University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

Papers in Natural Resources | Natural Resources, School of

11-12-1996

Prairie Legacies - Mammals

Russell A. Benedict
University of Nebraska State Museum

Patricia W. Freeman
University of Nebraska-Lincoln, pfreeman1@unl.edu

Hugh H. Genoways
University of Nebraska-Lincoln, h.h.genoways@gmail.com

Follow this and additional works at: http://digitalcommons.unl.edu/natrespapers

Part of the Natural Resources and Conservation Commons

Benedict, Russell A.; Freeman, Patricia W.; and Genoways, Hugh H., "Prairie Legacies - Mammals" (1996). *Papers in Natural Resources.* Paper 41.
http://digitalcommons.unl.edu/natrespapers/41

This Article is brought to you for free and open access by the Natural Resources, School of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Natural Resources by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Prairie Conservation

Preserving North America's Most Endangered Ecosystem

Edited by

Fred B. Samson

Fritz L. Knopf

CHAPTER 11

Prairie Legacies—Mammals

Russell A. Benedict
Patricia W. Freeman
Hugh H. Genoways

Few North American ecosystems have been as dramatically altered by humans as the prairies of the Great Plains. Occupying the immense interior of North America, these deceiving grassland oceans hid their complexity and diversity from many early travelers who saw this area merely as an obstacle to overcome in their westward journeys. But for the careful observer, prairies hold a tremendous quantity of life, arranged in a diverse mosaic of patches ranging in scale from minute anthills to the vastness of the Nebraska Sandhills or Kansas Flint Hills. Not only is a given ridgetop subdivided into a number of areas in varying stages of succession, but this ridge varies from the hilltop adjacent to it and from the valley separating the two. On a broader scale, prairies change substantially as one progresses west and north because of variation in soil characteristics, the rain-shadow effect of the Rocky Mountains, and increasing continentality of climate to the north.

But as fascinating and complex as these prairies are, they have a characteristic that may lead to their extinction: they perfectly meet the agricultural demands of a species that does not understand the value of conservation. Thousands of years of decomposing plant matter have created some of the richest soils on earth, and the living prairie plants fulfill the nutritional needs of livestock. Today, no piece of prairie exists that has not been impacted by humans in one way or another. The plant and animal communities that have occupied the Great Plains for thousands of years have been completely restructured by humans in the last two centuries. They have been impacted by such a variety of factors both intentional and unintentional that we will never understand them all.

Prairie Conservation
Island Press (Washington, DC • Covelo, CA)

Copyright © 1996 Island Press.
All rights of reproduction in any form reserved.

Prairie Mammals

Defining a community of prairie mammals is difficult because the species comprising it have changed dramatically during the last several hundred thousand years for several reasons. First, although landscapes dominated by grasses have been present in North America during the last 20 million years, prairie as we know it today appears to be quite young (Axelrod 1985; Risser et al. 1981). Taking modern form only in the last several million years, much of the flora and fauna of North American prairies was borrowed from ecosystems surrounding the Great Plains. For instance, many of the grass species that now dominate the plains originally evolved in the forest openings of the East, the meadows of the Rocky Mountains, or the deserts of the Southwest (Risser et al. 1981). Similarly, the community of prairie mammals is formed largely of species whose resource requirements were broad enough to allow them to move into the grasslands from other ecosystems. Additional evidence of the prairie's youth and turbulent history is the paucity of endemic species. Of the mammals found on the central and northern plains for instance, only 11.6 percent are considered true grassland species (Armstrong et al. 1986).

A second factor causing instability in the prairie mammal community was dramatic changes in climate that occurred during the Ice Age. These fluctuations caused rapid distributional shifts for many North American organisms and led to some degree of mixing of ecosystems (Graham 1986; Lundelius et al. 1983). As recently as ten thousand years ago, prairie mammals in the central and southern plains mixed with species typical of tundra (mammoth, lemmings, heather voles, caribou), northern boreal forests (mastodon, red-backed voles, red squirrel), and eastern deciduous forests (fox squirrel) to form a community unlike any found on earth today (Rhodes and Semken 1986; Voorhies and Corner 1985).

Third, near the end of the Ice Age, climate change, hunting pressure by early humans, or both caused an extinction event on the plains that affected large grazing mammals and their predators as well as other groups (Marshall 1984; Martin and Neuner 1978; Martin 1984). The diverse grazing community of horses, antelopes, camels, rhinos, bison, elephants, tapirs, and others was reduced to the modern assemblage dominated by only two or three species. Finally, moderate climatic shifts during the last ten thousand years (Bryson et al. 1970) have caused a continual reshuffling of the prairie mammal community that continues to this day (Frey 1992). The combined effect of the above factors created a temporally and spatially unstable mammal community on the plains and prevented the extensive evolution of endemic species.

