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PAST AND PRESENT DISTRIBUTION OF THE BROWN-HEADED COWBIRD IN THE ROCKY MOUNTAIN REGION

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Abstract. The Brown-headed Cowbird (*Molothrus ater*) historically occupied a range similar to that of the American bison (*Bison bison*). The range of the cowbird and bison on the Great Plains has been well documented. In the Rocky Mountains the bison range included both the eastern grasslands and higher-elevation ridges and mountain parks up to an elevation of 3900 m in Colorado. Based on the commensal relationship of the brood parasitic Brown-headed Cowbird with bison, we suggest that the cowbird had a larger elevational range in the Rocky Mountains than previously known, and subsequently has had a long-term host-parasite relationship with high-elevation breeding songbirds. The change from free-ranging bison herds of the past to the restricted movements of fenced cattle herds today has probably increased the duration and intensity of parasite pressure on cowbird hosts in localized areas.

Key Words: American bison, *Bison bison,* cowbirds, *Molothrus ater,* Rocky Mountains.

The Brown-headed Cowbird (*Molothrus ater*) is a well-studied obligate brood parasite (Rothstein 1975a, Friedmann et al. 1977, Rothstein 1990, Robinson et al. 1995a, Smith et al. in press) that historically occupied a range similar to that of the American bison (*Bison bison*) (Friedmann 1929). Cowbirds ranged over the Great Plains in commensal association with bison. "Buffalo birds" are thought to have foraged among the grazed grasslands for insects stirred up by herd movements (Friedmann 1929, Mayfield 1965, Thomas Say in Evans 1997:171). Cowbirds expanded their range with the clearing of forests and introduction of domestic livestock (Mayfield 1965, Rothstein 1994). In the Rocky Mountains, Brown-headed Cowbirds have undergone a recent elevational range expansion possibly due to habitat alteration and cattle grazing in the high country (Hanka 1985), as have cowbirds in the Sierra Nevada Range and the Far West (Rothstein et al. 1980, Rothstein 1994).

The historical range of bison on the Great Plains is well documented (Allen 1877, Roe 1970, McDonald 1981). In addition, mountain bison (*Bison bison athabascae*) ranged far west of the Great Plains (Christman 1971). While the subspecies separation of Great Plains bison (*B. b. bison*) from *athabascae* is not entirely clear (Meagher 1986), we use "mountain bison" to refer to those bison that ranged west of the Great Plains, in lowland shrub-steppe of the Great Basin and high-elevation coniferous forests, subalpine meadows, and alpine tundra. Mountain bison in the Rocky Mountains ranged above timberline in Colorado, Idaho, Montana, and Wyoming (Henderson 1870; Fryxell 1926, 1928; Warren 1927, Bergtold 1929, Davis 1935, Beidleman 1955, Pattie and Verbeek 1967, Armstrong 1972, Meaney and Van Vuren 1993). We suggest that, based on their commensal relationship with bison, Brown-headed Cowbirds have had a longer high-elevation range distribution in the Rocky Mountains than previously described, and that the recent elevational range expansion (Hanka 1985) is actually a re-expansion back to their former range.

Our purpose is to demonstrate that (a) bison occurred at high elevations in the mountains west of the Great Plains, (b) the first observations of cowbirds in the western states occurred during the period between extirpation of bison from and movement of cattle into the higher elevations, and (c) the number of high-elevation records of cowbirds has increased historically with increasing cattle numbers in the West in general, but also specifically at high-elevations. We argue that many hosts have had a long-term association with the cowbird in the West.

METHODS

We reviewed records of bison distribution (Christman 1971, McDonald 1981) and cowbird parasitism (Freidmann 1929, 1963; Freidmann et al. 1977, Chace and Cruz 1996) in the West. We reviewed agriculture statistics for Colorado, Idaho, Montana, Utah, and Wyoming (yearbook of the U.S. Department of Agriculture) to obtain the number of cattle in each state per year from 1896 to 1996 to determine the timing and abundance of cattle introductions to the Rocky Mountain states. Colorado counties east and west of the Front Range were analyzed separately, with Front Range counties containing >40% grassland habitat designated as eastern (see Chace and Cruz 1998 for delineation of counties). Cattle numbers were summed per year by eastern and western designation. This designation also has important bison implications. Eastern counties contained Great Plains bison, and a few along the eastern edge of the Front

Range may have also contained mountain bison; western counties had only mountain bison if they had any bison at all. Although cattle are not the only livestock that attract cowbirds (Rothstein et al. 1980), they are by far the most numerous and probably are a good index of livestock numbers in general.

