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Alexandra C. Latham '00
Illinois Wesleyan University

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A Senior Research Honors Paper
Presented by

Alexandra C. Latham
Department of Biology
Illinois Wesleyan University
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Approved for Research Honors by:

Sheryl Swartz Soukup, Project Advisor

R. Given Harper

William B. Jaeckle

Jeffrey A. Frick

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Alexandra C. Latham, Illinois Wesleyan University

ABSTRACT

The Brown-headed Cowbird (*Molothrus ater*) has long been associated with bison (*Bos bison*) in North America on the Great Plains (Friedmann 1929). As a result, I anticipated that cowbirds would parasitize host nests more frequently in the presence of bison than in their absence. I predicted that several common ground-nesting avian species, Dickcissels (*Spiza americana*), Grasshopper Sparrows (*Ammodramus savannarum*), and Eastern Meadowlarks (*Sturnella magna*), would suffer higher frequencies of brood parasitism in bison-grazed habitat than in ungrazed habitat on the tallgrass Konza Prairie Research Natural Area, located in northeastern Kansas. The frequency of cowbird parasitism for all species combined was significantly higher in bison-grazed (0.69) than in ungrazed habitat (0.44) ($p = 0.044$, $\chi^2 = 4.061$, $df = 1$). These results are consistent with the hypothesis and suggestion that bison-grazed habitat may be a more optimal site for cowbird brood parasitism than ungrazed habitat. I pose two principal explanations for the higher frequency of parasitism observed in the bison-grazed area. First, cowbirds may be able to forage more efficiently in the bison-grazed area, indirectly inflating parasitism frequencies by conferring a variety of energetic and nutritional advantages upon the females. Second, the cowbirds' abilities to find and parasitize nests may be enhanced by the shorter, less dense grass characteristic of grazed habitat. Further studies investigating the conservation implications of this phenomenon are merited.

Key words: bison, brood parasitism, Brown-headed Cowbird, Dickcissel, Eastern Meadowlark, Grasshopper Sparrow, Molothrus ater

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*), once commonly known as the "Buffalo Bird," is an obligate brood parasite and is the most abundant and widespread cowbird in North America. It has been documented to parasitize over 220 species of birds (Lowther 1993). Historically, the cowbird's range was restricted to the open grasslands of central North America (Mayfield 1965, Morris and Thompson 1998), an area that has been grazed by primitive bison for the last 100,000 years and more recently by the modern bison (*Bos bison*).

Bison, which once numbered 30-60 million on the Great Plains (McHugh 1972, Flores 1991, Benedict et al. 1996, Shaw and Lee 1997), played an important role in the existence of Brown-headed Cowbirds because cowbirds apparently subsisted on insects disturbed from the ground cover by the large ungulates (Mayfield 1965). In addition, bison altered the habitat by trampling and reducing vegetation cover (Hartnett et al. 1996), which may have enhanced cowbird foraging. However, the cowbird's bison-associated feeding habits would have been incompatible with territorial nesting due to the nomadic nature of the bison. Though it has been hypothesized that brood parasitism evolved as a means to overcome this incompatibility by removing cowbird nesting and parental demands (Widman 1907), the evolutionary time frame involved makes it virtually impossible to determine if this bison-associated foraging system was in place at the time of incipient brood parasitism. Others hypothesize that cowbirds probably evolved brood parasitism in South America (Friedmann 1929). Perhaps brood parasitism behavior in Brown-headed Cowbirds came about prior to cowbirds' contact with bison, and the cowbirds later opportunistically used their freedom from nesting activities to exploit the favorable foraging conditions generated by the bison (Ortega 1998).

In the late 1800's, bison numbers plummeted to less than 1,000 (McHugh 1972), and European settlers pushed westward bringing cattle *(Bos taurus)*, clearing forests, and plowing

tallgrass prairies along the way (Friedmann 1929, Mayfield 1965). At that time, the Brown-headed Cowbird began to move eastward through areas cleared by settlers, most likely as a result of the settlers impact creating habitat conducive to the cowbirds' survival and range expansion (Friedmann 1929, Mayfield 1965). Today, cowbirds are found throughout the United States (Lowther 1993) and often feed in shortgrass habitats such as croplands, horse corrals, and pasture (Friedmann 1929, Mayfield 1965, Thompson 1994).

