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RANGE EXPANSION BY BISON OF YELLOWSTONE NATIONAL PARK

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The bison (*Bison bison*) of Yellowstone National Park have existed as an isolated population since the park was established in 1872 (Meagher, 1973*a*). The bison that inhabited the Yellowstone River valley immediately north of the park were exterminated during the 1860s; those on the park's northern range were gone by the early 1890s. Bison from ranched herds introduced in 1902 interbred with the remnant original bison. The resulting population was influenced variously by ranching activities and regulation of population numbers by removals (reductions) through 1966. Except for a few males, bison seldom moved beyond park boundaries; they occupied traditional winter ranges with seasonal migrations to summer ranges (Meagher, 1973*a*).

During the past dozen years the population on the northern winter range expanded from the traditional core along the lower Lamar River, occupied new foraging areas within the park, and moved outside. Further expansion was disrupted because of conflicts with human interests (Meagher, 1973*b*, 1974, 1989). The factors which apparently contributed to the changes are presented here.

The study area (Fig. 1) encompassed all but the higher elevations at the fringes of the 100,000-ha northern winter range (Houston, 1982). Elevations ranged from about 2,030 m at the upper limits to 1,550 m at the lower. Bison foraged on discontinuous sites on open bottomlands and lower adjacent slopes, but their travel routes sometimes traversed forest areas and steep slopes. Long cold winters and short cool summers characterize the climate, but there is great variation in conditions across the winter range and between years (Houston, 1982). Much of the annual precipitation occurs as snow. During recent winters the ground was nearly snow-free much of the time near Gardiner at the north boundary.

Population counts, distribution, and group size were obtained by air, using a Piper Supercub. Ground observations provided supplemental detail. Movements were assessed by changes in group locations, visible travel trails in snow, and from unusual numbers of droppings along the road. Snow-course water-content records, supplemented by narrative field notes, provided information on winter severity.

The winter of 1975–1976 was exceptionally severe. As a result of two arctic storms in November followed by thaws the winter range was covered at the ground surface by a hard layer estimated at 150 mm in the Lamar area. Subsequently, more snow accumulated and consolidated. The snow courses recorded approximately 190% of the 20-year average water content for December 1975. During the entire winter, water content was well above 100%. The next winter was mild followed by 2 winters somewhat above average. All winters 1980–1987 were below average in severity.

Bison counted on the northern range in mid-winter increased approximately three-fold 1976–1987 (Table 1). The high count in 1985 of 661 bison included a temporary shift (Meagher, 1973*a*) of about 100 animals from Pelican Valley about 40 km south of the study area. During winter 1984–1985, the State of Montana removed 88 bison outside the park. The removal and the temporary nature of the shift from the south probably accounted for the drop to a count of 539 in 1986.

Beginning winter 1975–1976, mixed herds (females and juveniles with one to several older males) moved west of the traditional winter range. Initially, the major movement followed the Yellowstone River, with smaller movements most winters thereafter (Table 1). Attempts to block these movements (Meagher, 1989) precluded a detailed assessment of undisturbed movement patterns. These bison returned eastward in spring.