The prairie mammal community is dominated by species that colonized the grasslands from surrounding ecosystems. This topic has been examined most recently by Jones et al. (1983) and Armstrong et al. (1986) who analyzed affinities of mammals found in all habitats of the north-central prairie states. Of 138

species found in this region, only 16 (11.6 percent) are geographically centered on the Great Plains and likely evolved there (see table 11.1). The remaining 88.4 percent of the mammals apparently originated in other ecosystems and later colonized the plains. These mammals include 28 species from the coniferous forests of the mountains and northern North America, 25 species from the desert southwest, 18 that are widespread across the continent, 15 from the eastern deciduous forests, 12 from the southeastern United States, 5 from the Great Basin, and 5 of Neotropical origins. If we examine those 138 species listed by Armstrong et al. (1986) and omit mammals found in wetlands and forest habitats, we are left with 57 mammals found primarily in grasslands. This modification, however, still does not eliminate the bias toward nonendemics; the majority of these grassland mammals (41) still evolved in other ecosystems and later colonized the prairies. The present community of prairie mammals therefore represents a unique melting pot where grassland specialists interact and evolve with animals that originated in other regions of North America.

One more point that can be drawn from the data of Jones et al. (1983) and Armstrong et al. (1986) relates to the distribution of the grassland specialists, the

Table 11.1

Mammals whose distributions are centered on the grasslands of the Great Plains

Species	Habitat Affinity
White-tailed jackrabbit	Short–mixed-grass prairie
Franklin's ground squirrel	Tallgrass prairie
Richardson's ground squirrel	Short–mixed-grass prairie
Thirteen-lined ground squirrel	Widespread
Black-tailed prairie dog	Short–mixed-grass prairie
Plains pocket gopher	Widespread
Olive-backed pocket mouse	Short–mixed-grass prairie
Plains pocket mouse	Short–mixed-grass prairie
Hispid pocket mouse	Short–mixed-grass prairie
Plains harvest mouse	Short–mixed-grass prairie
Northern grasshopper mouse	Short–mixed-grass prairie
Prairie vole	Tallgrass prairie
Swift fox	Short–mixed-grass prairie
Black-footed ferret	Short–mixed-grass prairie
Spotted skunk	Widespread
Pronghorn	Short–mixed-grass prairie

Source: Modified from Armstrong et al. 1986, and Jones et al. 1983.

group most vulnerable to the prairie's decline. Of these sixteen endemic mammals, eleven are associated primarily with mixed-grass and shortgrass prairies of the central and western plains (see table 11.1). Only two species, Franklin's ground squirrel and the prairie vole, inhabit tallgrass prairies primarily, whereas the other three are fairly widespread, namely the spotted skunk, thirteen-lined ground squirrel, and plains pocket gopher.

Another important aspect of the prairie ecosystem is the impact of disturbance on the mammal community and the role of mammals in creating this disturbance. Historically, prairies were characterized by frequent perturbations, including fire, drought, grazing, storms, and local factors such as the digging activities of animals (Kaufman et al. 1988; Tomanek and Hulett 1970). The combined impact of these factors created a mosaic environment in which the microhabitat features at a given location could change dramatically in a few days (Collins and Barber 1985; Plumb and Dodd 1993). Prairie mammals were adapted to tolerate these conditions; many large mammals were somewhat migratory, whereas the reproductive capability and rapid dispersal of small mammals allowed them to quickly colonize and populate new patches of suitable habitat (Grant et al. 1982; Risser et al. 1981; Vinton et al. 1993).

Large-scale disturbances undoubtedly played a significant role in determining mammal use of an area. Fire, for example, has positive effects on some species (Coppock and Detling 1986; Kaufman et al. 1983; Vinton et al. 1993) and a negative impact on others (Kaufman et al. 1983; Vacanti and Geluso 1985). Likewise, grazing benefits some species by providing open habitat or by encouraging fresh growth of vegetation and reducing standing dead litter (Coppock et al. 1983b; Hansen and Gold 1977; Miller et al. 1994; Reading et al. 1989). In fact, Whicker and Detling (1988) cite previous research suggesting that female bison could potentially gain 25 percent more weight by preferentially feeding on prairie dog towns versus feeding in mixed-grass prairie. Alternatively, some species, especially those requiring dense litter, are negatively impacted by grazing (Birney et al. 1976; Grant et al. 1982). Drought also appears to have differential effects on various species, with some negatively impacted, others unaffected, and some responding favorably (Tomanek and Hulett 1970). On a landscape scale, the prairie mammal community was probably spatially and temporally diverse, with grazing and burning creating a continually shifting mosaic of habitats and the whole regional flora and fauna slowly recovering from past droughts.

