

**McCown's Longspur (*Calcarius mccownii*):
A Technical Conservation Assessment**

**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

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SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF MCCOWN'S LONGSPUR

Status

McCown's longspurs (*Calcarius mccownii*) are locally abundant breeding birds of the shortgrass prairies of the Great Plains. In Region 2 of the USDA Forest Service, they commonly breed only on the Pawnee National Grassland in Colorado and the Thunder Basin National Grassland in Wyoming. They winter mostly south of Region 2. Most populations appear to be stable or increasing, but due to a historical long-term decline in abundance on both their breeding and wintering grounds, this species is ranked by various state, federal, and private conservation organizations as a grassland "species of concern", "high priority", "imperiled", with "pressing needs", "state imperiled", or a species of "conservation concern".

Primary Threats

Loss of native shortgrass prairie to agriculture and development on both breeding and wintering grounds is the greatest threat to McCown's longspurs. Although most of the rangeland loss to agriculture was historical, more recent losses are not insignificant. In Colorado, for example, 3.8 percent of the remaining short and mixed-grass prairies east of the Rockies was lost to agriculture and urban expansion from 1982 to 1997 (Seidl et al. 2001). Habitat loss from increasing oil and gas development, especially in Wyoming, and the associated negative impacts of disturbance and fragmentation also pose a threat to McCown's longspurs. Fire suppression, prairie dog control, increasing recreational activities, and the use of pesticides are somewhat lesser threats. Any absolute changes in survival, or proportional changes in first-year and adult survival, will have major impacts on the population dynamics of this species.

Primary Conservation Elements, Management Implications and Considerations

Conservation of nesting and wintering habitats, broader conservation efforts to preserve prairie dogs and their habitats, minimization of the impacts of recreation, and proper management of livestock will benefit McCown's longspurs. Grazing management is the primary land management tool, and longspurs are often more abundant on heavily grazed grasslands. However, population response to grazing depends on regional soil type (Kantrud and Kologiski 1982), grazing history, and weather patterns. Prescribed burns may be necessary to maintain the stature of breeding habitat and to reflect the historic spatial extent and temporal pattern of prairie wildfires.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS) (**Figure 1**). McCown's longspur (*Calcarius mccownii*) is the focus of an assessment because it has been added to the Regional Forester's Sensitive Species List (Revised 2003). Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution (FSM 2670.5 (19)). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

This assessment addresses the biology and conservation of the McCown's longspur throughout its range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide managers, biologists, other agencies, and the public with a thorough discussion of the biology, ecology, conservation, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussions of broad

