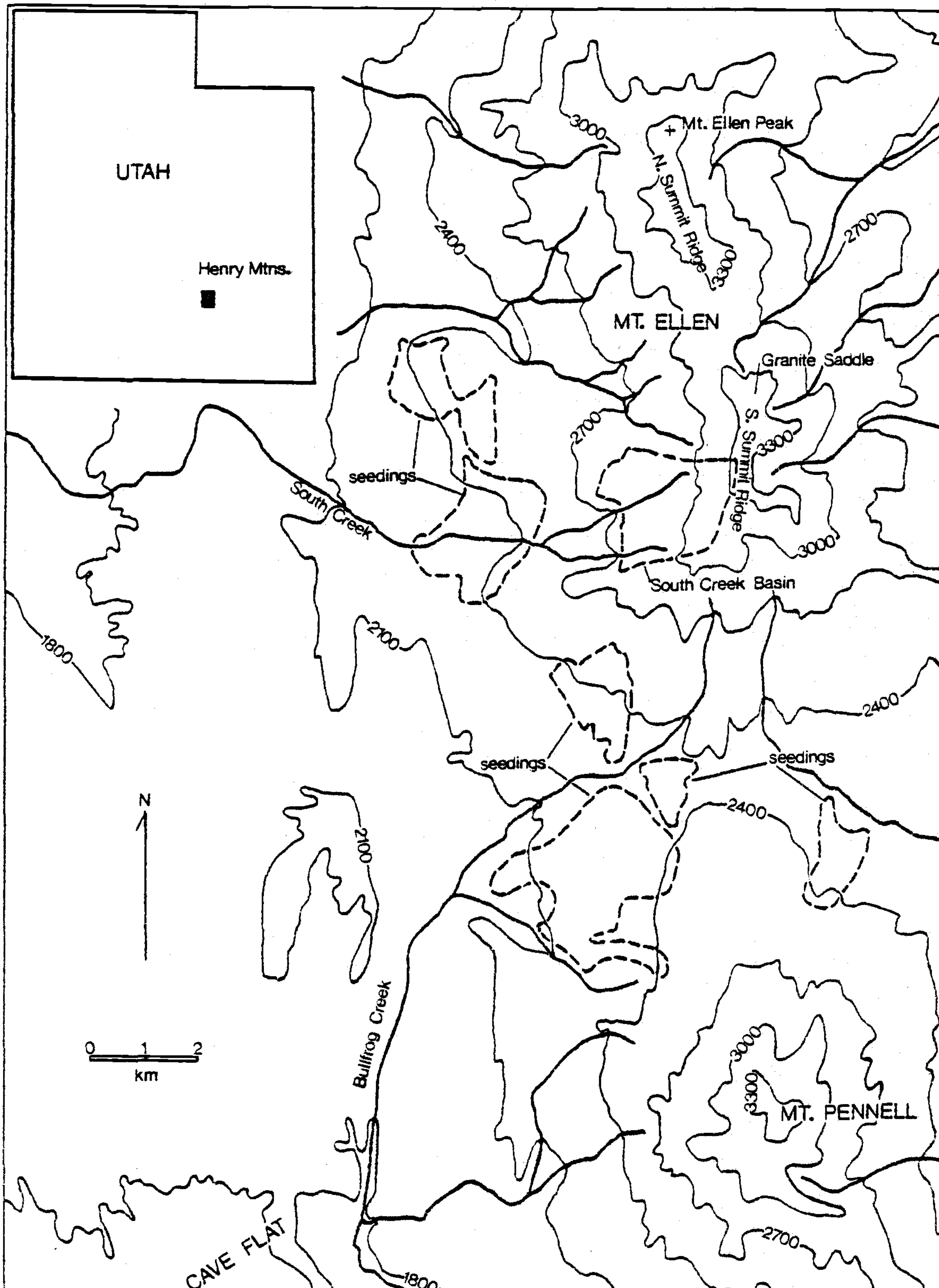

Fig. 1. Northern part of the Henry Mountains, Garfield County, Utah.

dominant shrub was big sagebrush (A. tridentata), with occasional areas of low sagebrush (A. nova). Other shrubs included snowberry (Symphoricarpos spp.), oak, bitterbrush (Purshia tridentata), rabbitbrush, wild rose (Rosa spp.), serviceberry (Amelanchier spp.), horsebrush (Tetradymia spp.) and barberry (Berberis spp.). Grasses were mostly native perennials, and included bluegrass (Poa fendleriana, P. sandbergii), needlegrass (Stipa lettermannii, S. comata), wheatgrass (Agropyron smithii, A. inerme), fescue (Festuca thurberi, F. ovina), bromegrass (Bromus ciliatus), squirreltail (Sitanion hystrix), junegrass (Koeleria cristata) and Indian ricegrass (Oryzopsis hymenoides), as well as several sedges (Carex spp.). Common forbs included penstemon (Penstemon spp.), locoweed (Oxytropis lambertii, Astragalus spp.), Indian paintbrush (Castilleja spp.), cinquefoil (Potentilla spp.), mountain dandelion (Agoseris spp.), prince's plume (Stanleya spp.) and onion (Allium spp.). The peaks above 3050 m occasionally supported dense meadows consisting primarily of Carex spp. or F. thurberi.

The upper slopes of Mount Ellen were steep and rugged. Slopes ranged from 0 to 40 degrees; most slopes exceeded 15 degrees and level areas were scarce. Precipitation varied with elevation, and ranged from an annual average of about 15 cm in the surrounding deserts to 50 cm or more on the upper slopes of Mount Ellen (BLM, unpublished data). Annual precipitation was irregular and unpredictable; at Hanksville, 35 km north of Mount Ellen, yearly totals (1931-1972) varied from 3.4 cm to 24.8 cm, with a mean of 13.3 cm (BLM, unpublished data).

All data on comparative ecology of bison and cattle were collected in South Creek Basin, an area of frequent co-use by bison and cattle. Cattle were present in the area throughout the period of data collection. South Creek Basin covered an area of about 4 km^2 on the west side of Mount Ellen, at the head of South Creek (Fig. 1). Elevation ranged from 2800 m on the west side of the basin to about 3260 m at the crest of South Summit Ridge on the east side. In contrast to other parts of Mount Ellen, South Creek Basin had a relatively large proportion of level areas. Slope increased from west to east, reaching a maximum of about 40 degrees. Most of the basin was unforested and supported sagebrush-grass communities.

METHODS

Data collection spanned 2 periods, 24 June through 6 September 1977 and 23 May through 1 October 1978. A field assistant helped collect data through most of the study, for a total of 10 man-months of field work.

The relationships between distribution of foraging bison and cattle, and elevation, slope, distance from water, and aspect were evaluated through direct observation. South Creek Basin was the only area on the upper slopes of Mount Ellen that was used frequently during the study by both bison and cattle. Furthermore, activity of bison and cattle throughout most of the basin could be monitored from any of several locations.

About 100 days were spent recording bison and cattle use in South Creek Basin. At 30-minute intervals, all bison and cattle that were feeding were located, and elevation, slope, distance from nearest water (both horizontal and vertical) and aspect of the location of each animal were recorded. A 15-minute topographic map was used to determine elevation, distance from water, and aspect. Slope was measured with a clinometer. Any direct interactions between bison and cattle were noted.

To compare availability of preferred forages to distribution of bison and cattle, 6 sites were selected in South Creek Basin that received heavy use by 1 or both species in 1977. Each site corresponded approximately to 1 plant community; boundaries were drawn where plant composition changed noticeably. During summer 1978, the numbers of bison and cattle feeding on each of the 6 sites were recorded at 30-minute intervals on an almost daily basis. Bison use and cattle use in South Creek Basin in 1978 occurred primarily during a 6-week period from 25 July to 7 September. At the end of this period, 40 plots (each 0.75 x 1.50 m) were located randomly on each of the 6 sites. All plant species in each plot were recorded, clipped separately and weighed to the nearest gram on a pan balance accurate to 0.1 g. Percent utilization of each species was estimated prior to clipping. After vegetation sampling was completed, a 30-g sample of each species was clipped, weighed, air dried for 72 hours, and reweighed to determine percent dry matter. For each of the 6 sites, percent of total forage utilized and percent availability were calculated for each plant species. A relative preference index (RPI) for each plant species was derived using the following formula adapted from Krueger (1972):

$$\frac{\text{\% of total forage utilized x frequency of utilization}}{\text{\% availability x frequency of occurrence}}$$

For each site, dry weights of preferred forages (indicated by a RPI of greater than 1) were summed for each plot and a mean kg/ha of preferred forages was calculated.