Recent conservation efforts and economic factors have been responsible for enlarging bison populations on public and private grasslands in the Great Plains (Hartnett et al. 1997, Torok et al. 1998). Understanding current patterns of cowbird parasitism in the context of bison grazing is interesting in light of the cowbird's proposed long history of association with the bison, and is also relevant to the conservation of host species. Cowbird parasitism usually reduces the reproductive success of host species (Payne 1977, Rothstein 1990, Ortega 1998) and has had a dramatic negative impact on populations of a number of hosts (Mayfield 1965, Post and Wiley 1976, Wiley 1985, Ortega 1998).

In this study, I examined the effects of bison grazing on cowbird parasitism frequencies on the tallgrass prairie of northeastern Kansas. The Brown-headed Cowbird readily parasitizes the nests of a number of prevalent ground-nesting prairie summer resident birds, including Dickcissels (*Spiza americana)*, Grasshopper Sparrows (*Ammodramus savannarum*), and Eastern Meadowlarks (*Sturnella magna*) (Mayfield 1965, Elliott 1978, Zimmerman 1983, Zimmerman 1993). I tested my hypothesis that these species suffer higher frequencies of parasitism in bison-grazed habitat than in ungrazed habitat. Since bison populations are expected to continue to grow in the future (Torok et al. 1998), understanding cowbird breeding behavior and the intensity of adverse effects on hosts in bison-grazed habitat is valuable. However, despite the large number of studies examining breeding ecology, host

interactions, and parasitism rates of Brown-headed Cowbirds, to date no study has tested the effects of bison on brood parasitism frequencies by cowbirds.

METHODS

Study Site

Konza Prairie Research Natural Area is a 3,486 ha reserve located in the Flint Hills of Riley County in northeastern Kansas, U.S.A. (Reichman 1987). The vegetation of the area consists of native tallgrass prairie dominated by the perennial grasses Big Bluestem (*Andropogon gerardii*), Little Bluestem (*Andropogon scoparius*), Indian Grass (*Sorghastrum nutans*), and Switchgrass (*Panicum virgatum*) (Freeman and Hulbert 1985, Steinauer and Collins 1996).

The research focus of studies at Konza has been to investigate the role of grazing, fire frequency, and their interactions on tallgrass prairie ecosystem processes (Zimmermann 1993). In 1977, a watershed-level fire-frequency experiment was initiated that included annual, 2, 4, 10, and 20-year fire frequencies. Bison were subsequently placed on Konza in 1987, and the burning regime was expanded to incorporate bison-grazed and ungrazed sites. A herd of approximately 200 bison currently grazes within a 1,000-ha fenced area of the reserve (McMillan 1999).

Watersheds N4C and K4A of the Konza Prairie Research Natural Area were used in this study (Fig. 1). Each site is burned in the spring at four-year intervals. Site N4C was last burned in 1998, and site K4A was last burned in 1997. The 78-ha N4C watershed has been grazed by bison since 1987, and the 55-ha K4A watershed has been ungrazed by bison since they were extirpated from the region in the middle to late 1800's (Knapp and Seastedt 1998). However, both watersheds were grazed by cattle from that time until the land was acquired by The Nature Conservancy in 1977 (Freeman and Hulbert 1985).

Nest Surveys

Approximately 210 hours were spent locating nests. Nest searches were conducted daily by walking north-south transects, 30 m apart, at varying times between dawn and dusk from 6 June to 19 July 1999. Nests were located by observing nest-building activities, territorial behavior, presence of the female, food-carrying, and defensive behavior exhibited by both the host males and females. In addition, both Grasshopper Sparrow and Eastern Meadowlark nests were frequently discovered when females were flushed from their nests by the investigator.

Orange plastic flags attached to stakes approximately 1 m tall were placed 10 m from newly discovered nests to facilitate later visits. At each visit, the number of host eggs, parasitic eggs, host nestlings, and parasitic nestlings were recorded. If nests were found during the incubation stage, they were revisited every three days until all eggs had hatched or until the nests failed. Nests were no longer revisited once all eggs had hatched.