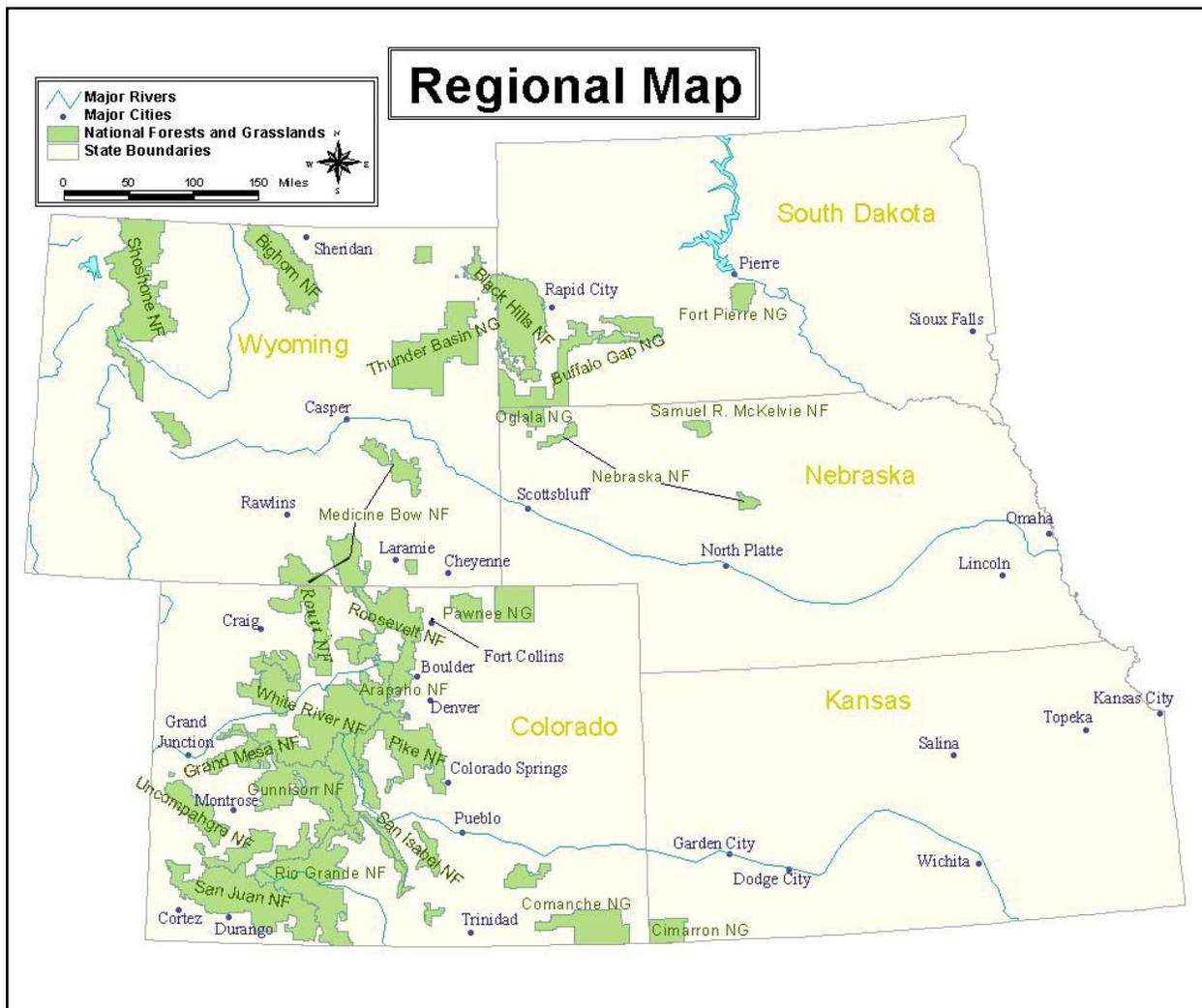


Figure 1. USDA Forest Service Region 2. National grasslands and forest are shaded in green.

implications of that knowledge, and outlines information needs. While the assessment does not develop specific land management prescriptions. Rather it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e. management implications). This information can be used by managers to direct land management decisions. Furthermore this assessment cites management recommendations proposed elsewhere, and when these have been implemented, the assessment examines the success of their implementation.

Scope

This species conservation assessment examines the biology, ecology, conservation, and management of the McCown's longspur with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although much of the literature on the species originates from field investigation outside the region, this document places that literature in the ecological and social context of the Rocky Mountain Region. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of McCown's longspur in the context of the current environment. The evolutionary environment of the species is considered in conducting the syntheses, but placed in a current context.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on McCown's longspur are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications and reports were used in this assessment when refereed information was unavailable. However, these were regarded with greater skepticism. Unpublished data (e.g. Natural Heritage Program records) were important in estimating the geographic distribution of the species. These data required special attention because of the diversity of persons and methods used in collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of

the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, we note the strength of evidence for particular ideas, and we describe alternative explanations where appropriate.

Publication of Assessment on the World Wide Web

To facilitate the use of species conservation assessments, they are being published on the USFS Region 2 World Wide Web site. Placing the documents on the web makes them available to biologists and the public more rapidly than publishing them as reports. More important, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the web. This report was reviewed through a process administered by the Society for Conservation Biology, employing at least two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

McCown's longspur is endemic to the Great Plains as a breeding bird. It is not federally listed or a candidate for listing under the Endangered Species Act. However, due to a historical, long-term decline in abundance on both the breeding and wintering grounds, this species is ranked by various state, federal, and private conservation organizations as a grassland "species of concern", "high priority", "imperiled", with "pressing needs", "state imperiled", or a species of "conservation concern". **Table 1** summarizes these rankings.

Table 1. Management status of McCown’s longspur by federal and state agency and private conservation organizations.