Simple linear regression (Dixon and Massey 1969:193) was used to compare foraging distribution of bison and of cattle to elevation, slope, horizontal distance from water, vertical distance from water, and amount of preferred forage. Square root transformation of the independent variable was attempted wherever the regression relationship appeared curvilinear. A "difference in proportions" test (Dixon and Massey 1969:249) was used to compare occurrence of bison and cattle on the basis of aspect.

Geographic distribution of bison was evaluated by weekly surveys of the upper slopes of Mount Ellen, the seedings, Cave Flat, and adjacent areas; as many bison as possible were located during each survey. Altitudinal distribution of bison on the upper slopes of Mount Ellen was evaluated by recording the elevation of bison whenever they were encountered.

The size of bison cow groups was determined by counting individuals whenever such groups were observed. Many sagebrush flats and openings on the upper slopes of Mount Ellen were bounded by physiographic features such as dense forests or ravines, that permitted delineation of each opening. The area of each opening was calculated with an aerial photograph and a compensating polar planimeter, and the sizes of all bison cow groups observed in each opening were recorded. Simple linear regression was used to compare group sizes to the areas of forest openings in which they occurred.

Seven bison cows were recognizable individually on the basis of natural markings. Observations of these cows were used to evaluate stability of bison cow groups. Each of the 7 cows was seen repeatedly during the study, in groups of varying sizes. Whenever 1 of the cows was observed in a group, the group was counted and all members were classified by age and sex. Assuming that a particular cow belonged to a stable subgroup, such as a clan, that stable subgroup was probably equal in size or smaller than the smallest group in which the marked cow was observed. Similarly, the largest size of each age-sex class within the hypothetical stable subgroup was the minimum number observed. This procedure was used to evaluate the maximum size and composition of the hypothetical stable subgroup associated with each cow.

An additional measure of group stability was obtained by observing each of 4 of the naturally marked cows for 28 consecutive days. Any persistent associations between a marked cow and other individual bison were recorded. Temporary stability of bison groups was evaluated by noting the time that a particular group persisted before dividing or combining with another group. Group persistence was compared to the distance from the group to the nearest bison of another group, averaged for all days that the group persisted. Also, the procedure of observing individual cows yielded data on the length of time that a bison group remained at a particular location.

RESULTS AND DISCUSSION

Comparative Foraging Ecology

A total of 7793 observations of bison and 1249 observations of cattle were recorded in South Creek Basin.

Foraging distribution of neither species was correlated ($P > 0.05$) to elevation (Fig. 2). However, cattle never were observed grazing at elevations greater than 3080 m, whereas bison were observed frequently at elevations up to 3260 m. Almost one-half (49%) of all bison observations were recorded above 3000 m, compared to just 7% of cattle observations. Cattle grazed most frequently at 2800 m and 2930 m; most level areas in South Creek Basin were located at either of these elevations.

Distribution of bison was not correlated ($P > 0.05$) to horizontal distance from water, whereas cattle distribution decreased, in general, with increased horizontal distance from water (Fig. 2). Although the correlation was significant ($P < 0.01$), horizontal distance from water accounted for less than one-half ($r^2 = 0.45$) of the variability in cattle distribution. Furthermore, cattle frequently were observed feeding at distances of 600 m or more from water, which indicated that horizontal distance from water was not an important factor limiting cattle distribution. Cattle grazed near water more often than bison; almost one-half (48%) of cattle observations were within 200 m of water, compared to 18% of bison observations.

Bison grazed most frequently on the steepest slopes present in South Creek Basin, although the relationship between bison distribution and slope was not significant ($P > 0.05$, Fig. 3). Conversely, cattle distribution was negatively correlated ($P < 0.01$) to slope. A square root transformation of slope accounted for over 70% ($r^2 = 0.72$) of the variability in distribution of feeding cattle. About one-third of slopes in South Creek Basin were 25 degrees or more, yet less than 10% of cattle observations were recorded on such slopes, compared to 65% of bison observations.

Bison use decreased with increasing vertical distance from water;

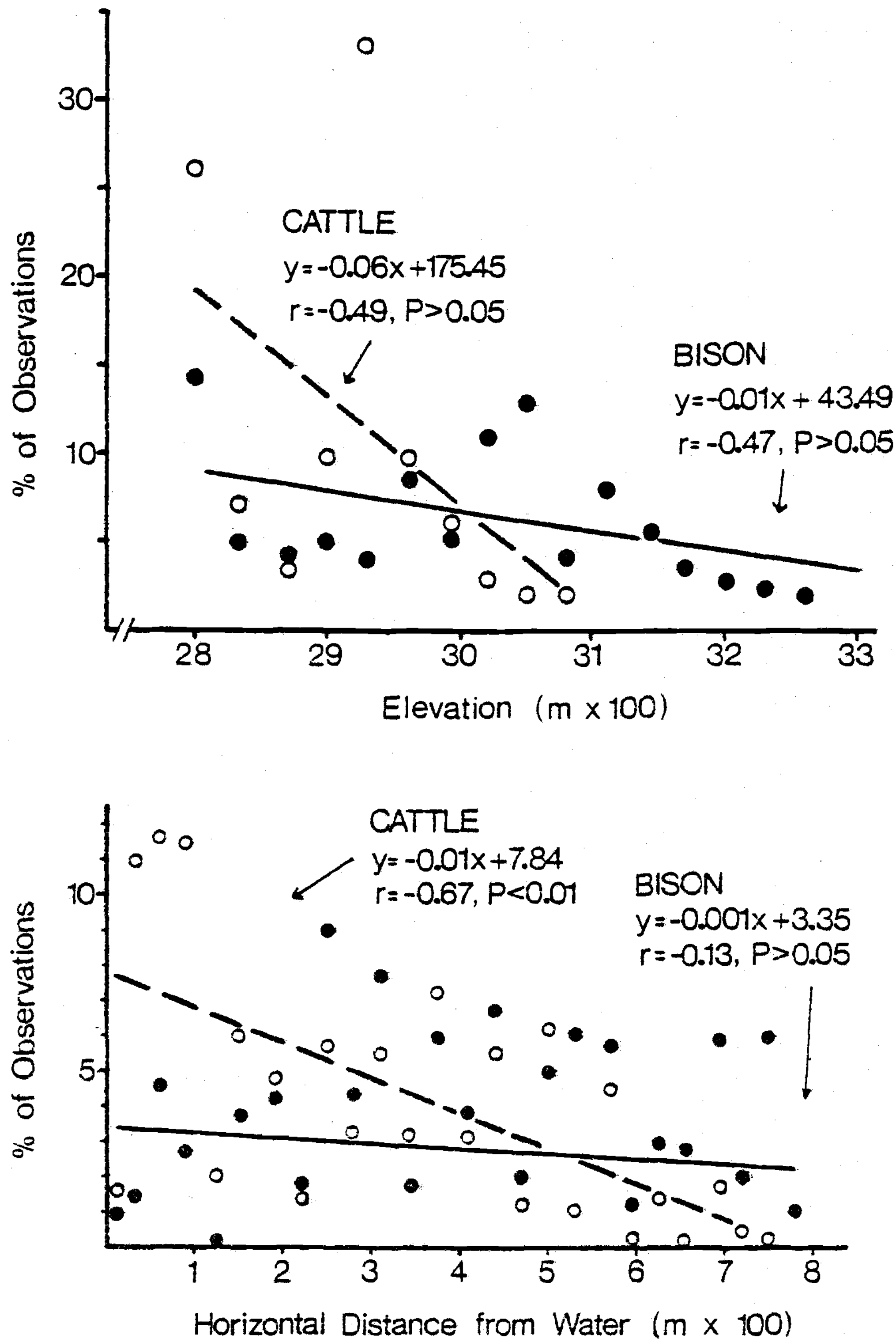

Fig. 2. Comparison of distribution of foraging bison and cattle to elevation (upper graph) and horizontal distance from water (lower graph), during summer 1977 and summer 1978 in South Creek Basin, Henry Mountains, Utah. Solid circles and lines denote bison, and open circles and broken lines denote cattle.