RESULTS

The maximum range expansion of the bison was achieved approximately 2000 years before present (BP), although mountain bison remains have been found as early as 10,000 years BP (Lyman and Livingston 1983). Mountain bison ranged far west of the Great Plains and throughout the Rocky Mountain region and occurred at all elevations (Christman 1971, Meagher 1986). Archeological findings include mountain bison kill sites in Waterton Valley in southwestern Alberta as old as 7500 years BP (Reeves 1978), and 7000 years BP in southwestern Idaho (Agenbroad 1978). Other archeological localities with, presumably, mountain bison stretch west beyond the Great Plains to eastern Washington and Oregon, to the Sierra Nevada of California, south to Arizona and New Mexico, and north, at least to southwestern Alberta (Christman 1971, Butler 1978, Reeves 1978, Lyman and Livingston 1983, Van Vuren and Bray 1985). Nearly half the specimens of mountain bison between 1500 to 600 years BP in Colorado, Arizona, and New Mexico were associated with low-elevation ponderosa pine and pinyon-juniper forests (Christman 1971).

Mountain bison were found not only west of the Great Plains but also at high elevations. Bergtold (1929) speculated that bison were widely distributed across the high country of Colorado at least during the last 300 years, which was verified by Meaney and Van Vuren (1993). Meaney and Van Vuren (1993) recorded all known bison specimens in Colorado west of the Great Plains, from which we calculated that 56.9% of 116 bison specimens were collected above 2500 m. In Montana, Fryxell (1928) found a "fairly complete and perfect skeleton of a very large bull buffalo on top of Pryor Mountains [2750 m] in south central Montana," which confirmed Grinnell's earlier comment to Fryxell (1928) that "I have frequently seen bison living at and above timberline . . . in Montana . . . ." Indeed, Pattie and Verbeek (1967) found skeletal evidence of bull, cow, and calf bison in the Beartooth Mountains. Bison also ranged at high elevations in Wyoming. Henderson (1870) commented that in June ". . . thousands of buffalo [were] quietly grazing" on Buffalo Plateau, Yellowstone National Park. Additionally, bison remains have been found in the Medicine Bow Mountains (2850–3600 m) and slopes of the Gros Ventre Mountains above Jackson Hole, Wyoming (Fryxell 1928). We found no records that suggest a similar use of high-elevation areas in Utah or Idaho, even though bison were found in high numbers at lower elevations (Ross in Davis 1935, Roe 1970).

Current free-ranging mountain bison herds have seasonal elevational movements through open ponderosa pine (*Pinus ponderosa*), pinyon-juniper woodlands (*P. monophylla* and *Juniperus scopulorum*), and across subalpine forest-parkland habitat (Fuller 1962, Van Vuren 1983, Van Vuren and Bray 1986, Shaw and Carter 1990). Furthermore, based on specimens taken (Figgins 1933), some herds of mountain bison wintered in the high-elevation montane grasslands (parks) and migrated into alpine zones through forested communities during the summer (Meaney and Van Vuren 1993). Some mountain bison may have wintered on the wind-swept alpine tundra, like the 5% to 10% of the Rocky Mountain National Park elk herd today (Stevens 1980). Mountain bison achieved maximum abundance west of the Rocky Mountains approximately 3000 to 1500 years BP (Butler 1978) but never reached the population densities found on the plains east of the Rockies (Schroedl 1973). Extant reintroduced free-ranging bison in forested montane habitats of the Henry Mountains of Utah have smaller group sizes and larger home ranges than bison of the Great Plains, and this was probably true of former high-elevation mountain bison herds in the Rocky Mountains (Van Vuren 1983, Van Vuren and Bray 1986, Meaney and Van Vuren 1993).