But prairie mammals do more than passively respond to disturbance; they create disturbance and thus greatly impact the diversity of the whole prairie ecosystem. Mammals affect vegetative structure and composition by feeding on plants and by disturbing the soil. Several authors (Anderson 1982; Axelrod 1985; Plumb and Dodd 1993; Risser et al. 1981) have suggested that grazing played a substantial role in the development of North America's prairies by decreasing

woody vegetation and favoring the evolution of grazing-tolerant plants. Modern grasslands appear to represent an extreme in the level of herbivory, with rates of removal of annual aboveground net productivity ranging between 50 to 80 percent (Coppock et al. 1983a; McNaughton et al. 1988). Mammalian grazing affects plant structure and species composition and represents a major link in nutrient cycling pathways. By feeding selectively on certain plants, grazers reduce the dominance of these species and allow subdominant plants to become a more important component of the vegetation (Risser et al. 1981). Bison feed heavily on grasses and are thought to have been numerous enough to have significantly impacted the prairie vegetation at a local scale (England and DeVos 1969; Peden et al. 1974; Plumb and Dodd 1993). In addition, other grazers, such as pronghorn, prairie dogs, wapiti, voles, and pocket gophers, were abundant and increased the impact on the prairie vegetation. To attempt to manage today's prairies without some form of grazing ignores the importance of this process in maintenance of the ecosystem and may lead to overdominance by a few species (Howe 1994b).

Mammals also affect vegetative composition and structure by disturbing the soil. Wallowing by bison and digging by badgers, pocket gophers, prairie dogs, and other mammals provide unique microhabitats, affect soil conditions, and break the dominance of perennial grasses to provide habitat for annual forbs and grasses (Collins and Barker 1985; Huntly and Inouye 1988; Munn 1993; Platt and Weiss 1985; Whicker and Detling 1988). The abundance of these disturbances on the prairies of the past undoubtedly led to a substantial increase in vegetative diversity and further enhanced the mosaic nature of grasslands. Unfortunately, of the three most important groups of mammals involved in soil disturbance (pocket gophers, prairie dogs, and bison), the latter two have been drastically reduced in number.

A final aspect of herbivory that potentially has a significant impact on prairie vegetation is the activity of seed-eating mammals and other animals. Although this topic has received little attention in prairies, research conducted in a transitional area between desert scrub habitat and grassland in Arizona has found that kangaroo rats exert such an important force on the vegetation that their removal results in a dramatic change in habitat (Heske et al. 1993). Through seed predation and soil disturbance, these rodents decrease grass cover by nearly threefold and appear to have greater local impact than grazing by cattle.

Present Community

The mammal community that inhabited the prairies of the Great Plains three hundred years ago has been radically restructured by recent human activities. Keystone species have been eliminated or drastically reduced; other species have declined, while still others have increased. Additionally, the prairie ecosystem

that these mammals inhabited, the evolutionary landscape in which they evolved and continue to evolve, has been converted, fragmented, and otherwise altered.

Humans have caused the decline or disappearance of a large number of mammals, both directly through overhunting and extermination, and indirectly through habitat modifications (see table 11.2). The removal of several of these animals has resulted in changes in the whole prairie ecosystem because of the im-

Table 11.2

Great Plains mammals extirpated, declining, or extinct

Species	Status
White-tailed jackrabbit[a]	D
Eastern chipmunk	D
Franklin's ground squirrel[a]	D
Black-tailed prairie dog[a]	D
Gray squirrel	D
Southern flying squirrel	D?
Plains pocket mouse[a]	D - L
Plains harvest mouse[a]	D - L
Prairie vole[a]	D? - L
Woodland vole	D?
Gray wolf[a]	Extinct
Swift fox[a]	D
Black bear	Ex
Grizzly bear[a]	Ex
Black-footed ferret[a]	Ex
Wolverine	Ex
Badger[a]	D? - L
Eastern spotted skunk[a]	D?
River otter	D (reintroduced)
Mountain lion	D
Lynx	D
Wapiti[a]	Ex (reintroduced)
Pronghorn[a]	D (now increasing)
Bison[a]	Ex (reintroduced)
Mountain sheep[a]	Extinct

Source: Includes information from Bowles 1981, and Jones et al. 1983.

Note: D = declining; D? = status somewhat unclear, but appears to be declining; D - L = declining in local portions of ranges; Ex = extirpated.

[a]Primarily inhabiting grasslands.

portant role these species played in regulating communities and modifying vegetation.

The near elimination of bison has had a substantial impact on prairies. Grazing activities of bison created patches of open habitat that differed vegetatively from surrounding ungrazed prairie. Further, the wallowing, trampling, rubbing, and excretion of waste of 30 to 60 million bison created a habitat that was highly variable both spatially and temporally (Axelrod 1985; England and DeVos 1969; Plumb and Dodd 1993; Risser et al. 1981). Several species of birds and small mammals (Risser et al. 1981) were apparently adapted to utilize these temporary open patches created by bison activities. Although bison have been replaced by cattle and other livestock in most regions of the prairie, the impact is not the same (Noss et al. 1995). Bison eat different plants than cattle (Peden et al. 1974; Plumb and Dodd 1993), and the confinement of cattle creates an environment that is not as spatially or temporally diverse (Howe 1994a; Knopf 1994). The role that free-ranging bison played in altering vegetative and faunal communities is poorly understood, especially on a landscape scale, and needs further research if genuine attempts are to be made to restore large prairie reserves.