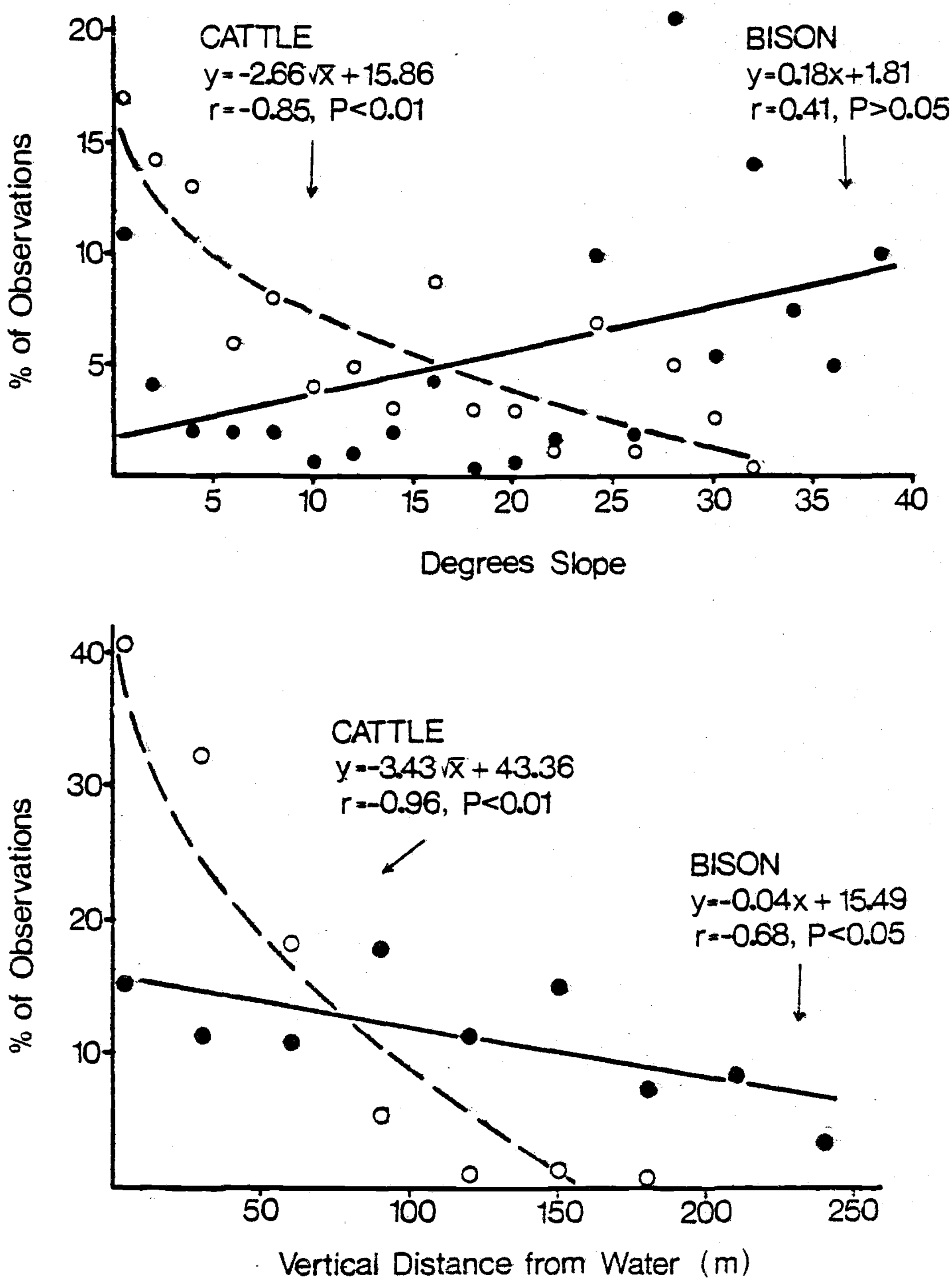

Fig. 3. Comparison of distribution of foraging bison and cattle to slope (upper graph) and vertical distance from water (lower graph), during summer 1977 and summer 1978 in South Creek Basin, Henry Mountains, Utah. Solid circles and lines denote bison, and open circles and broken lines denote cattle.

although the correlation was significant ($P<0.05$), vertical distance from water accounted for less than one-half ($r^2=0.46$) of the variability in bison distribution (Fig. 3). Moreover, bison frequently grazed sites up to 240 m above the nearest water source, which was the maximum distance for any site in the basin. Cattle distribution was negatively correlated ($P<0.01$) to vertical distance from water; a square root transformation accounted for 92% ($r^2=0.92$) of the variability in cattle distribution. Furthermore, cattle seldom grazed more than 90 m above water, which indicated that vertical distance from water limited cattle distribution.

Bison and cattle both ate primarily grasses and grass-likes in South Creek Basin in summer 1978 (Appendix B), and hence forages preferred by the 2 species were similar. Bison grazed most often on sites that had the most preferred forage (Fig. 4). Frequency of use among the 6 sites was positively correlated ($P<0.05$) to amount of preferred forage. Conversely, there was a negative relationship between frequency of cattle use and amount of preferred forage, although the relationship was not significant ($P>0.05$). This negative relationship probably was not caused by an aversion to food, but rather an aversion to steep slopes; slope and amount of preferred forage among the 6 sites were correlated ($P<0.01$, Table 1). Similarly, frequent use of steep slopes by bison probably was a response to a greater availability of preferred forages associated with these slopes, rather than a preference for steep slopes.

Bison fed on north facing slopes more often ($P<0.01$) than did cattle, whereas cattle were found more often ($P<0.01$) on south and southwest slopes (Table 2). These differences probably were not the result of differing responses to aspect by bison and cattle, but rather to associated factors. Most north slopes were 100 m or more above water, beyond the range of most cattle in South Creek Basin, and most south and southwest slopes were adjacent to large level areas that averaged less than 100 kg/ha of preferred forage. Bison and cattle rarely used northeast, east and southeast slopes, because there were few such slopes in South Creek Basin.