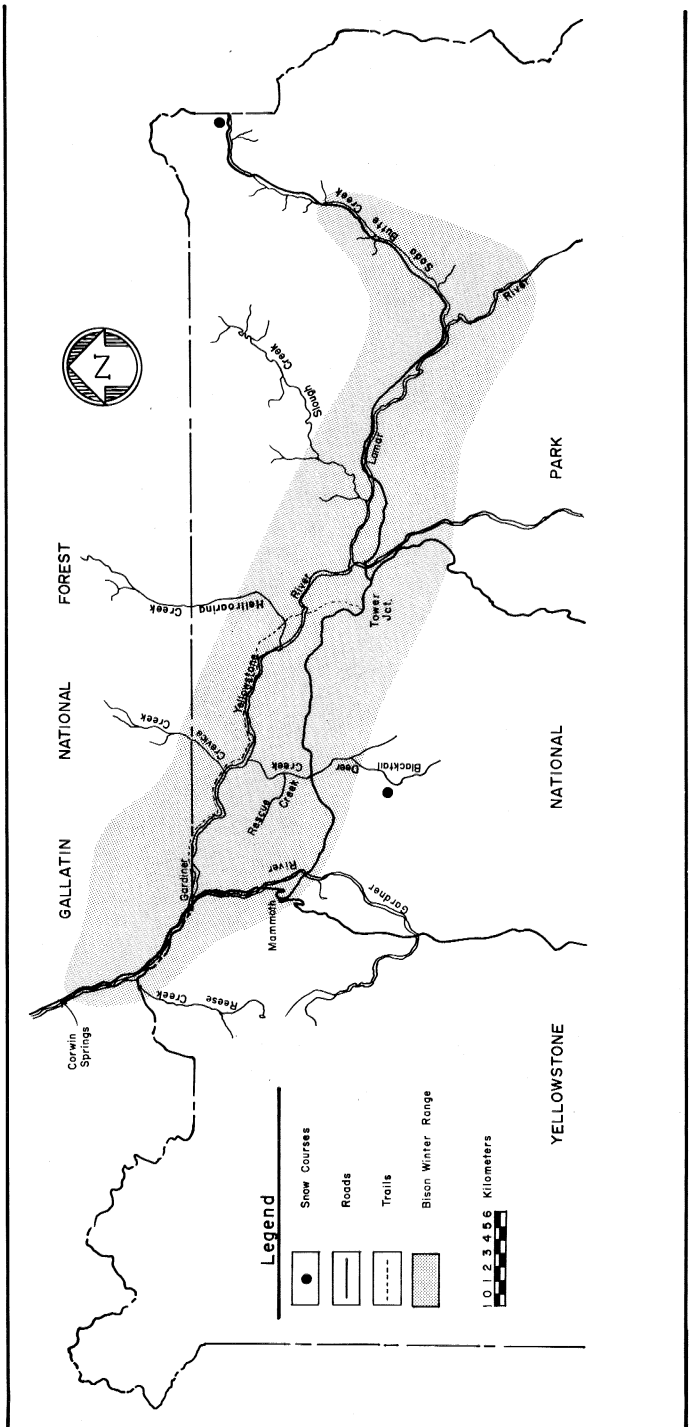

FIG. 1.—The northern winter range of bison in Yellowstone National Park.

TABLE 1.—*Period of bison use and maximum numbers west of the traditional northern winter range, Yellowstone National Park, 1976–1987.*[a]

Winter	Blacktail area			Mammoth-Gardiner-Reese			River Trail			Winter count
	First date	Last date	Maximum numbers	First date	Last date	Maximum numbers	First date	Last date	Maximum numbers	
1975–1976	5 Feb.	21 Mar.	59	29 Mar.	12 Apr.	7[b]	5 Feb.	31 Mar.	84	200
1976–1977		no activity			no activity			a few males		209
1977–1978		a few males			a few males		24 Feb.	28 Mar.	78	219
1978–1979		a few males			a few males		14 Mar.	19 Mar.	80	262
1979–1980		moved through		24 Feb.	8 Apr.	12[b]	2 Mar.	8 Apr.	29	233
1980–1981	1 Dec.	18 Dec.	34		a few males			no activity		255
1981–1982	17 Feb.	18 Feb.	15	8 Apr.	29 Apr.	9[b]	12 Feb.	18 Feb.	11	329
1982–1983	15 Jan.	mid Feb.	75	21 Feb.	21 Mar.	51		no activity		434
1983–1984	30 Nov.	19 May	28	26 Feb.	19 Apr.	64	5 Mar.	10 Mar.	14	416
1984–1985	16 Jan.	3 Mar.	60	16 Nov.	26 Apr.	79	27 Feb.	14 Mar.	67	661
1985–1986	20 Nov.	6 Apr.	151	7 Dec.	5 Apr.	241		Mar.	48	539
1986–1987	20 Nov.	30 Apr.	297	25 Nov.	1 Apr.	229	1 Dec.	20 Feb.	44	594

[a] Movements during fall are not included. Maximum numbers are not additive.
[b] Mammoth area only, group composed mainly of males.

In early January 1976, bison were first seen traveling the plowed road westward from the Tower area. A group of 15 moved about 10 km west the 3rd week of January; by 13 February a group of 13 was observed near Blacktail Deer Creek. A maximum of 59 bison was recorded in the Blacktail area the 3rd week of March 1976 (Table 1). Travel has occurred annually since December 1980; the bison generally have moved earlier and in greater numbers since then. Beginning winter 1982–1983, mixed groups continued beyond Blacktail to Mammoth and Gardiner. Later some groups apparently bypassed the Blacktail area and other foraging sites enroute to travel directly to lower elevations. Return to the traditional winter range occurred in spring.

The bison used two major travel routes (Fig. 1). The natural topographic route along the Yellowstone River from Tower to Gardiner was the primary route initially (Table 1). In 1982–1983, the plowed road became the primary route. Bison sometimes traveled the 32 km from Tower to Mammoth in 1 day. Numbers of animals on the road route were much greater than those on the river route. When human interference precluded use of the primary routes, the bison detoured across steep terrain, or traveled along tributary drainages.