Statistical Analyses

Frequency of cowbird parasitism (proportion of nests parasitized) was calculated for all host species combined as well as for individual species for the two sites. Although nests discovered in the incubation stage were followed through to the nestling stage whenever possible, some nests failed before reaching the nestling stage. When computing parasitism frequencies and comparing them in grazed and ungrazed habitats, parasitism data for both the nests at the nestling stage and additional nests that failed in the incubation stage were combined, with each nest represented only once in the sample. This yielded more conservative statistical results than when considering parasitism frequencies only of nests that survived to the nestling stage. A chi-square 2 x 2 contingency table test (Zar 1999) was used to determine whether or not the frequency of cowbird parasitism on the nests of the combined species differed

significantly between sites. In addition, a chi-square 2 x 2 contingency table analysis was used to determine whether or not the frequency of cowbird parasitism of Dickcissel nests differed significantly between bison-grazed and ungrazed habitat. It was not possible to determine whether or not frequency of cowbird parasitism differed between study sites in the case of Grasshopper Sparrows or Eastern Meadowlarks due to small sample sizes of those species. Means and standard errors of the number of host eggs and nestlings were also calculated for the combined species and individual species at each site. A two-tailed t-test was used to determine if there was a significant difference between host egg means for combined species in bison-grazed and ungrazed study sites. A two-tailed t-test was also used to determine if there was a significant difference between host nestling means for combined species in bison-grazed and ungrazed study sites.

RESULTS

Sixty-six nests were located in the two sites (Table 1). The mean number of host eggs for the combined species did not differ significantly between the bison-grazed site (3.67 ± 0.33 SE, n=6) and the ungrazed site (3.50 ± 0.50, n=8) (t=0.257, p=0.802, df=12). The mean number of host nestlings also did not differ significantly between the bison grazed site (3.32 ± 0.13, n=31) and the ungrazed site (3.39 ± 0.17, n=31) (t=0.303, df=60, p=0.763). Table 2 reports the means for individual species in the two habitats.

The frequency of cowbird parasitism for all species combined was significantly higher in bison-grazed than in ungrazed habitat ($p = 0.044$, $\chi^2 = 4.061$, df = 1, Table 1). Frequency of parasitism of Dickcissel nests was higher but not significantly different in bison-grazed habitat than ungrazed habitat ($p = 0.071$, $\chi^2 = 3.252$, df = 1, Table 1).

Multiple parasitism (more than one cowbird egg or nestling in a nest) was discovered in only one nest. A Dickcissel nest located in the bison-grazed site had two cowbird nestlings present.

DISCUSSION

The significantly higher frequency of cowbird parasitism for all species combined in the bison-grazed study site compared to the ungrazed study site supports my hypothesis that bison grazed habitat is a more optimal habitat for brood parasitism purposes compared with ungrazed habitat. In the case of the Dickcissel, frequency of brood parasitism was higher but not significantly different in bison-grazed habitat than ungrazed habitat. Results also indicated that host egg means for combined species were not significantly different between the two sites, and mean number of host nestlings for combined species were also not significantly different between the two sites. Clutch size therefore did not affect parasitism frequencies.

Bison-grazing affects a habitat by reducing canopy height, vegetative cover, and accumulation of plant litter (Hartnett et al. 1997). As a result, I believe two primary explanations may account for the overall higher frequency of parasitism observed in the bison-grazed area. First, cowbird foraging efficiency in bison-grazed habitat may be greater than in ungrazed habitat due to both the physical presence of the bison and the changes in structural composition caused by grazing (Morris and Thompson 1998). Increased foraging efficiency may indirectly contribute to higher frequencies of parasitism by conferring a variety of energy and nutritional advantages upon the females. Second, changes in structural composition resulting from grazing may enhance cowbird searches for host nests in bison-grazed habitats, thus increasing parasitism rates.

Cowbirds may benefit from the effects of bison grazing with respect to the first of these factors, foraging efficiency, in a number of ways. Prey items are more visible and may therefore be located more quickly and captured more successfully in bison-grazed than ungrazed areas (Morris and Thompson 1998). Invertebrates may also be disturbed from the vegetation by the grazing bison (Morris and Thompson 1998). In addition, studies have documented higher invertebrate densities in grazed versus ungrazed habitats (Holmes et al. 1979, Jepson-Innes and Bock 1989, Morris and Thompson 1998). Invertebrates, which are protein-rich food items, comprise an estimated 52% of the cowbird's diet during the breeding season (Lowther 1993). Though most species of birds draw on their body reserves for egg production, female cowbirds appear to acquire all of their protein and some of their calcium and fat for egg production directly from their diet (Ankney and Scott 1980). As a result, insects are of particular importance to female cowbirds, since females have the capacity to lay an egg almost daily (Lowther 1993). The greater abundance of protein-rich food items in bison-grazed habitat may enable females to maximize egg production and quality.