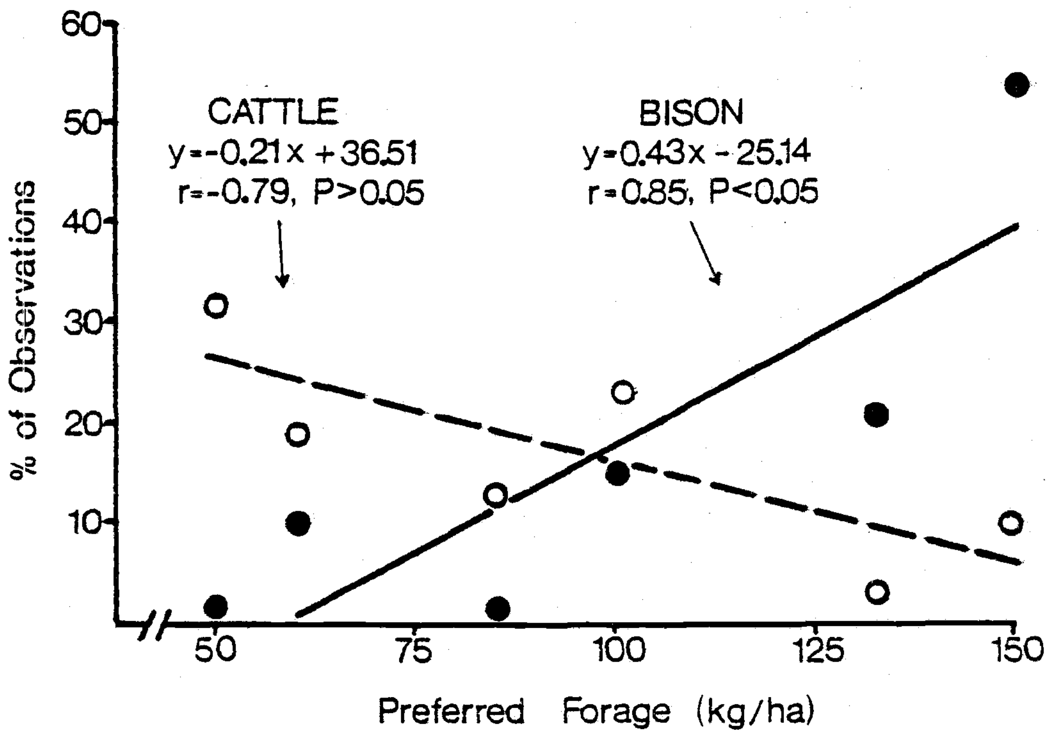

Fig. 4. Comparison of distribution of foraging bison and cattle to amount of preferred forage among 6 sites, during summer 1978 in South Creek Basin, Henry Mountains, Utah. Solid circles and lines denote bison, and open circles and broken lines denote cattle.

Table 1. Simple correlation coefficients for regression between amount of preferred forage and 4 site characteristics, at 6 sites in South Creek Basin, Henry Mountains, Utah during summer 1978.

	Amount of preferred forage
Elevation	0.43
Horizontal distance from water	0.06
Slope	0.93[a]
Vertical distance from	0.67

[a] $P<0.01$

Table 2. Aspect and percent use by bison and cattle in South Creek Basin, Henry Mountains, Utah during summer 1977 and summer 1978.

	Percent use, by aspect							
	N[a]	NE	E	SE	S[a]	SW[a]	W	NW
Bison	41	0	1	2	0	4	29	24
Cattle	19	0	2	1	9	10	32	27

[a] Different between species ($P<0.01$)

Bison and cattle were observed less than 20 m apart on 58 occasions. Activities included feeding (31 observations), resting (13), drinking (6), licking salt (5) and moving (3). Neither species altered behavior noticeably until the distance between them closed to an average of 4 m ($N = 26$, $SE = 0.6$, range = 1-15). At this distance, cattle either altered direction or moved aside as bison approached. Bison never were displaced by cattle. Bison were openly aggressive toward cattle on 16 occasions, but only when the 2 species were less than 5 m apart. Cattle were subordinate to bison in all interactions and were driven off an average 4 m ($N = 16$, $SE = 1.1$, range = 1-15). Yearling bison initiated 15 of 16 aggressive encounters with cattle, possibly because yearlings were subordinate in the bison dominance hierarchy (McHugh 1958); McHugh (1958) found that subordinate bison engaged in a higher percentage of aggressive encounters with conspecifics than did more dominant bison. On one occasion in this study a domestic cow charged a group of bison at a salt lick, but was itself driven off.

During at least 7 days in late May 1978, a domestic cow accompanied a group of 20 bison and was seemingly treated as a conspecific by bison in the group. The cow participated in all group activities, and migrated northward with the group at least 15 km to an area that was not used by cattle.

In summary, distribution of foraging bison in South Creek Basin was positively related to availability of preferred forage, whereas distribution of foraging cattle was negatively related to vertical distance from water and slope. Vertical distance from water and slope were at least partially independent in their effects on cattle distribution, because these 2 factors were poorly correlated ($r^2 = 0.04$) when compared in areas where cattle occurred. Elevation, horizontal distance from water, and aspect showed little or no relationship to distribution of either bison or cattle. Interspecific interactions did not affect distribution of either species until the distance between them closed to a few meters, and resulted in the displacement of cattle by bison.

Behavior

Movements and Distribution.—Bison moved frequently. In 57 observations, groups remained an average of only 1.9 days (SE = 0.3, range = 1–14) at any one location, and 95% of all groups observed left an area within 3 days.

Geographic distribution of bison in the Henry Mountains was similar between years in several respects. In both summers, bison followed a pattern of early use of the northern part of the range and a gradual southward shift as the summer progressed (Table 3). Furthermore, the north and east slopes of Mount Ellen Peak, the west side of North Summit Ridge, and South Creek Basin were used in the same sequence and at about the same time during both summers.

Differences in geographic distribution of bison between summers were evident. The area around Granite Saddle was used by 30–60% of the herd during June and July 1977, but was not visited at all by bison in 1978. This area, located at 3290–3440 m elevation, was the highest site used by bison during the study. During summer 1977, bison did not frequent the seedings at all before August; in 1978 the seedings supported at least 30% of the herd throughout the summer. Moreover, bison were absent from Cave Flat during summer 1977 until early September, whereas in 1978 groups of 40–50 bison were seen there irregularly through much of the summer. Cave Flat was considered part of the winter range of the herd (BLM 1974).

Altitudinal distribution of bison on the upper slopes of Mount Ellen (above 2530 m) also was different between years. During summer 1977, bison frequented higher elevations than in summer 1978 (Fig. 5).

Bison distribution, both geographical and altitudinal, varied between summers possibly because of different forage availability during the 2 summers. Summer 1977 was the 2nd year of a 2-year drought in the Henry Mountains, and little or no herbaceous growth was visible on Cave Flat or any of the seedings. Bison moved to the higher elevation areas on Mount Ellen, particularly Granite Saddle, probably because more forage was available on those areas; precipitation, and presumably forage production, increased with elevation. Heavy snowfall

Table 3. Geographic distribution of bison, at weekly intervals, during summer 1977 and summer 1978 in the Henry Mountains, Utah. Concentrations of activity are indicated by (+), and when combined for each week, represent at least 60% of the bison herd.

		1977						1978					
Month	Week	Cave Flat	Seedings	South Creek Basin	Granite Saddle	West side, N. Summit Ridge	N. & E. slopes of Mt. Ellen Pk.	Cave Flat	Seedings	South Creek Basin	Granite Saddle	West side, N. Summit Ridge	N. & E. slopes of Mt. Ellen Pk.
May	4			no data					+				
June	1			↓					+			+	+
	2			↓					+			+	+
	3				+	+	+		+			+	+
	4				+	+	+		+			+	+
July	1				+	+	+		+			+	+
	2					+			+			+	
	3				+	+		+	+			+	
	4			+	+	+			+	+		+	
August	1		+	+		+			+	+		+	
	2		+	+		+			+	+			
	3		+	+				+	+				
	4		+	+					+				
Sept	1	+	+						+	+			
	2			no data				+	+	+			
	3			↓				+	+				
	4			↓				+	+				