A second keystone species that has been enormously impacted by the activities of humans is prairie dogs. Historically occupying roughly 400,000 km^2, or 20 percent of the available shortgrass and mixed-grass prairies, prairie dogs alter vegetation, create open habitat, modify soil conditions, affect energy and nutrient cycles, and create burrows that are used by a host of other animals (Munn 1993; Whicker and Detling 1993 and citations therein). In fact, nearly 170 vertebrates have been recorded using prairie dog towns (Miller et al. 1994), although this number is somewhat inflated since it includes birds flying over and not really using the town's unique habitat. Depending on the species, the degree of use may include foraging on the town, use of abandoned burrows as hibernacula, consuming prairie dogs or animals attracted to their colonies, or even total dependence upon prairie dogs. Feeding and clipping activities of prairie dogs stimulate fresh vegetative growth and reduce standing dead biomass, which provides nutritious forage (Coppock et al. 1983a). As a result bison, wapiti, and pronghorn prefer to feed in prairie dog towns (Coppock et al. 1983b; Miller et al. 1994). Although the typical prairie dog colony of today is fairly small and isolated (Miller et al. 1994), towns during presettlement times often stretched for miles. One prairie dog town in Texas covered roughly 40,234 km^2 and contained an estimated 400 million prairie dogs (Bailey 1905).

Because of early reports of competition between prairie dogs and cattle and the possible role of these rodents in transmitting diseases such as plague to humans, eradication programs were instituted in the late 1800s and continue to this day. During four years in the early 1980s, over 185,000 ha of prairie dog colonies were poisoned, at a cost of $6.2 million. Two agencies of the federal government and numerous state offices are responsible for the control of prairie dogs on an

estimated 80,000 ha annually (Miller et al. 1994 and citations therein). In reality, cattle prefer to graze in prairie dog colonies (Miller et al. 1994) and their weight gain is not significantly different from cattle grazing away from towns (O'Meilia et al. 1982; Uresk 1993). In addition, direct transmission of plague from prairie dogs to humans accounts for only 3 percent of the two to twenty human cases per year (Barnes 1993). Although local control of prairie dogs might be justified, the mass elimination of this group of species is not. Populations of prairie dogs have been reduced by roughly 98 percent according to current estimates (Whicker and Detling 1993). Today, local populations are in serious danger of elimination from further poisonings and outbreaks of sylvatic plague, and colonies are so isolated that repopulation through immigration is becoming less and less likely (Miller et al. 1994). Evidence suggests that fragmentation of prairie dog populations has already impacted the genetic and population structure of colonies (Pizzimenti 1981). Given the significance of prairie dogs in creating large patches of habitat that differ from the surrounding prairie and their importance in providing habitat for many other animals, the program of widespread eradication of prairie dogs must be reconsidered.

The effects of removing a keystone species is evident in the plight of the black-footed ferret. Totally dependent on prairie dogs as a food source and to provide burrows, this North American endemic was reduced to dangerously low levels in the mid-1980s when the remaining eighteen wild animals were captured for breeding (Forrest et al. 1988; Thorne and Williams 1988). Because ferrets require a large number of prairie dogs within a small geographic area, decline in populations of ferrets is attributable primarily to the decimation of prairie dog colonies. Further, canine distemper has eliminated local populations because of the ferret's lack of immunity. Assuming canine distemper is a native disease, presettlement ferret populations probably remained stable because of immigration from large surrounding populations that recolonized areas decimated by the disease. The highly fragmented and isolated conditions of recent populations of ferrets made local extinction more probable and recolonization unlikely (Forrest et al. 1988). Although the captive ferret population is reproducing, reintroduction programs are hampered by the continued presence of distemper, sylvatic plague outbreaks that affect populations of prairie dogs, and the continuing eradication of prairie dogs (Oldemeyer et al. 1993).

Another group of animals decimated by human activities on the plains was the midsize grazers, including white-tailed and mule deer, wapiti, mountain sheep, and pronghorn. All members of this group decreased because of overhunting or the introduction of nonnative diseases (Genoways 1986; Genoways et al. 1979), but modification of habitat as the human population on the plains increased further hurt their numbers. Wapiti were extirpated from most of the Great Plains; the subspecies that was native to the plains is now extinct (Jones et al. 1983). Similarly, the native prairie subspecies of mountain sheep, which was probably

fairly common in the western prairies prior to settlement, is now extinct (Jones et al. 1983). Pronghorn, mule deer, and white-tailed deer decreased to dangerously low levels near the beginning of the 1900s but have rebounded to varying extent due to regulated hunting. Mule deer will likely not return to their previous population levels due to habitat modification and the resulting increase in white-tailed deer. The impact of the loss of wapiti and the decrease of the western midsize grazers on the prairie community is difficult to assess. Wapiti were once quite common in the eastern prairies (England and DeVos 1969; Jones et al. 1983) and apparently have some impact on the vegetation in areas where they are still extant (Frank and McNaughton 1993).