The ease with which cowbirds can locate host nests is the second factor I view as valuable in explaining the effects of grazing on parasitism frequencies. Cowbirds employ three different techniques while searching for hosts. They watch silently for nesting activities of hosts from perches, they walk silently on the ground, and they make a series of short aerial searches from a few feet above the vegetation (Friedmann 1929, Norman and Robertson 1975, Payne 1977). Each of these nest-searching techniques may be enhanced in bison-grazed habitat, because the more penetrable, less dense undergrowth and reduced amounts of leaf litter characteristic of bison-grazed areas would allow greater visibility and ease of movement for the cowbirds (Norman and Robertson 1975, Larison et al. 1998). Host nests would also be more exposed and conspicuous in the bison-grazed area, due to reduced density and height

of growth as well as reduced amounts of leaf litter. Personal observations during nest searches support these ideas. Five nests discovered in the bison-grazed study site were partially exposed from above and were noticed with the naked eye. However, no nests within the ungrazed site were located simply by looking down and spotting them. Instead, nests in the ungrazed site were invariably concealed by the vegetation. To locate most nests in either site, it was necessary to observe the parents' activities (usually identified by alarm-calls) and search around in the grass or scrub. Once defensive parents had been identified by the researcher, the nests in the bison-grazed site were usually located more easily and quickly than those in the ungrazed site. This seemed to be related to the thickness of the vegetation found within the ungrazed site, as the nests were often hidden deep beneath the leaf litter. Presumably, cowbirds would experience similar difficulties when searching for host nests in ungrazed sites. As a result, parasitism levels may be reduced in ungrazed areas due to difficulty in finding host nests.

The effects of bison grazing on cowbird foraging efficiency and ease of finding host nests may also interact to generate the observed pattern of greater cowbird parasitism frequency in the grazed than in the ungrazed site. For instance, a cowbird's daily routine consists of egg laying, nest searching, courtship, and mating in the morning, and foraging in the afternoon (Ortega 1998). If cowbirds are feeding in a grazed area that facilitates more efficient foraging, they can invest less time foraging than would be necessary in an ungrazed area with taller, denser vegetation. The conserved time may be used for additional host-nest searches, potentially increasing the probability of locating host nests. Thus, the increased foraging efficiency in grazed sites may increase cowbird nest-finding success in these sites. Furthermore, Brown-headed Cowbirds have been documented feeding and breeding in separate locations (Payne 1965, Rich 1978, Rothstein et al. 1984). In fact, they have been

documented to fly up to 7 km per day between feeding and breeding sites (Rothstein et al. 1984). If a breeding area is a suboptimal site for foraging, cowbirds can relocate to an area of higher foraging quality for feeding purposes (Rothstein et al. 1984). In the case of the sites involved in this study, it is possible that the bison-grazed habitat may be better for foraging than the taller, denser, ungrazed habitat. Thus, cowbirds breeding in the bison-grazed study site may also remain there to forage. In contrast, for cowbirds breeding within the ungrazed site, the benefits of relocating to the shorter, grazed area to feed may outweigh the costs of doing so. Nonetheless, these relocating birds would pay a cost, including additional time and energy expenditure for travel. As a result, cowbirds breeding in the ungrazed habitat would face increased food demands and therefore foraging time, which may lead to a reduction of time spent searching for hosts. The idea that cowbirds use different sites for feeding and breeding is consistent with my observations on Konza. On numerous occasions I observed large groups of cowbirds feeding in the vicinity of the bison. When disturbed, they would fly up and then promptly settle back down to the ground near the bison. No such groups were observed foraging away from the bison. This suggests that the cowbirds at Konza may fly to the bison-grazed area, forage efficiently there on the ground in large groups, and then return to nest-searching areas. I assume that some of these foraging cowbirds remain within the bison-grazed area to breed and others relocate to ungrazed areas for breeding.