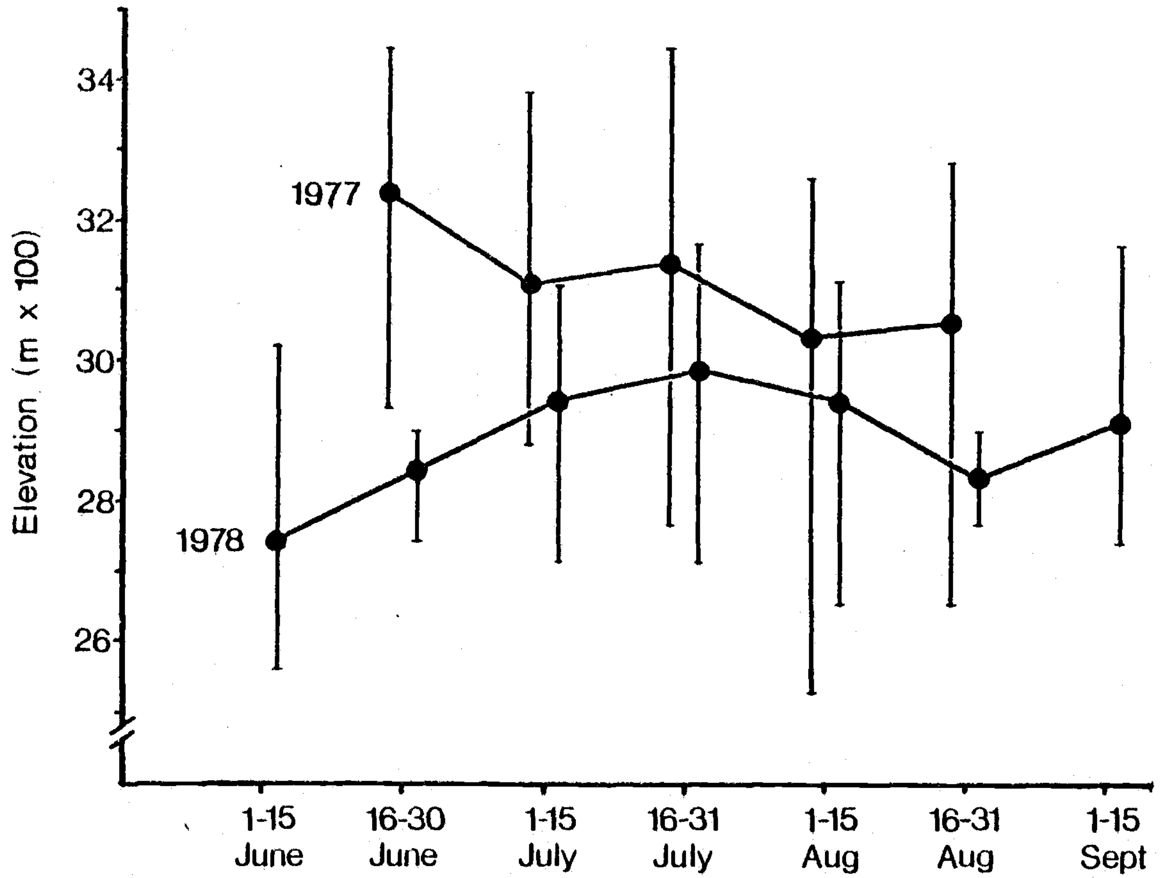

Fig. 5. Means and associated ranges in elevation of bison observed above 2530 m on Mount Ellen, Henry Mountains, Utah.

during winter 1977-78 resulted in abundant forage production on Cave Flat, the seedings and the upper slopes of Mount Ellen. The bison probably found sufficient forage throughout much of their range during summer 1978, and consequently herd distribution was more variable than in summer 1977. A large part of the herd remained on the seedings, where forage was abundant, throughout the summer. Animals that moved onto the upper slopes of Mount Ellen probably found sufficient forage between about 2500 m and 3000 m, and hence did not continue to the highest peaks.

Group Size.—Bison cow groups were small; almost one-half (49%) of 191 groups totalled 15 animals or less (Fig. 6). These results were consistent with those of Fuller (1960), Egerton (1962) and Shackleton (1968), who also found that bison groups in forested habitats usually totalled less than 30 animals.

Group size was correlated ($P<0.01$) to the size of forest openings in which they were observed; larger groups were found more often in the larger openings (Fig. 7). Furthermore, the size of the largest group observed in each opening was correlated ($P<0.01$) to the area of each opening, which indicated that group size was limited, in part, by opening size. These results document a close relationship between habitat structure and size of bison groups.

Group Stability.—Cows that had calves were always observed with their calves. In addition, several cows that were observed repeatedly throughout the summer were accompanied by a yearling. Most yearlings in cow-yearling pairs suckled regularly and were undoubtedly the offspring of the suckled cows. No other persistent associations between recognizably distinct bison were documented. The maximum sizes of hypothetical stable subgroups to which each of 7 cows belonged, based on a comparison of the groups in which each cow was observed, ranged from 3 to 8 individuals (Table 4). These results indicated that if stable subgroups existed at all in the social structure of the Henry Mountain herd, they totalled only a few animals and included at most 1-4 cows with or without calves, 1-2 yearlings, and 1 adult bull. Cows with calves or yearling offspring possibly were the only stable subgroups in the Henry Mountain herd.

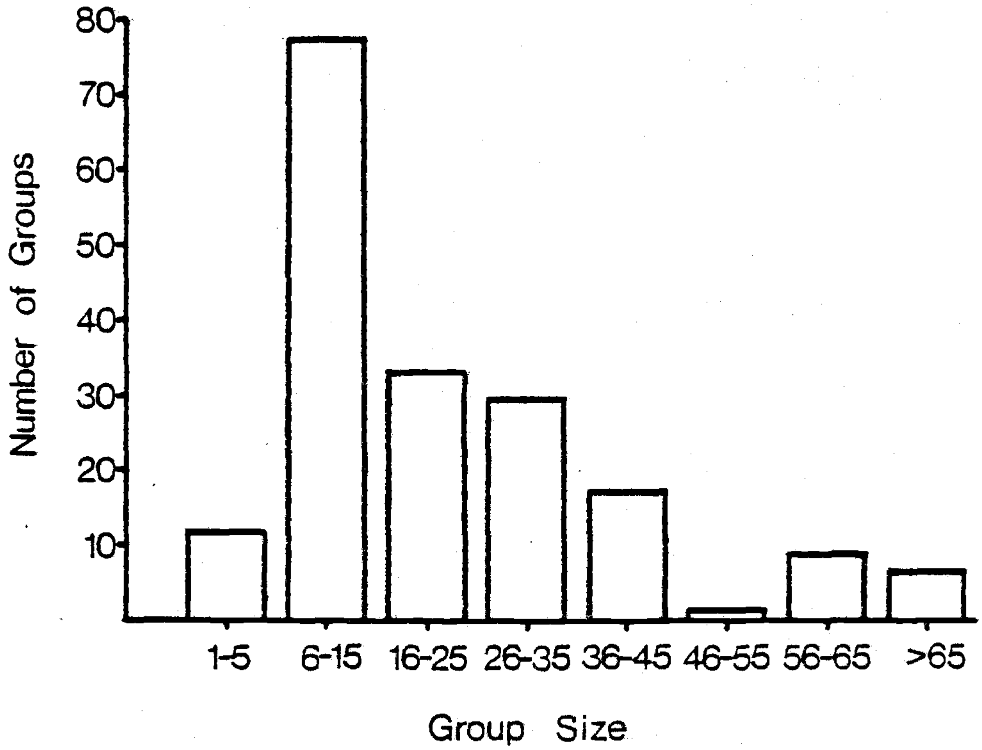

Fig. 6. Size distribution of 191 bison cow groups counted during summer 1977 and summer 1978, above 2530 m on Mount Ellen, Henry Mountains, Utah.