In the 1960s the area between the bridge at Tower and the Lamar Canyon about 10 km to the east formed the core winter range (Fig. 1). Although mixed herds occasionally were found from Soda Butte west to the Hellroaring area (Meagher, 1973*a*), most groups concentrated on the Slough Creek bottoms, and sedge flats and swales across the valley of the lower Lamar River. A mixed herd of 12–20 first used the meadows west of the Yellowstone River at Tower in March 1975 for about a month; use was annual thereafter.

Use by mixed herds in the Blacktail area during the winter of 1975–1976 was confined to foraging sites north of the road, especially near the ponds. Annual use begain in 1980–1981, and expanded to creek bottoms south of the road in 1985–1986. During the mild winter of 1986–1987, use was widespread north and south of the road including upland sites where groups were not seen before.

Six males and one female visited Mammoth in April 1976. Annual use by a few males began the next winter. In late February 1980, three females and nine males appeared in Mammoth. Mixed herds with a larger proportion of females and calves began to use the Mammoth area in winter 1982–1983, and moved toward Gardiner. In 1983–1984 the bison began to cross the park boundary on Reese Crek.

In winter 1984–1985 some of the first groups bypassed the Blacktail area enroute to Mammoth and beyond. On 22 November 1984 a mixed herd of 14 appeared near Gardiner; by 26 November they crossed Reese Creek. On 20 November 1986, 68 were seen in the Blacktail area; on the 21st this herd increased to 100 and moved west. They encountered a newly installed cattleguard and fence, but by 25 November 1986, moved to lower elevations using the Rescue Creek drainage.

The bison foraged on suitable sedge bottoms and swale areas throughout the Mammoth-Gardiner area. Similar sites were used between Gardiner and the boundary at Reese Creek, but use patterns were complicated by occasional human disturbance. Beyond the boundary the bison were disturbed intentionally by attempts to force them back into the park (Meagher, 1989).

Nearly two-thirds (385) of the northern range bison were west of the traditional winter range on 22 January 1987. Attempts by mixed herds north of the Yellowstone River to expand beyond the park boundary occurred most winters after 1975–1976. Similar attempted expansion south of the river has occurred since 1983–1984.

The unusually severe winter of 1975–1976 apparently provided the initial impetus that led to the westward movements or stress dispersal of bison on the northern winter range. However, winter conditions subsequent to 1975–1976 did not appear to be sufficiently severe to contribute to the continued movements and increase in numbers. Movements on the river route occurred during winters of 1977–1978 and 1978–1979 which were above average in severity, but snowfall (and severity) every winter since has been below average. The largest movements recorded to date, spanning the entire winter, occurred during exceptionally mild conditions of 1986–1987. Intensive management at the Buffalo Ranch at Lamar Ranger Station apparently precluded similar movements by bison after a comparable stress dispersal in 1943 when approximately 130 of about 750 bison moved down the river trail. The next winter, 405 of 757 bison were removed (Meagher, 1973*a*). This removal probably included many of the older experienced females, commonly the leaders (McHugh, 1958), and may have been a more significant factor than other ranch activities such as winter feeding of hay. After daily road plowing between Tower and Mammoth began in the late 1940s (B. Hape, pers. comm.), a few males sometimes travelled this route, but mixed herds did not until 1975–1976.

The movements of 1976–1987 were not significantly correlated (r - 0.39, $P > 0.05$) with population increases on the northern range. Brief fall movements of groups, first seen September 1984, might be termed excursions or explorations, and were suggestive of a population at ecological carrying capacity (Caughley, 1979). However, availability of adequate forage for increased numbers of bison did not appear to be a factor in the movements during recent mild winters. In 1986–1987 available forage for the increased population

appeared more than ample, as a reuslt of a wet summer in 1986 and lack of snow in winter. The northern range was pock-marked throughout the winter with the feeding craters of elk (*Cervus elaphus*) and bison, indicating that both species could travel and forage essentially at will. Yet the first movement of about 100 bison occurred when the snow cover west of Tower was 60–80 mm, with little more to the east. These animals initially bypassed the extensive, easily accessible Blacktail foraging areas. Also, park records indicated that ≥200 bison usually wintered in the Lamar area from about 1952 through 1964 regardless of the severity of the winter. During the mild winter of 1986–1987 <200 bison were counted there on 11 aerial surveys.

Use of the plowed road for relatively easy and energy-efficient travel probably facilitated learning and a rapid increase in numbers. The road traverses suitable foraging sites, and that would have further encouraged use. This route appears to be the least likely under undisturbed conditions. The Yellowstone River gradient (Fig. 1) forms a natural topographic route for several species of wildlife, where the trail maintained by the National Park Service probably has facilitated travel in a few rough areas. Movement might have been confined to the river trail in the absence of the plowed road, but it seems probable that without human efforts to block the river trail, major movements there also would have increased.