Although my results are consistent with my hypothesis that bison grazing increases cowbird parasitism frequencies, alternative explanations for the higher parasitism frequencies in the grazed than in the ungrazed sites do exist. For instance, studies by Zimmerman (1983, 1996) suggest that the key dependent variable in my study, parasitism frequency, may have the potential to bias my results. Specifically, the results of Zimmerman's studies enable us to infer that cowbird success in locating nests could be affected by both the physical ease of locating

host nests and the abundance of nests within a habitat. Zimmerman found that the relative abundance of breeding birds in bison-grazed habitat declined after the introduction of bison. For instance, the relative abundance of Dickcissel nests was lowest in prairie that was both burned and grazed and was significantly different from nest abundance in ungrazed treatments for all months except August and May (Zimmerman 1996). However, the frequency of cowbird parasitism on Dickcissel nests was significantly and inversely associated with the density of available nests (Zimmerman 1983). Perhaps frequency of parasitism was higher in bison-grazed habitat because there were fewer nests to parasitize in the bison-grazed area; thus, a greater proportion of nests were parasitized. By using "parasitism frequency" as the key dependent variable in my study, it is possible that a reduced abundance of potential host nests in the grazed areas increased the likelihood that any one nest in the grazed site would be parasitized. However, since nest density was not determined, the extent to which this argument applies to my study is unknown.

A second possible alternative explanation for my results stems from the observation that cowbirds frequently use perches to observe the activities of potential hosts (Friedmann 1929, Norman and Robertson 1975). Cowbirds exhibited this perching behavior throughout the summer on Konza. Common perches included trees, shrubs, and fence lines. Both study sites had fences bordering part of the area. However, the ungrazed site had gallery forest bordering it to the north, but had few trees scattered within the site. In contrast, the bison-grazed site was not bordered by gallery forest on any side, but did contain an abundance of scattered tall trees from which cowbirds could perch and observe activities in all directions. Though unquantified, it appeared that woody vegetation was less abundant in the ungrazed site than in the grazed site. Studies have suggested that the availability of perches may increase parasitism levels (Freeman et al. 1990, Johnson et al. 1990), as a greater abundance of

perches would better facilitate the cowbirds' silent, watching technique. As a result, this "tree-density" variable confounds interpretation of my results.

This study indicates that bison-grazed habitat may, in fact, be a more optimal site for cowbird brood parasitism, since parasitism frequencies were higher in the grazed than in the ungrazed site. Two principal factors may explain the higher frequency of parasitism observed in the bison-grazed area. First, cowbirds may forage with greater efficiency in grazed areas, which may indirectly contribute to higher frequencies of parasitism. Additionally, the cowbirds' abilities to locate host nests may be enhanced by the shorter and less dense grass characteristic of grazed habitat. Further studies would be valuable to determine the relative importance of these two factors. In addition, since bison numbers have been increasing on the Great Plains due to conservation efforts and as a replacement for cattle (Hartnett et al. 1997, Torok 1998) and cowbird brood parasitism is known to reduce the reproductive success of host species (Payne 1977, Rothstein 1990), further investigations of the conservation implications of this study are merited.

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Table 1. Sample size and frequency of parasitism for each species and all species combined in bison-grazed and ungrazed study sites.

	TREATMENT			
	K4A (ungrazed)		N4C (grazed)	
SPECIES	**N**	**PARASITISM FREQUENCY**	**N**	**PARASITISM FREQUENCY**
Dickcissel	20	0.55	23	0.78
Grasshopper Sparrow	10	0.40	5	0.80
Eastern Meadowlark	4	0	4	0
All Species Combined	34	0.44	32	0.69

Table 2. Mean host eggs and host nestlings for each species and all species combined in bison-grazed and ungrazed study sites. Nests discovered during the incubation stage that survived to the nestling stage appear in both the "host eggs" and "host nestlings" portions of the table.