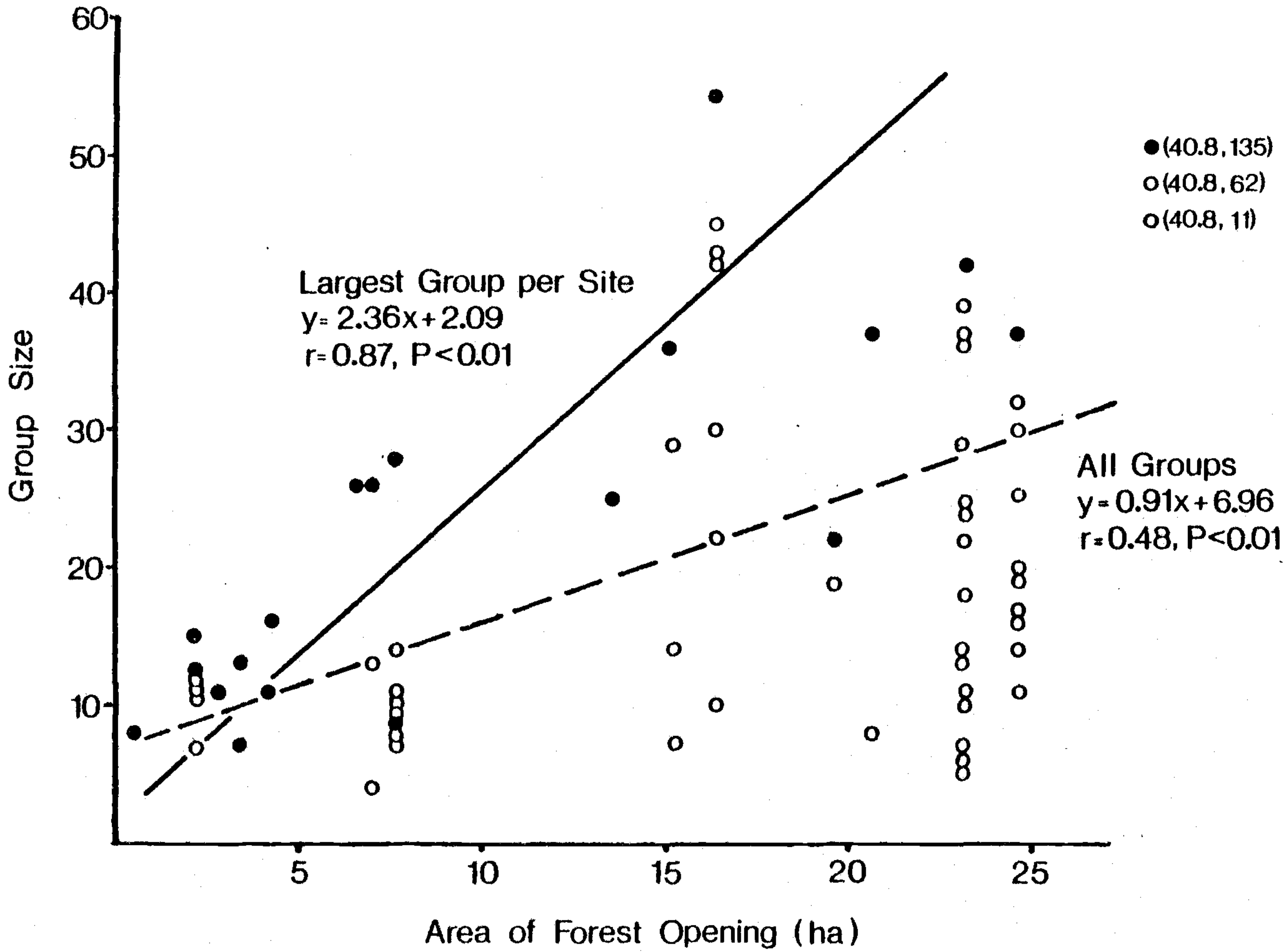

Fig. 7. Comparison of bison cow group size and area of the forest opening in which each group was observed, during summer 1977 and summer 1978, above 2530 m on Mount Ellen, Henry Mountains, Utah. The solid line and solid circles denote the largest group recorded on each of 20 forest openings. Open circles denote all other groups found on each opening. The broken line represents all groups.

Table 4. Maximum size and composition of hypothetical stable subgroups that included 1 of 7 recognizable bison cows, in the Henry Mountain bison herd, during summer 1977 and summer 1978.

Cow No.	Year	No. groups in which cow was observed	Hypothetical subgroup				
			Size	Bulls	Cows	Yearlings	Calves
1	1977	15	8	1	4	1	2
	1978	7	5	1	3	1	0
2	1978	20	3	1	1	1	0
3	1978	18	5	0	3	2	0
4	1977	6	8	0	4	1	3
	1978	18	5	1	3	1	0
5	1977	6	7	1	4	0	2
6	1978	11	4	1	1	2	0
7	1978	6	7	2	3	2	0

Once formed, most bison cow groups persisted for only 1-4 days before dividing or combining with another group (Fig. 8). The time a group persisted was positively correlated ($P<0.01$) to the average distance to the nearest bison of another group, which indicated that group persistence was related to the probability of encountering other bison.

Bison groups in this study possessed little or no stability. Groups changed composition whenever other groups were encountered, and those that persisted did so in part through a lack of contact with other bison. Stable subgroups, if they existed at all, comprised only a few animals.

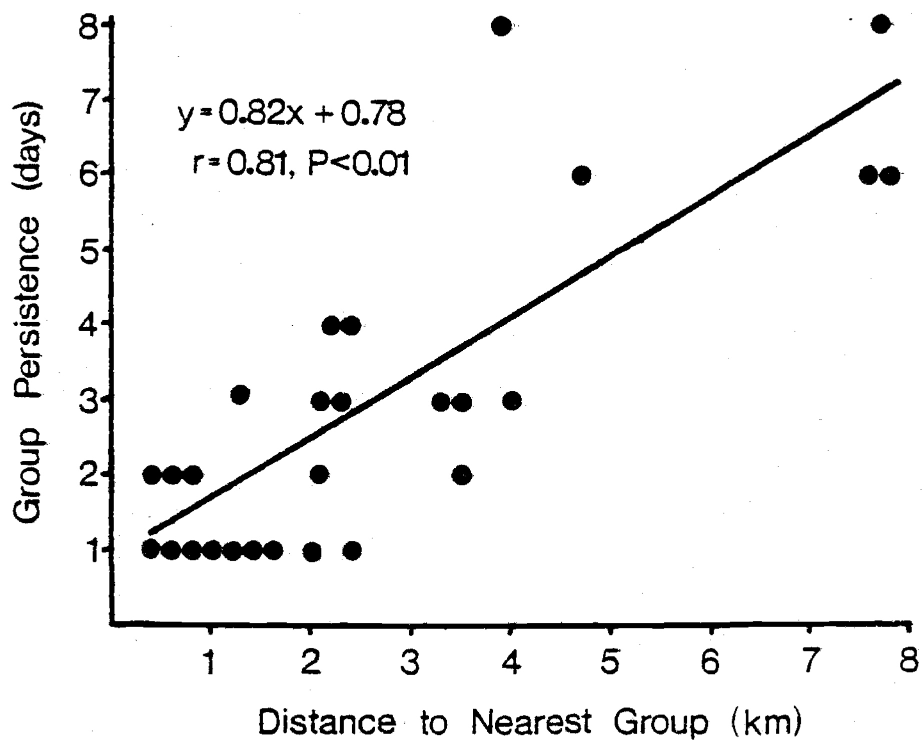

Fig. 8. Comparison of the number of days that bison cow groups persisted and the average daily distance to the nearest bison of another group, during summer 1977 and summer 1978 on Mount Ellen, Henry Mountains, Utah.

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APPENDICES

Appendix A: Population Dynamics

The entire study area was searched for bison 5 times in 1977 and 4 times in 1978. All individuals observed during each survey were counted and classified according to age and sex. In addition, all bison groups were counted whenever encountered during the study, and members were classified according to age and sex. A weighted average of the age and sex proportions of all groups yielded another estimate of age and sex composition of the herd.

The herd totalled about 220 animals during both summers. This estimate was based on counts in both years that approached 200 animals (Table 5). Typically, 10-20 bison were excluded from these totals because of the possibility that they already were counted. The addition of these animals increased at least 1 count in each summer to a total of about 220.

Calves comprised about 21% of the herd in summer 1977, but less than 4% in 1978; few cows calved in 1978. Possibly, the severe drought during 1977 had a negative effect on the health of bison cows through reduced forage production, and resulted in a very low calving rate in 1978.

Yearlings comprised about the same percentage in the herd in 1978 as they comprised as calves in 1977, which indicated that most calves survived the winter of 1977-78. High survival of calves during a winter that followed a severe drought possibly was because of parental care; many bison suckled regularly until at least 16 months old.

Appendix B: Diets of Bison and Cattle

Numerous studies of cattle diets, including Stephens (1966), Mackie (1970), Miller and Krueger (1976), Cook and Harris (1977), and Vavra et al. (1978), documented that grasses and grass-likes were the forages eaten most often. Only 4 published studies evaluated bison diets; all reported that bison ate mostly grasses and sedges (Meagher 1973, Peden et al. 1974, Peden 1976, Reynolds et al. 1978). Peden et al. (1974) compared diets of bison and cattle, and found that bison

Table 5. Age and sex proportions in the Henry Mountain bison herd, 1977-1978. A dash denotes no data.