Prior experience with particular routes and new foraging areas may have been a major factor in the rapid increase in large movements. Leadership may shift among several older females (McHugh, 1958). This, with intermingling and shifting of group members (Lott and Minta, 1983; Rutberg, 1984; Van Vuren, 1983), would facilitate learning. Repetitive air observations indicated that knowledge of various travel routes and new foraging areas was widespread.

The acquired knowledge of areas having less snow appears to have added impetus to the bison movements. Apparently bison have inhabited deep snow areas in Yellowstone for centuries (Meagher, 1973*a*). Mixed groups were observed to forage regularly in snows 600 mm deep (Houston, 1982); however, Telfer and Kelsall (1984) rated bison as poorly adapted for snow. They may do best where deep snows do not persist.

Historically, bixon were extremely gregarious (Roe, 1970). Group size appears related to habitat interspersion, with larger groups in more open habitat (Van Vuren, 1983), and on flatter ground (Rutberg, 1984). Bison appear to be generalist foragers, requiring large quantities of forage (Houston, 1982). The habitat in Yellowstone National Park is mostly forested except for the valleys which are the ungulate winter ranges. Houston (1982) noted that a combination of wet meadows, swales, and mesic grasslands accounted for 70–90% of bison observed feeding, but there are relatively few such sites that are both extensive and accessible for the aggregation of large groups in winter. Eleven aerial surveys in winter 1986–1987 suggested that larger aggregations occurred more often in the new areas, but the correlation was not significant (r Blacktail = 0.42, r Mammoth-Gardiner-Reese = 0.38; $P > 0.05$). The ultimate cause of large groups of bison is not clear. Homogeneity and density of forage, facilitation of sight and communication among individuals, less snow, or some combination of these factors may be involved.

Bison distribution on the northern winter range appeared to be unstable geographically by 1987. In contrast, the northern Yellowstone elk appear to have undergone a gradual expansion of habitat use and reestablishment of migratory patterns. Elk movements involved only a portion of the population, with a variably sized migratory segment which correlated with severity of winter weather (Houston, 1982). In bison, essentially all the population was moving except for some scattered males, regardless of winter conditions. McCullough (1985) characterized bison as showing truly nomadic long-range movements with migratory patterns demonstrable in some locations. The present northern Yellowstone situation may represent an intermediate stage between a migratory and a nomadic pattern of land use.

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POLYGYNY IN A WILD WOLF PACK

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Wolf (*Canis lupus*) mating systems vary considerably, but it is difficult to obtain data on the subject from wild wolves (Harrington et al., 1982). To date, no clear record of polygyny in wild wolves has been reported, although male wolves that we studied have bred different females in different years. Herein, we document the breeding of two females by a single male wolf during the same breeding season and the raising of pups by both females.

All three animals were radio-tagged and aerially radio-tracked in the central Superior National Forest of northeastern Minnesota (Mech, 1974). The two females were thought to be littermates born in 1984; one was captured as a pup on 24 November 1984, and the other as a probable yearling 2 km away on 16 July 1985. During winter 1984–1985, the aforementioned female was part of a pack of six (Fig. 1).

From the date that both females were radio-tagged to 30 September 1986, their ranges overlapped considerably (Fig. 1), and they were found by telemetry either near each other or together two of 45 times they were located, 3 and 7 October 1985. Their ranges were primarily outside the known territory of the pack of six (Fig. 1). On 7 May 1986, the first-captured female was found 64 km E of its previous locations, but it returned to its natal range a week later.

A male wolf, radio-collared on 11 July 1986, was an adult member of a pack of ≥ 10 whose territory lay about 18 km S of the ranges of the two females. The last time the male was known to be in its pack's territory was 30 October 1986. Subsequently, it was found twice between areas occupied by its pack and those of the females. The first time the male was located in the range of the females, 24 November 1986, it was seen with both of them. At five locations determined between 7 October and 10 November 1986, the females were near or with each other twice.

From 24 November 1986 through 3 April 1987, the three animals were located together based on telemetry 49 of 50 times (Fig. 1); on 1 December 1986 the female marked in 1985 was away from the other two wolves. All three were observed together 19 times, and no other wolves were ever seen near them. The breeding season in this region can be from 28 January through 4 March (Mech and Knick, 1978), so the male was the only possible consort of these females.

After 3 April 1987, the latter female was never found with either of the other two wolves. It may be significant that it lacked a hind foot. On 6 April 1987, the crippled female was near the area where the other female later denned while it was about 1 km away. The crippled female was first known to den on 17 April 1987 about 21 km W of where the other female denned between 17 and 24 April (Fig. 1). From 6 April through 5 August 1987, the latter female was found by telemetry with or near the male during 16 of 32 times they were located. The male was found near the den of the female caught in 1984 several times

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