Bison are not well adapted for deep snow (Telfer and Kelsall 1984). In Colorado, Benedict (1993, and pers. comm.) speculates that bison were extirpated from the Estes Park area by 1859 in part because of deep snow during the spring of 1844. The heavy snowfall during the winter of 1837–1838 had a similar effect on bison herds in Idaho and Utah (Stansbury 1852, Roe 1970), and deep snow accumulation continues to exact a heavy toll on the Yellowstone bison population (Meagher 1976). Increased hunting pressure with the arrival of Europeans probably restricted the seasonal movements of mountain bison as they did Great Plains bison. Higher numbers of mountain bison were probably forced to stay at higher elevations in large open parks and meadows during the winter where the effects of deep snow and less forage would have reduced numbers. The harsh winters of 1837–1838 and 1843–1844 in combination with market hunting may have been the cause of the bison decline in the Rocky Mountains in general. Most wild bison in western states were extirpat-

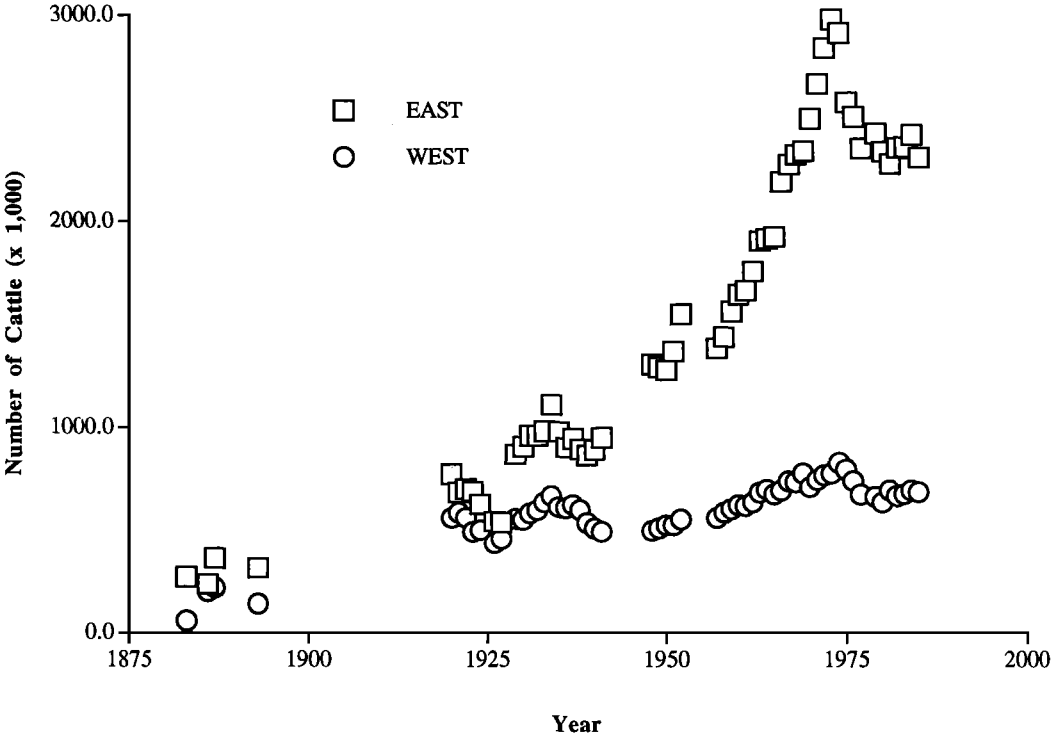

FIGURE 1. Number of cattle in Colorado, east and west of the Continential Divide (1883–1985).

ed by the 1880s, although a few may have survived until 1904 (Warren 1906).

Although the first livestock were introduced to the West in 1598 in New Mexico (Scurlock and Finch 1997), it was not for another 250 years that cattle reached substantial numbers. Bison abundance was very low by the late 1800s when cattle were becoming fairly abundant in the Rocky Mountains. In Colorado, nearly equal numbers of cattle occurred in eastern (plains) counties and western (higher elevation) counties through the 1920s (Fig. 1). Western counties reached their present levels of cattle by 1959 with a peak in 1974. Since 1941, the number of cattle in eastern counties consistently doubled the number of cattle west of the plains, with a peak in 1973 (~ 3 million head). We feel that the trend of high-elevation cattle numbers lagging behind numbers in low-elevation grasslands in Colorado is consistent with other western states. Although the total abundance of cattle differs among states, the increase of cattle from 1940 to 1975 is consistent across states (Fig. 2). Overall, cattle number patterns are similar among Colorado and Montana, and Wyoming and Idaho (Fig. 2). Utah shows only a slow, steady increase in cattle numbers (Fig. 2). For the first 50 years of recorded cattle abundance in Colorado, Idaho, Montana, Utah, and Wyoming, the total number ranged between 3.5 and 6 million head. Following 1940 the number of cattle increased to a peak of nearly 12 million in the mid-1970s. Cowbirds began to be recorded at high elevations in the west during this period of peak cattle abundance.