Another group missing from today's prairies are the large predators, including gray wolf, grizzly bear, black bear, and mountain lion. All these animals were apparently somewhat common on the Great Plains but were quickly eliminated as human settlement increased (Jones et al. 1983). The subspecies of gray wolf that inhabited the plains is now extinct. Results of these eliminations may be substantial since mountain lions and wolves are top predators. The recent increase in number of white-tailed deer, raccoons, opossum, coyotes, and red foxes may be attributable at least in part to the removal of these predators-competitors (Jones et al. 1983). Wolves, grizzly bears, and mountain lions have been shown to impact numbers of prey in regions where they are still extant (Bianchet et al. 1994; Messier 1994).

While most of the above reductions or extirpations have been fairly well documented, other prairie mammals have undergone declines quietly (see table 11.2). Documenting declines in population or range for less visible, often small and nocturnal mammals is difficult because intensive trapping or periods of observation are necessary to prove an animal is no longer present or is reduced in number. As a result, the status of many secretive or infrequently trapped species remains uncertain.

Although locally abundant, most of the inconspicuous species that rely on grasslands have decreased throughout their ranges because of wide-scale conversion of prairie to agricultural lands (Armstrong et al. 1986; Bowles 1981; Lovell et al. 1985). Tallgrass prairies of the eastern plains have been eliminated more than other grasslands (Noss et al. 1995; Samson and Knopf 1994), and the landscape of this region bears little resemblance to that which occurred there two centuries ago. Prairie remnants are small and widely isolated, and the only common grassland habitats remaining are roadside right-of-ways, fencerows, streamcourses, and areas too steep or rocky to plow. Without fire, however, the few somewhat natural areas remaining are filling in with woody vegetation. Most of the larger mammals requiring grasslands are either gone or greatly reduced, including white-tailed jackrabbit, black-tailed prairie dog, badger, spotted skunk, mule deer, and wapiti. Of the small mammals inhabiting the tallgrass prairies, many are unspecialized enough to utilize the remaining strips of grasses and may

be locally abundant. Perhaps the only mammal that is somewhat restricted to tallgrass prairies is the Franklin's ground squirrel, a species that is, not surprisingly, declining (Bowles 1981; Jones et al. 1983). The prairie vole, a species that likely evolved in the tallgrass prairies, has apparently declined to some extent over much of its original range but now has expanded east to occupy grasslands created as humans cleared eastern forests (Bowles 1981; Jones et al. 1983).

Population and community changes that have occurred in less conspicuous mammals of mixed- and shortgrass prairies are poorly known. In areas where these prairies have been heavily converted, results are likely similar to that discussed for tallgrass prairies. Populations of grassland species have probably declined overall with roadside right-of-ways and fencerows serving as the only somewhat appropriate habitat remaining. Since mixed-grass and shortgrass prairies contain more grassland specialists than eastern prairies, the impact of habitat reduction and fragmentation may be greater. In areas where prairies remain intact, some species are still abundant, while others may be substantially reduced because of the decrease in habitat diversity caused by the control of fire, the near elimination of native grazers, and the control of prairie dogs. So little is known of the community of small mammals in these habitats prior to settlement that more specific statements are not possible. Attempts should be made to quantify the remaining community of mammals in these prairies for use in conservation efforts and to establish data to compare with future surveys.

Although many prairie mammals have undergone declines in recent decades, few of them are reduced to threatened or endangered status. This fact may lead to the false assumption that prairie mammals are not negatively affected by humans. However the negative impact is real because of the decrease in genetic diversity that occurs when populations are reduced or destroyed in large portions of the range of a species (Risser 1988). Like most organisms, mammals, especially smaller and less mobile species, show considerable genetic and morphological variation across their ranges, probably attributable to selection to local environmental conditions. Current methods of measuring biodiversity do not take into account the importance of this genetic diversity to the survival and evolutionary potential of a species. If the next hundred thousand years are as climatically unstable as the last hundred thousand, the loss of genetic diversity will seriously decrease the viability and threaten the existence of many prairie species.

Although this book deals with prairie conservation, nonprairie mammals need mentioning. Forests on the Great Plains have varied considerably in the past. Prior to settlement, strips of true eastern deciduous forest penetrated the plains on steep bluffs along major rivers mostly in the tallgrass prairie region. With the arrival of European settlers, these forests, and the true deciduous forest mammals that require them, were negatively impacted. Unlike white-tailed deer and fox squirrels, species such as woodland voles, gray squirrels, eastern chipmunks, and southern flying squirrels require fairly mature oak-hickory forests for survival.

All of these eastern deciduous forest species have decreased on the Great Plains, probably because of logging, grazing, cultivation, and other modifications (Bowles 1981; Jones et al. 1983). Populations of these mammals are important to conserve since they represent species living on the very edge of their tolerable habitat. As such, these populations might represent evolutionary hot spots where small populations and unique environments lead to genetic diversity and possibly speciation (Frey 1993; Mayr and Ashlock 1991). Similar declines have been found in mammals of the boreal forests that penetrate the northern prairies (Armstrong et al. 1986; Jones et al. 1983). Additional attention must be paid to relict populations of mammals such as the eastern woodrat isolated along the central Niobrara River in Nebraska. Such isolates also represent potential for speciation should selection or random processes lead to sufficient divergence.