Agency/organization	Rank given McCown’s longspur
USDA Forest Service	Sensitive species in Region 2
U.S. Fish and Wildlife Service	High priority declining grassland species of the northern prairie; Bird of Conservation Concern throughout its breeding and wintering ranges (ranked nationally in Regions 2 and 6, and in all Bird Conservation Regions where the species occurs)
Natural Heritage Program	G4 – apparently secure overall, but dramatic declines in northern part of range
National Audubon Society	Red Watchlist species; declining rapidly, small population or limited range, conservation threats
Partners in Flight	High Priority; Breeding Score of 27 (extreme high priority) for both the Wyoming Basin and Central Shortgrass Prairie physiographic areas S86 and S36, respectively
<u>State of Wyoming</u>	
Department of Game and Fish	Species of Special Concern
Natural Heritage Program	S3B/SZN – breeding population vulnerable; no non-breeding occurrences
<u>State of Nebraska</u>	
Department Game, Fish, and Parks	Species of Concern
Natural Heritage Program	S3 – vulnerable
<u>State of Colorado</u>	
Natural Heritage Program	S2B/SZN – breeding population imperiled; no non-breeding occurrences
<u>State of South Dakota</u>	
Natural Heritage Program	SUB/SZN – unrankable breeding population; no non-breeding population
<u>State of Kansas</u>	
No special status	

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Laws, regulations, and management direction

There are no existing legal mechanisms, management plans, or conservations strategies that apply specifically to the McCown’s longspur. However, this species is protected by several laws that apply to most wildlife species, including the Migratory Bird Treaty Act (1918), the National Forest Management Act (1976), and the Neotropical Migratory Bird Conservation Act (2000).

The Migratory Bird Treaty Act prohibits, with certain exceptions, the pursuit, hunting, capture, killing, taking, sale, purchase, transport, receipt for shipment, or export of any migratory bird, or the nest or eggs of such

birds (16 U.S.C. 703; <http://laws.fws.gov/lawsdigest/migtrea.html>). Furthermore, international treaties serving as the foundation of the Act or formed subsequent to and implemented by the Act require the federal government to protect ecosystems of special importance to migratory birds against pollution, detrimental alterations, and other environmental degradations.

The National Forest Management Act and its implementing regulations and policies require the USFS to sustain habitats that support healthy, well-distributed populations of native and desired non-native plant and animal species on National Forest System lands. One means of redeeming this statutory responsibility is through the Sensitive Species policy (FSM 2670.5 (19)). Under this policy, Regional Forester’s may identify species for which current or predicted downward trends in populations and/or habitats have been identified. These identified “sensitive species” are accorded

special analysis and management attention. Currently, McCown's longspur is classified as a sensitive species in Region 2.

The standards and guidelines of the Government Performance Results Act of 1993 are intended to ensure that resources under federal jurisdiction are managed in a sustainable manner. The National Environmental Policy Act requires agencies to specify environmentally preferable alternatives in land use management planning. Additional laws with which the USFS must comply are the Endangered Species, Clean Water, Clean Air, Mineral Leasing, Federal Onshore Oil and Gas Leasing Reform, and Mining and Minerals Policy acts; all are potentially relevant to McCown's longspur conservation.

The Neotropical Bird Conservation Act provides grants to U.S., Latin American, and Caribbean organizations for the conservation of birds breeding in the U.S. and wintering south of the U.S. border. It encourages habitat protection, education, research, monitoring, and the long-term protection of neotropical migratory birds (<http://laws.fws.gov/lawsdigest/neotrop.html>).

National monitoring and conservation-related programs relevant to the McCown's longspur include the North American Breeding Bird Survey (BBS) and the Monitoring of Avian Productivity and Survivorship program (MAPS). The BBS (<http://www.mbr-pwrc.usgs.gov/bbb/intro00.html>), which started in 1966, is a nationwide (including southern Canada) effort of >3500 roadside avian surveys conducted during the breeding season. The main objective of the BBS is to estimate long-term trends in avian populations. The MAPS program was created in 1989 to assess and monitor the reproductive success and population dynamics of >120 species of North American landbirds (<http://www.birdpop.org/maps.htm>). Using banding and constant-effort mist-netting, MAPS data are used to describe spatial and temporal patterns in species' reproductive success and population trends with regard to landscape-level habitat characteristics, weather, and species' ecological characteristics. Goals are to monitor and identify causes of population decline, to maintain healthy populations, and to evaluate the effectiveness of management and conservation actions.