Early records of cowbird parasitism or cowbird presence rarely mentioned exact elevation. Naturalists in Colorado recorded cowbirds as occurring in the grasslands and lower foothills (Drew 1885, Gale 1893 unpublished field notes, Cooke 1897, Sclater 1912, Saunders 1921, Hayward 1941, 1945). Since 1966 cowbirds have been recorded at higher elevations (3300 m) in Colorado (Hanka 1985, Spencer 1985), Montana (Pattie and Verbeek 1966), and (2500 m) Utah (Hayward et al. 1976, Behle et al. 1985). Recent evidence in California and Colorado suggests that cowbirds expanded their elevational range in response to montane livestock (Rothstein et al. 1980, Hanka 1985), and cowbirds subsequently have parasitized species at those elevations (Table 1).

DISCUSSION

Over the past 5000 years in the Rocky Mountain states cowbirds probably had a historical,

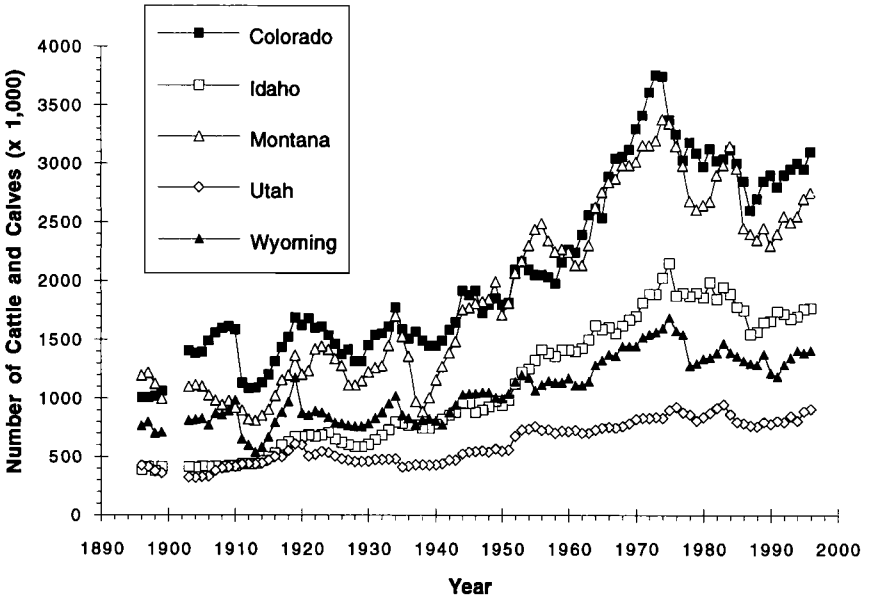

FIGURE 2. Hundred-year trend in cattle abundance for Colorado, Idaho, Montana, Utah, and Wyoming (1896–1996).

geographical, temporal, and elevational distribution similar to that of the bison, with an upper elevational limit at ca. 3800 m. Even though they occurred at lower densities than Great Plains bison, mountain bison probably were numerous enough to support commensal flocks of cowbirds during the avian breeding season. While deep snows may have been present into the early summer and prevented bison, and consequently cowbirds, from reaching the habitats of forest breeding birds until after incubation, we cannot rule out the possibility that mountain bison wintered above treeline and thus provided cowbirds with a foraging location next to subalpine forest breeding birds. As bison approached extirpation in the mid-1800s, herds were small and scattered and cowbirds probably were mostly restricted to lower elevations where cattle were just beginning to occur in appreciable numbers in the mountain West (Fig. 2). During the late 1800s and early 1900s cowbirds probably became associated with the growing low-elevation cattle herds. By the turn of the century, naturalists had covered many high elevation areas in the region and reported cowbirds as birds of the grasslands and foothills. Even though higher elevations were surveyed (Drew 1885, Sclater 1912), cowbirds were primarily found from the grasslands up to the foothills and mountain parks < 2500 m (Gale 1893 unpublished field notes, Cooke 1897), although Friedmann (1929) reported one observation of a female cowbird in association with horses at 2895 m in Colorado. Cowbirds began to be recorded at high elevations during the peak of cattle abundance in the Rocky Mountian states from the