Period	Source	Date	Total	Percentages				Bulls: 100 cows	Calves: 100 cows
				Calf	Yearling	Cow	Bull		
Summer 1977	Count 1	1 July	177	19.8	12.1	—	—	—	—
	Count 2	8 July	163	21.2	12.4	—	—	—	—
	Count 3	31 July	189	21.6	14.6	36.6	27.4	75	60
	Count 4	12 Aug	151	18.5	13.2	35.8	32.5	91	52
	Count 5	27 Aug	174	22.4	11.5	38.3	26.6	69	58
	Weighted group average			21.4	13.0	35.7	30.0	84	60
Summer 1978	Count 1	5 June	198	4.4	24.4	45.0	26.0	58	10
	Count 2	8 July	199	4.5	19.0	44.6	31.8	71	10
	Count 3	21 Aug	188	4.4	23.1	50.0	21.9	44	9
	Count 4	13 Sept	150	3.3	18.3	50.4	29.0	58	8
	Weighted group average			3.4	21.7	47.6	27.7	58	7

on the shortgrass plains of Colorado ate mostly grasses in all seasons and under both heavy and light grazing intensities. Cattle at the same site, however, varied intake of grasses as season and grazing intensity changed, and included substantial quantities of forbs and shrubs in their diets. No study has compared diets of bison and cattle in a sagebrush - grass community.

Diets of bison and cattle in South Creek Basin were evaluated by utilization estimates and by fecal analysis. Of the 6 sites in South Creek Basin that were sampled for preferred forage, 1 was used exclusively by cattle. A 2nd site was used mostly by bison; the small amount of cattle use was limited to the edge of the site, where no vegetation sampling plots were located. Calculations of forage utilization on the cattle site and the bison site represented exclusive use by both species and hence were estimates of the diets of the 2 species.

On 10 August 1978, a 1-tablespoon sample was collected from each of 35 bison and 35 cattle feces in South Creek Basin. Bison feces were dropped by 6-10 individuals and cattle feces were dropped by 10-15 individuals. All had grazed in adjacent parts of South Creek Basin for at least 4½ days immediately prior to collection. Samples were preserved with an equal volume of salt, labeled, and sent for microhistological analysis to Composition Analysis Laboratory, Colorado State University. After the samples were ground separately in a Wiley Mill, microscope slides were prepared from each of the 70 samples. Plant fragments were identified by examination of 100 microscope fields. Frequency of occurrence of plant fragments was converted to percent relative density; Sparks and Malechek (1968) found that percent relative density was equivalent to percent dry matter for many plant species.

Bison feces were dropped by animals that grazed primarily on 2 of 6 sites where the amount of preferred forage was determined. Similarly, cattle feces were dropped by animals that grazed primarily on 2 other of the 6 sites. Weighted averages of forage availability on the 2 bison sites and the 2 cattle sites were used as estimates of forage availability for comparison with diets derived from fecal analysis.

Researchers have compared methods of diet determination in herbivores and found that utilization estimates on several plots yielded 1 of the more accurate estimates of diets (Laycock et al. 1972, McInnis 1977). Conversely, fecal analysis was the least accurate method of diet determination; grasses were consistently overestimated and forbs were consistently underestimated (Vavra et al. 1970, Slater and Jones 1971, Anthony and Smith 1974, McInnis 1977, Vavra et al. 1978). The use of both techniques in this study provided complementary information on diets of bison and cattle. Utilization estimates gave reasonably accurate percentages of forages in diets, but a lack of replicates precluded statistical comparison between bison and cattle. Fecal analysis, although inaccurate, provided replicates useful in comparison of diets between species; a necessary assumption was that inaccuracies were consistent among both bison and cattle.

Bison ate about 90% grasses and sedges; 7 of 9 grasses and sedges were preferred or were eaten at about the same frequency and amount as they occurred (Table 6). Forbs and browse each contributed only about 5% to the bison diet. All forbs and browses available were strongly rejected.

Cattle were primarily grazers, but also included substantial quantities of forbs in their diet (Table 6). Most available grasses and sedges were preferred, but not as highly as by bison. Furthermore, cattle strongly preferred 1 forb (Penstemon spp.) and ate another (Oxytropis lambertii) at almost the same frequency and amount as it occurred on the site. Browse was not found in the cattle diet, possibly because of low palatability of sagebrush (Artemisia spp.), the only available browse.

Results from fecal analysis confirmed basic differences in diets of bison and cattle that were suggested by utilization estimates. Bison ate more (t-test, $P<0.01$) grass than did cattle, whereas cattle ate more ($P<0.01$) forbs (Table 7). Moreover, results from both methods demonstrated the importance in the cattle diet of Oxytropis lambertii, a plant that was poisonous to cattle (Marsh 1929, Kingsbury 1964:307). Bison ate little O. lambertii, and strongly rejected it when encountered. Penstemon spp., a forage that appeared in both bison

Table 6. Diets of bison and cattle in South Creek Basin, Henry Mountains, Utah, during summer 1978, based on utilization estimates.

	Bison			Cattle		
Forage	% Avail.	% Diet	RPI	% Avail.	% Diet	RPI
Browse	52.8	5.5	0.01	30.9	0	0
Artemisia tridentata	8.9	0	0	24.6	0	0
A. nova				6.3	0	0
Berberis spp.	0.03	0	0			
Chrysothamnus viscidiflorus	3.0	0	0			
Rosa spp.	0.4	0.3	0.19			
Symphoricarpos spp.	40.5	5.2	0.02			
Forb	12.3	5.1	0.20	16.5	19.4	0.79
Agoseris spp.	0.1	0	0	0.6	0	0
Oxytropis lambertii	6.8	2.2	0.07	7.4	12.1	0.93
Astragalus spp.	1.4	0.9	0.43	3.5	1.3	0.15
Hymenoxys spp.				1.1	0.1	0.02
Penstemon spp.	4.0	2.0	0.20	1.4	7.0	5.00
Potentilla spp.				2.4	0.2	0.01
Stanleya spp.				0.3	0	0
Grass & Grass-like	34.7	89.6	2.58	52.4	80.5	1.54
Agropyron smithii	1.9	5.1	1.83			
Carex spp.	1.1	3.4	2.68	1.2	3.1	1.61
Bromus ciliatus	1.9	3.1	1.00			
Festuca ovina	2.4	1.0	0.26	4.3	1.0	0.09
F. thurberi	8.8	42.3	4.81			
Poa fendleriana/ P. sandbergii	8.8	9.2	1.01	27.0	23.8	0.88
Stipa comata	2.6	7.9	2.24	1.4	4.3	1.84
S. lettermannii	5.9	15.7	2.39	14.3	44.1	3.01
Sitanion hystrix	1.3	1.9	0.60	3.9	2.9	0.19

Table 7. Diets of bison and cattle in South Creek Basin, Henry Mountains, Utah during summer 1978, based on analysis of 35 fecal samples from each species. An asterisk denotes forages occurring in significantly different amounts ($P < 0.01$) in bison and cattle feces. Forages that comprised an average of less than 0.1% of both bison and cattle feces are combined as "other" or denoted "tr".