	HOST EGGS						HOST NESTLINGS					
	K4A (ungrazed)			N4C (grazed)			K4A (ungrazed)			N4C (grazed)		
SPECIES	**n**	**x Host Eggs**	**S. D.**	**n**	**x Host Eggs**	**S.D.**	**n**	**x Host Nestlings**	**S.D.**	**n**	**x Host Nestlings**	**S.D.**
Dickcissel	5	3.20	1.64	5	3.80	0.84	18	3.11	0.96	22	3.18	0.73
Grasshopper Sparrow	2	3.50	0.71	1	3.00	0.00	9	3.44	0.53	5	3.40	0.55
Eastern Meadowlark	1	5.00	0.00	0	0	0.00	4	4.50	0.58	4	4.00	0.82
All Species Combined	8	3.50	1.41	6	3.67	0.82	31	3.39	0.92	31	3.32	0.75

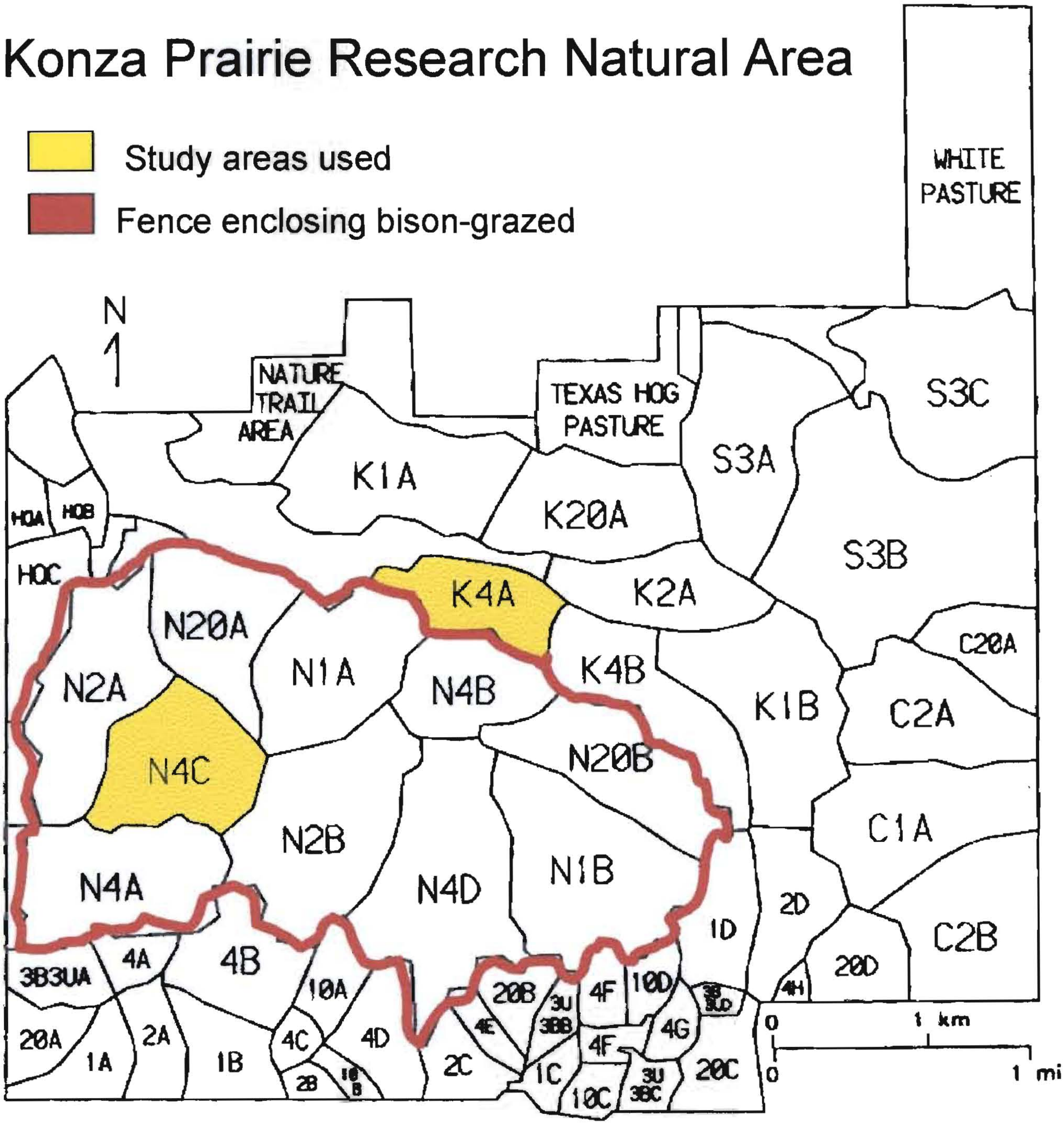

Figure 1. Bison-grazed (N4C) and ungrazed (K4A) study sites on Konza Prairie Research Natural Area