TABLE 1. PASSERINE SPECIES PARASITIZED AT HIGH ELEVATIONS IN COLORADO

Species	Number	Year	Elevation	Reference
Poecile gambeli	1	1984	2280 m	Brockner 1984
Regulus calendula	3	1985	>2400 m	Chace and Cruz 1996
Wilsonia pusilla	1	1985	3180 m	Spencer 1985
Wilsonia pusilla	7	1990, 1992	>2800 m	Chace and Cruz 1996
Catharus guttatus	2	1990, 1994	2400 m	Chace and Cruz 1996
Dendroica petechia	1	1990	2800 m	Chace and Cruz 1996
Spizella passerina	1	1985	>2400 m	Spencer 1985
Melospiza lincolnii	3	1990, 1992	>2800 m	Chace and Cruz 1996
Euphagus cyanocephalus	18	1985	2895 m	Hanka 1985

mid-1960s to the present (Keeler-Wolf et al. 1972, Hanka 1985). The association of cowbirds with herding ungulates is strong, and their historical elevational distribution may be as great as the former range of the bison, and now cattle. We suggest that Brown-headed Cowbirds occurred at high elevations in the Rocky Mountains until the extirpation of bison and have recently regained their former range with introduction of domestic livestock.

Cowbird distribution is not wholly dependent on the presence of bison, cattle, or other large ungulates. Rothstein (1994) suggested that despite the presence of preferred habitat, elk herds, and potential hosts, cowbirds were absent from the Central Valley of California until 1922. Cowbirds entered this region in 1922 following anthropogenic changes (irrigation and agriculture) that improved feeding and breeding conditions for the cowbird (Rothstein 1994). We feel that along the Rocky Mountains the long-term presence of mountain bison probably enabled cowbirds to move easily between high-elevation bison herds and those of the Great Plains. High-elevation herds provided foraging opportunities and allowed cowbirds to parasitize the nests of many high-elevation songbirds.

As in the Sierra Nevada of California (Verner and Ritter 1983, Rothstein 1994), present-day populations of cowbirds in the Rocky Mountains often forage among large grazing animals. Feeding sites are anthropogenic, e.g., horse corrals, pastures with livestock, bird feeders, or campgrounds. From 1986–1989, 164 Brown-headed Cowbirds were trapped and banded at a feeding station on Mount Evans, Colorado (elev. 3260 m). Cowbirds were trapped from April to August, with highest numbers in May (mean captures per month = 29.0); males outnumbered females 2.35:1 (L. E. Reiner, unpubl. data).

The center of cowbird abundance today (Robinson et al. 1995a) overlaps the former center of bison abundance among the grasslands of the Great Plains (McDonald 1981, Meagher 1986). Although mountain bison have been recorded in the high-elevation areas in the Rocky Mountains, little is known about the distribution of cowbirds in the Great Basin prior to the extirpation of the bison. They were probably located along major tributaries, such as the Colorado River (Rothstein 1994), and were associated with far western mountain bison herds. Following cattle introductions in the Great Basin, western populations of cowbirds may also have re-expanded their elevational distribution; however, a distributional change along the west slope of the Rocky Mountains has not been as well documented as along the east slope.

Prior to the extirpation of bison in the late 1800s, Brown-headed Cowbirds probably parasitized the nests of many songbird species in the high-elevation regions. Cowbird numbers at higher elevations likely declined as bison were extirpated, then resurged following the introduction of cattle. When cowbirds followed the nomadic bison herds, their parasitic efforts and eggs were dispersed over the range of the seasonal movements of the bison herds, whereas now cowbird breeding populations are as stationary as the herds of livestock around which they forage. While free-ranging herds occur at lower densities and may disperse cowbird activity over a larger area, many cattle containment areas are at high densities and largely stationary through the early part of the breeding season. The implications of this changing pattern on songbird communities are likely very important. Where once songbird communities may have encountered brood parasitism for only a portion of their breeding season, now the pressure of parasitism is pronounced throughout their reproductive season. In addition, because of the strong site fidelity of many songbirds (Greenwood and Harvey 1982, Holmes and Sherry 1992) and annual timing of cattle movement among pastures, the pressure of parasitism may exist throughout the lifetime reproductive effort of many individual birds.

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