The beaver is another nonprairie mammal that requires brief mention. Occurring in riverine habitats in the prairies, this keystone species was decimated by early fur trappers leading to extirpation throughout much of its original range (Bowles 1981; Genoways 1986; Jones 1964). Although this animal has recovered well on the plains, its status requires future monitoring because of the great importance of its damming activities to many other organisms.

The increasing human presence on the prairies has not led to the decline of all species (see table 11.3). Many generalists and successional forest-edge species have increased and expanded their ranges into the plains. Other species have increased as a result of climatic change. Although many of these species are not mammals of grasslands, they are important members of the Great Plains fauna and often have an impact on prairies and prairie mammals.

Habitat and dietary generalists that have increased in the last century are raccoon, opossum, red fox, and coyote (Bowles 1981; Jones et al. 1983). Probable reasons for these increases are numerous and include climatic change, increased habitat, and the ability to live in close contact with humans and feed opportunistically on the abundant food we provide. The impact of these mammals on others in the Great Plains may be substantial because these animals act as predators, competitors, or both, of other, more specialized mammals. Although little attempt has been made to quantify the impact of these increasing mammalian generalists, similar increases in generalist species of birds have been linked to the decline of more specialized birds (Robinson et al. 1995).

Another group expanding its population and geographic range are those species associated with successional forests and forest edges, including white-tailed deer, white-footed mouse, fox squirrel, eastern cottontail, woodchuck, and probably some relatively unspecialized bats (Bowles 1981; Jones et al. 1983). Although oak-hickory forests and their associated fauna have decreased, fast-growing woody plants, both native and nonnative, have increased in abundance on the Great Plains because of the control of prairie fire, decreased flooding, and intentional planting (Johnson 1994). This increase has been most dramatic along

Table 11.3

Great Plains mammals that have increased in populations, range, or both since settlement

Species	Status
Opossum	RI/PI
Masked shrew	RI
Big brown bat	PI?
Red bat	PI?
Hoary bat	PI?
Eastern cottontail	RI/PI?
Black-tailed jackrabbit	RI
Woodchuck	RI/PI?
Fox squirrel	RI/PI
White-footed mouse	RI/PI
Hispid cotton rat	RI
Meadow vole	RI/PI?
House mouse	Introduced
Norway rat	Introduced
Black rat	Introduced, cities only
Meadow jumping mouse	RI
Domestic dog	Introduced, some feral
Coyote	PI
Red fox	RI/PI
Gray fox	RI?
Domestic cat	Introduced, some feral
Raccoon	PI
Least weasel	RI
White-tailed deer	RI/PI

Source: Includes information from Bowles 1981, and Jones et al. 1983.

Note: PI = increase in populations; RI = increase in range; ? = status is uncertain but species appears to be increasing.

rivers, where forested corridors of cottonwood, ash, hackberry, and Russian olive now connect eastern and western woodlands. The impact of this connection on mammals is not at all clear, but in birds, the increased woody vegetation has resulted in the meeting, and occasional hybridization, of faunas that were previously isolated, a conservation issue termed faunal mixing (Knopf 1994). Although mammals have spread west more slowly than birds, the next few decades will see the meeting of the rapidly expanding eastern mammals (white-tailed deer, fox squirrel, white-footed mouse, eastern cottontail) with mammals of

western forests, if this is not already occurring. Whether any western mammals will spread east is unknown, but two species of birds, the black-billed magpie and house finch, have apparently done just that. Additionally, the impact of these forest mammals on animals of surrounding prairies is unclear. At least one of these species, the white-tailed deer, probably has a negative impact on its prairie counterpart, the mule deer, through hybridization (Carr et al. 1986) and possibly competition.

Interestingly, of the increasing populations discussed above, none currently require any special conservation efforts. But these are the very species that most often benefit from many Midwest wildlife preserves, game enhancement plantings, and tree planting programs. In addition, the increasing numbers of these often conspicuous species distract the public's attention away from those more secretive species whose populations have been negatively impacted.

Another group of mammals that has appeared recently on the Great Plains includes several introduced species—the house mouse, Norway rat, black rat, domestic cat, and domestic dog. Although the two rats are associated primarily with human dwellings, the house mouse is becoming increasingly common in grassland habitats in the Midwest, especially in the east. It is possible that this species will become an important competitor of native rodents. Domestic dogs and cats also represent a threat to native species through predation and hybridization.

A final example of species that have increased in numbers and geographic range on the plains recently is a group of grassland generalists that probably are reacting to changes in climate. The masked shrew, meadow vole, meadow jumping mouse, and least weasel have northern origins and appear to be spreading south because of an overall cooling trend in the Great Plains since the mid-1960s (Frey 1992; Jones 1964). Apparently responding to climatic warming on the plains during the last several thousand years, species of southern origin including the nine-banded armadillo, opossum, and hispid cotton rat are expanding (Genoways and Schlitter 1967; Jones et al. 1983). The seemingly contradictory nature of the above expansions is probably attributable to the differing time scales of the climatic changes to which the mammals are responding.