Enforcement of existing laws and regulations

Enforcement of existing laws and regulations should be adequate. On the Pawnee National Grassland, which is one of the two Region 2 grasslands that support breeding populations of McCown's longspurs, "intensive

and extensive" species monitoring began in 1997. This includes USFS data collection and cooperative research agreements with Colorado State University, U.S. Fish and Wildlife Service (USFWS), Colorado Natural Heritage Program, and Rocky Mountain Bird Observatory. Key habitat conditions for the mountain plover (*Charadrius montanus*) were maintained by prescribed burning of areas of taller grasses; because of habitat associations with McCown's longspur, such management should benefit that species, as well. Additionally, access was restricted during key vulnerable seasons to eliminate disturbance (seasonal closures or mitigation on project implementation) to threatened and endangered species, including the mountain plover; again this should also benefit McCown's. Road closures to improve wildlife habitat were not effective, however, due to budgetary constraints. Grazing allotments were monitored to evaluate rangeland health and to determine long-term trends; adjustments were made in allotment management.

The Thunder Basin National Grassland Land and Resource Management Plan includes two key objectives pertinent to McCown's longspur conservation: 1) ensure long-term grassland health, and 2) maintain and enhance the viability of native plant and animal species. Specifically, grazing will be varied with broad resource emphasis, range vegetation emphasis, and natural-appearing-landscape emphasis; few to no prairie dog (*Cynomys* spp.) areas will be controlled with poison; certain prairie dog complexes will be managed for black-footed ferret (*Mustela nigripes*) reintroductions; some areas will be protected for research, education, biological diversity, and wilderness; and off-road travel will be restricted. To minimize oil and gas activities on the Thunder Basin National Grassland, required mitigation includes limiting noise on oil and gas production facilities, restricting distance from certain vegetation types of concern, minimizing drill site traffic and vegetation disturbance, and reclaiming production sites.

Challenges for the USFS on shortgrass prairies include:

- ❖ an increasing urban population and its accompanying desire for recreation, conflicting with livestock grazing on range allotments
- ❖ incomplete inventories of roads and trails, which limit knowledge related to grassland fragmentation issues
- ❖ maintaining species viability

- ❖ dealing with the increasing impact of oil and gas drilling activities
- ❖ managing for desired plant species composition, structure, and pattern
- ❖ monitoring for plant, animal, and ecosystem processes and functions
- ❖ maintaining sustainable community relationships and ecosystem functions
- ❖ using grazing to achieve desired vegetative conditions.

Biology and Ecology

Systematics and species description

McCown's longspur is in the order Passeriformes and in the family Emberizidae. It is a heavy, stocky bird, 15 cm long and weighing about 25 to 26 g (With 1994a). The elongated nail of the hallux gives the "longspur" its name. The tail pattern is diagnostic: white, with an inverted black "T". McCown's tends to appear paler and grayer than other longspurs, is distinctively plain-faced, and generally lacks streaking on the underparts. Its bill is longer than that of other longspurs; it is swollen at the base and usually pink in non-breeding birds. The breeding male has a pale gray look, a black cap and malar streak, a chestnut patch on the median wing coverts, and a black crescent on the breast. In winter, the male shows at least a shadow of dark breast patch. Breeding females are drab and pale, but with at least a wash of chestnut on the median wing coverts; females share the diagnostic tail pattern (With 1994a, Sibley 2000).

The species has a larger bill and shorter hallux nail compared to the other *Calcarius* longspurs. Sibley and Pettingill (1955) reported a hybrid between McCown's and chestnut-collared longspurs (*C. ornatus*). No geographic variation or subspecies have been described (With 1994a).

Distribution and abundance

The distribution of breeding populations is disjunct, corresponding to the now fragmented distribution of the shortgrass prairies of the Great Plains and the southern fringe of the Canadian Prairie Provinces (**Figure 2**). Furthermore, both breeding and winter distributions (**Figure 3**) may shift annually as McCown's is nomadic to some extent, making

"somewhat erratic appearances and disappearance" at certain times and in certain places (Bent 1968). McCown's longspurs breed in loose colonies from southeastern Alberta east to southern Saskatchewan, south through Montana, eastern and central Wyoming, to western North Dakota and South Dakota, and western Nebraska to northeastern Colorado (Godfrey 1986, With 1994a, Dechant et al. 1999). They winter in the southern U.S. from western Oklahoma south through eastern New Mexico and central and west Texas into northern Mexico (mainly on the Plateau from northern Sonora and Chihuahua to northern Durango). Some wintering birds extend as far west as southeastern Arizona and southwestern New Mexico. They may rarely winter in southern California, southeastern Colorado, and western Kansas (With 1994a, Howell and Webb 1995). Christmas Bird Count (CBC) data reveal major annual shifts in the distribution of wintering populations, presumably due to fluctuating weather patterns and conditions on the wintering grounds. Winter abundance estimates show dramatic fluctuations as well; for the period from 1982 to 2002, total numbers seen per party hour ranged from a low of 0.0046 (391 individuals) to a high of 0.269 (2846 individuals) (National Audubon Society 2002).