	Bison		Cattle	
Forage	% Avail.	% Diet ($\bar{x} \pm SE$)	% Avail.	% Diet ($\bar{x} \pm SE$)
Browse	36.9	0.4 ± 0.08	70.5	0.4 ± 0.50
Artemisia spp.	11.0	tr	65.4	0.2 ± 0.06
Symphoricarpos spp.	24.1	tr	4.0	0
Other	1.8	0.3	1.1	0.2
Forb(*)	23.7	0.7 ± 0.09	8.7	4.5 ± 0.54
Astragalus/Oxytropis(*)	14.6	tr	4.9	3.8 ± 0.52
Erigeron spp.	0.3	0.2 ± 0.05	0	tr
Lesquerella spp.	0	0.2 ± 0.05	0	tr
Oenothera spp.	0	0.2 ± 0.01	0	0
Penstemon spp.	8.2	0	0.4	0
Phlox spp.	0	0.1 ± 0.04	0	tr
Potentilla spp.	0.2	0	0.7	0.4 ± 0.08
Other	0.4	tr	2.7	0.2
Grass & Grass-like(*)	39.4	98.7 ± 0.13	20.7	95.0 ± 0.54
Agropyron spp.	3.0	2.1 ± 0.40	0.2	2.1 ± 0.28
Bouteloua gracilis	0	0.1 ± 0.04	0	tr
Bromus spp.	1.0	3.0 ± 0.51	0.6	3.7 ± 0.54
Carex spp.(*)	0.7	2.6 ± 0.35	0.4	0.5 ± 0.12
Festuca spp.	12.7	12.5 ± 2.53	1.5	9.9 ± 0.68
Koeleria cristata(*)	a	12.8 ± 0.85	a	21.9 ± 1.37
Oryzopsis hymenoides	0	0.3 ± 0.09	0	1.4 ± 0.37
Poa spp.(*)	13.5	66.2 ± 2.16	10.5	49.8 ± 1.83
Sitanion hystrix	1.1	tr	1.5	tr
Stipa spp.(*)	7.3	1.2 ± 0.14	6.1	5.6 ± 0.91
Other	0	0.2	0	tr

[a] Incorrectly identified during vegetation sampling and included in *Poa*.

and cattle diets based on utilization estimates, was not recorded in any feces. Possibly, this forb was destroyed totally during digestion or sample preparation; it was the most succulent forage (37.2% dry matter) recorded in the study.

The findings of this study were consistent with other research on diets of bison and cattle. Bison ate grasses almost exclusively, whereas cattle ate substantial amounts of forbs in addition to grass.

Appendix C: Comparison of Utilization Estimates and Fecal Analysis to Determine Diets of Bison and Cattle

Researchers have attributed the inaccuracy of the fecal analysis method to differential digestibility of forages (Vavra et al. 1970, Hansen et al. 1973, Anthony and Smith 1974, McInnis 1977, Vavra et al. 1978), or loss of plant fragments during analysis (McInnis 1977). Vavra and Holechek (unpublished manuscript) subjected several forage mixtures of known composition to *in vitro* digestion and then analyzed them according to various microhistological procedures. They found that digestion changed forage composition, primarily through partial loss of all forbs and 1 shrub, snowberry (*Symphoricarpos albus*). When analytical procedures were used that were similar to those used in this study, digestion reduced the proportion of forbs by 80%, and reduced snowberry according to the following regression relationship: $y = 4.86 + 1.29x$. Sample preparation and analysis had little effect on results.

In the present study, forbs were important in diets of cattle and snowberry was eaten in small amounts by bison. Utililization estimates yielded different values for bison and cattle diets than did fecal analysis, possibly because of differential digestibility of these forages. To test this, the correction factors derived by Vavra and Holechek were used to adjust diets derived from utilization estimates. The adjusted diets, which represented the effects of *in vitro* digestion, were compared to results of fecal analysis.

Adjusted diets were very similar to diets derived from fecal analysis (Table 8). Loss of forbs and snowberry through digestion

Table 8. Diets of bison and cattle in South Creek Basin, Henry Mountains, Utah during summer 1978. Diets were determined by utilization estimates, fecal analysis, and utilization estimates adjusted for loss of forbs and snowberry during digestion.

	Bison			Cattle		
Forage	Utiliz.	Fecal	Adjusted Utiliz.	Utiliz.	Fecal	Adjusted Utiliz.
Grasses	89.6[a]	98.7	98.4	80.5[a]	95.0	95.4
Forbs	5.1[a]	0.7	1.1[a]	19.4[a]	4.5	4.6
Browse	5.5[a]	0.4	0.5	0	0.4	0

[a] Different ($P<0.01$) from fecal estimate

accounted for most differences between the utilization estimate method and the fecal analysis method. These results substantiated the numerical relationships between digested and undigested forages that were reported by Vavra and Holechek. Predetermined correction factors, that accounted for forages lost during digestion, increased the accuracy and utility of the fecal analysis method of determining herbivore diets.

Appendix D: Impact of Bison Wallows

The impact of bison wallows was evaluated by a thorough survey of all wallows above 2530 m on Mount Ellen. Most wallows occurred on forest openings. The diameter of each wallow was measured to the nearest meter and then used to calculate area. Total area of those wallows that occurred in a forest opening was compared to the area of the opening.

A total of 274 wallows was located, most of them 2-3 m in diameter (Table 9). Total area impacted by wallows was about 0.3 ha. Wallows impacted about 1% or less of any forest opening on Mount Ellen; many areas had no wallows at all.

Appendix E: Reaction by Bison to Humans

Bison in the Henry Mountains were extremely wary when humans were present; detection of a person by either sight or smell usually caused a stampede. Once stampeded, bison ran an average 1.8 km ($N = 34$, $SE = 0.24$, range = 0.8-5.0). Occasionally, bison tolerated the presence of a human as close as about 400 m, but usually only if the bison were above the person, up a steep slope. Bison were much more tolerant of automobiles, provided no one left a vehicle and consequently became recognizable as a human. A similar tolerance of automobiles was reported in bison (Engelhard 1970) and in Thomson's gazelle (*Gazella thomsoni*) (Walther 1969).

Table 9. Location and size of bison wallows above 2530 m on Mount Ellen, Henry Mountains, Utah. Percent area impacted by wallows is shown for openings that had delineated boundaries.

Location	No. of wallows, by diameter (m)											Total No.	Total area(m^2)	Area of opening(ha)	% area in wallows
	1	2	3	4	5	6	7	8	9	11	17				
1			1									1	7.1		
2			2	1								3	26.8	0.6	0.45
3		1	3									4	24.4	13.6	0.02
4		9	5	6	1		1					22	197.1	9.7	0.20
5		15	7	3								25	134.0	2.0	0.67
6		12	5	3	2	1						23	178.0	1.8	0.99
7		7	9	4	6	1			1			28	345.5	5.7	0.61
8							1					1	38.5	3.6	0.11
9		6	12	2	5	4	1	1	1			32	492.6	4.2	1.17
10		6	4	2	3							15	131.0		
11		2	1		1							4	32.9		
12		9	8	6	7	2	1	1		1	1	36	764.9	18.5	0.41
13		16	5					1				22	135.4		
14		9	4	2								15	81.5	10.0	0.08
15		2	1									3	13.3	8.2	0.02
16			3	1								4	33.9		
17			1	1								2	19.7		
18			1									1	7.1		
19		10	9	4	1							24	164.9	22.0	0.07
20			2	1								3	26.8	20.8	0.01
21		1	3	1		1						6	65.3	20.8	0.03
Totals		105	86	37	26	9	4	3	2	1	1	274	2920.7		

Appendix F: Time Spent at Water by Bison

Bison in the Henry Mountains seldom spent much time near a water source. Typically, a group walked from a feeding area to a water source, located up to 1.6 km distant. Once at water, bison remained an average 21.3 minutes ($N = 726$, $SE = 0.51$, range $= 2$–45), then usually returned to where they were previously or moved to a new area. They seldom rested or fed near water.

Appendix G: Suggestions for Further Research on Bison

The relationship between bison distribution and food availability should be studied more thoroughly. Bison distribution and movements should be quantified regularly throughout the year, and then compared to a comprehensive evaluation of food availability. Many sites throughout the range of the herd should be sampled regularly for quantity and quality of all plant species (i.e., nutritive value, phenology, dry weight and green weight). Experimental manipulation of forage availability, such as burning or seeding of specific sites, could lead to a better understanding of possible effects on bison distribution.

Diets of bison and cattle should be compared in a scheme of varied forage availability, such as in different seasons or in different plant communities.

Associations between individual bison should be described and quantified to evaluate more thoroughly the stability of bison groups. The home range of free-ranging bison should be determined by tracking marked individuals.