Conservation

The most obvious factor impacting mammals of the prairie is the widespread conversion of native grasslands into agricultural fields. As discussed elsewhere in this volume, the loss of prairie habitat ranges from 20 to >99 percent depending on the region. The habitat that has replaced the prairie is primarily monocultural row crops. Although utilization of agricultural fields by large mammals has been mostly unstudied, use of this habitat by small mammals has received some research effort. In the east, use of crop fields by small mammals appears to be limited largely to three species—the deer mouse, white-footed mouse, and house

mouse (Houtcooper 1977, 1978; Whitaker 1966); all are generalist species typical of disturbed or successional habitats. Only the deer mouse uses crop fields once they have been plowed. Research by Navo and Fleharty (1983) in western Kansas found that several species used wheat and sorghum fields temporarily, but only the deer mouse used these habitats extensively. They also cited previous research that found that plowed fields had very low abundance of small mammals. Finally, work in western Kansas by Fleharty and Navo (1983) and Reed and Choate (1986) found that irrigated crop fields offered good habitat for several species during some of the year, but the surrounding fencerows were important because they housed permanent populations that could colonize the crop fields when conditions were adequate. Most of the species that used these fields were either generalists or highly mobile species, including northern grasshopper mice, hispid pocket mice, plains pocket mice, western harvest mice, deer mice, white-footed mice, and Ord's kangaroo rats, which are adapted for utilizing temporary booms in resources. Additionally, Fleharty and Navo (1983) suggested that these rodents were not pests, but rather were useful since they consumed waste grain and insect crop pests and benefited the soil through burrowing activities. From these studies it appears that crop fields are used during certain times of year by some species that are generalists or adapted to utilize disturbances but are avoided by more specialized species.

Another habitat feature common in some areas is fields that have been replanted with nonnative pasture grasses or, more recently, native grasses. Many of these fields are enrolled in the Conservation Reserve Program (CRP) instituted by the federal government in 1985 and renewed in 1995. In some areas these fields are quite common, making up over 5 percent of the cropland in shortgrass prairie states and 3.4 percent in mixed-grass–transition states (Knopf 1994). The importance of these plantings to mammals is poorly understood. Generally, the fields are planted with one to four species of grasses and are quite poor in forb diversity. Based on this information it is likely that planted fields are used by mammal species requiring dense cover but lack the vegetative diversity to support a diverse mammal community on a landscape scale. Research in Texas found that although the CRP fields planted in nonnative grasses supported a community with similar values of diversity as local native prairies, the species that were present differed (Hall and Willig 1994). The authors suggested that one of the important differences between prairies and CRP fields was the lack of disturbance in the latter. Further research to understand the importance of CRP fields and nonnative pastures to prairie mammals is badly needed.

Even in areas where prairie vegetation is still intact, overall vegetative structure and diversity are probably quite different from presettlement conditions because of the decrease in perturbations (fire and prairie dogs) and the altered grazing regime. The foraging pattern of cattle is different from that of bison because cattle eat more forbs and shrubs. Confined cattle also create an environment less

spatially or temporally diverse than that likely created by free-ranging bison (Howe 1994b; Knopf 1994). The combination of these factors leads to a landscape with different vegetative composition, one that does not contain the diversity of habitats, and one that is not as frequently affected by random disturbance. The impact of this altered vegetative environment on mammals is unknown, although research has shown that grazing by cattle has an impact on small mammals of the prairie, especially in tallgrass or mesic prairies (Birney et al. 1976; Grant et al. 1982; Moulton et al. 1981). From a conservation standpoint, the most important issue is to determine how the current, cattle-dominated landscape differs from the presettlement ecosystem modified by bison, prairie dogs, and fire.

Fragmentation of habitat and isolation of populations are important, but unstudied, issues in conservation of prairie mammals. With increasing loss of habitat, fragmentation gives rise to isolated populations of organisms more likely to become extinct, less likely to be recolonized, more genetically isolated from surrounding populations, and more likely to suffer the negative impacts of inbreeding and genetic drift (Andren 1994; Franklin 1986; Wilcox 1986). In addition, small patches of habitat typically contain fewer species than expected because of a lack of microhabitat diversity and the absence of rare or patchily distributed organisms. These trends become more important as body size of the organism increases (usually lower population density) and vagility decreases (usually lower colonization and immigration rate). To understand the importance of these factors to a given species or ecosystem, additional information, including the life history of the organisms involved and the degree of connectedness of the habitat patches, must be known. To our knowledge, little effort has been made to determine the importance of fragmentation and isolation to the prairie mammal community (but see Robinson et al. 1992). In regions where fragmentation is less intense, flow of animals from patch to patch may be substantial, given the mobility of larger prairie species and the ability of many smaller mammals to use connecting corridors such as fence lines and roadside right-of-ways. In more intensely fragmented areas, those prairie species that are unable to utilize other habitats at least for dispersal may be experiencing the problems associated with small, isolated populations. Finally, the role of interstate highways and channelized rivers in isolating or, in some cases, connecting populations needs to be determined (Genoways 1985).

Simply reading a roster of mammals listed as threatened or endangered by the U.S. Fish and Wildlife Service, one might come to the conclusion that the prairie mammal community has been little affected by activities of humans. Nothing could be further from the truth. The wide-scale destruction of habitat, the alteration of remaining habitat, the extermination or decimation of keystone mammals and top predators, the increase in generalist and introduced animals, and the reduction in genetic diversity within individual species have all contributed

to the complete restructuring of the community of prairie mammals. Three characteristics of this community—the relative lack of endemics, the broad resource requirements of many of its species, and the adaptations of many mammals of the prairie to tolerate frequent disturbance—have proved fortuitous from a conservation standpoint. Had the prairies been heavily populated by specialists with narrow geographic ranges and ecological niches, the biological disaster that we are currently battling would have been much worse. Even with this advantage however, prairie mammals need protection to preserve dwindling species, maintain genetic diversity, and retain what remains of the original mammal community structure. The importance of conserving the mammal community of the prairie should be evident to all prairie ecologists and conservationists. For among all the animals that inhabit the prairies, no other group plays as important a role in creating the habitat mosaic that characterizes the prairies of North America.

Action Plan

To protect mammals and other organisms that inhabit the prairies of North America, several courses of action need to be implemented soon. Basic information to make intelligent conservation decisions for managing preserves, public lands, and private holdings is lacking. One of the most important issues to resolve is determining how the current cattle-dominated prairie landscape differs in vegetative and faunal composition from the ecosystem modified by the accumulating effects of bison, prairie dogs, and fire. Although most remaining herds of bison are fairly small and somewhat confined, study of these areas would still be valuable, especially if the area also contains prairie dogs and is managed with fire. We know little about temporal and spatial patterns of grazing by presettlement bison, and some attempt to mimic original conditions could be worthwhile. Especially valuable would be research conducted on preserves containing herds of differing sizes, densities, and degrees of confinement. This research could be compared to similar studies on adjacent cattle-grazed landscapes and would provide a much better understanding of the prairie ecosystem. In addition, this information would be valuable in managing prairie preserves and could lead to means of minimizing the impact of nonnative grazers on the prairie flora and fauna. Research analyzing some of these questions is underway at several locations throughout the Great Plains, and preliminary results can be found in the literature (Pfeiffer and Steuter 1994; Steuter et al. 1995).

Other needed research includes the importance and characteristics of linear grassland remnants (roadside right-of-ways, fencerows, etc.) and planted pastures (including CRP fields) to mammal communities. Because these habitats represent some of the only remaining grasslands in intensively cultivated areas, their use by mammals as corridors and permanent habitat needs clarification.

Many of these areas are heavily managed by grazing, mowing, and planting, and the impact of this management is almost unknown (but see Grimm and Yahner 1987). Additionally, the effects of habitat fragmentation and isolation have been nearly unexplored in prairie mammals. Grassland specialists, such as the black-tailed prairie dog, plains harvest mouse, and plains pocket mouse, in the heavily impacted eastern and central prairies might be suffering from problems characteristic of small, isolated populations that result in declines greater than expected based on the quantity of remaining habitat. Additionally, further surveys to quantify the populations and distributions of prairie mammals, especially those that specialize in grasslands, will provide important information for conservation and supply baseline information against which future changes can be measured. In addition to research, the following actions are recommended:

1. Preservation of large tracts of remaining prairies is crucial to preserving the prairie mammal community. Protecting entire ecosystems is more efficient than conservation measures that work on a species-by-species basis (Noss et al. 1995). Remaining tracts of fairly undisturbed prairies exist, especially in the central and western plains.

2. Existing and future prairie preserves should be managed with the same forces that have impacted this ecosystem for millennia, namely temporally and spatially unpredictable disturbances caused by grazing and digging animals and by fire (Howe 1994a). The results of these management tools will require careful monitoring to determine their impact on other management objectives, such as the control of nonnative, cool-season grasses. Current management techniques, which often prevent grazing and use early-season fires year after year, likely will lead to long-term loss of vegetative diversity and the subsequent loss of faunal diversity.

3. By working with landowners and state road departments, managers could use roadside right-of-ways and fencerows to provide useful habitat and corridors that allow immigration of some mammals between existing patches of prairie.

4. The current trend in using bison to gain income from grazing should be encouraged, especially if research can show how to use bison to restore more native conditions.

5. The senseless eradication of prairie dogs is economically costly (Collins et al. 1984), agriculturally unnecessary, and ecologically detrimental. Government subsidizing of this program should be stopped; prairie dog control and hunting on public lands should be prevented; and educational efforts to improve the image of the prairie dog must be implemented.

6. When it becomes necessary to reintroduce extirpated species, every attempt must be made to use reintroduction stock that is as close to native as possible. Although the release of nonnative genetic stock may be acceptable when the na-

tive gene pool is extinct, the introduction of foreign forms in regions where native individuals are still present contaminates the gene pools that evolved in that area for thousands of years. The reintroduction of river otters in several states for instance, involved subspecies from Louisiana and northwestern North America, even though in some cases native individuals were still present in the region (Genoways 1986).