The species is most numerous (breeding) in southwestern Saskatchewan and locally in Montana and Wyoming (Sauer et al. 2001). Andrews and Righter (1992) categorized the McCown's longspur as a common to abundant summer resident and common to abundant local migrant in Colorado. On the wintering grounds, McCown's longspurs occur at highest densities in the Texas panhandle, western Texas, and eastern New Mexico.

McCown's longspurs have undergone noticeable declines during historic times, with their breeding range "drastically reduced" (Bent 1968). Their breeding range formerly included Oklahoma (no records since 1914: Nice 1931, Sutton 1967), western Minnesota (Currie 1890, Brown 1891; no records after 1900: Bent 1968, Green and Janssen 1975), South Dakota (no breeding records since 1910: Visher 1913, 1914; Bent 1968; but territorial behavior observed in 1993: Peterson 1995; annual but local in the northwest: Martin personal communication 2004), and Manitoba (Taverner 1927). In North Dakota, the species formerly bred in the northwestern and southwestern parts of the state but has gradually disappeared; it may still breed irregularly in the extreme western part of the state (Bent 1968, Martin personal communication 2004). In addition, the species may formerly have been more abundant across its present range.

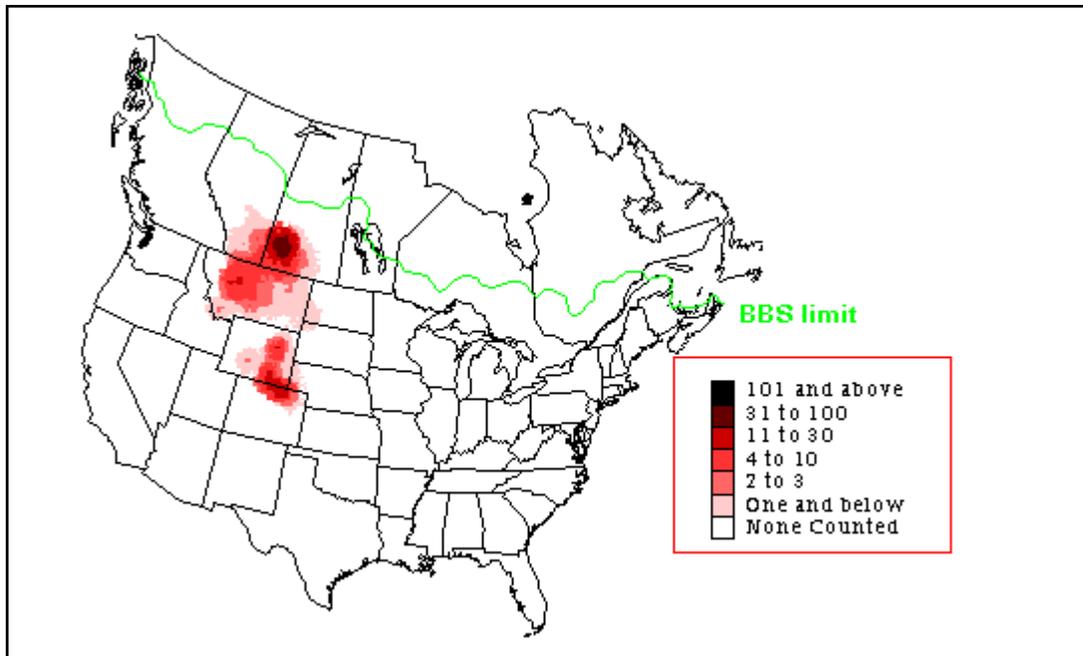


Figure 2. Relative breeding season abundance (average number of birds per route) of McCown's longspur based on Breeding Bird Survey data, 1982 to 1996.

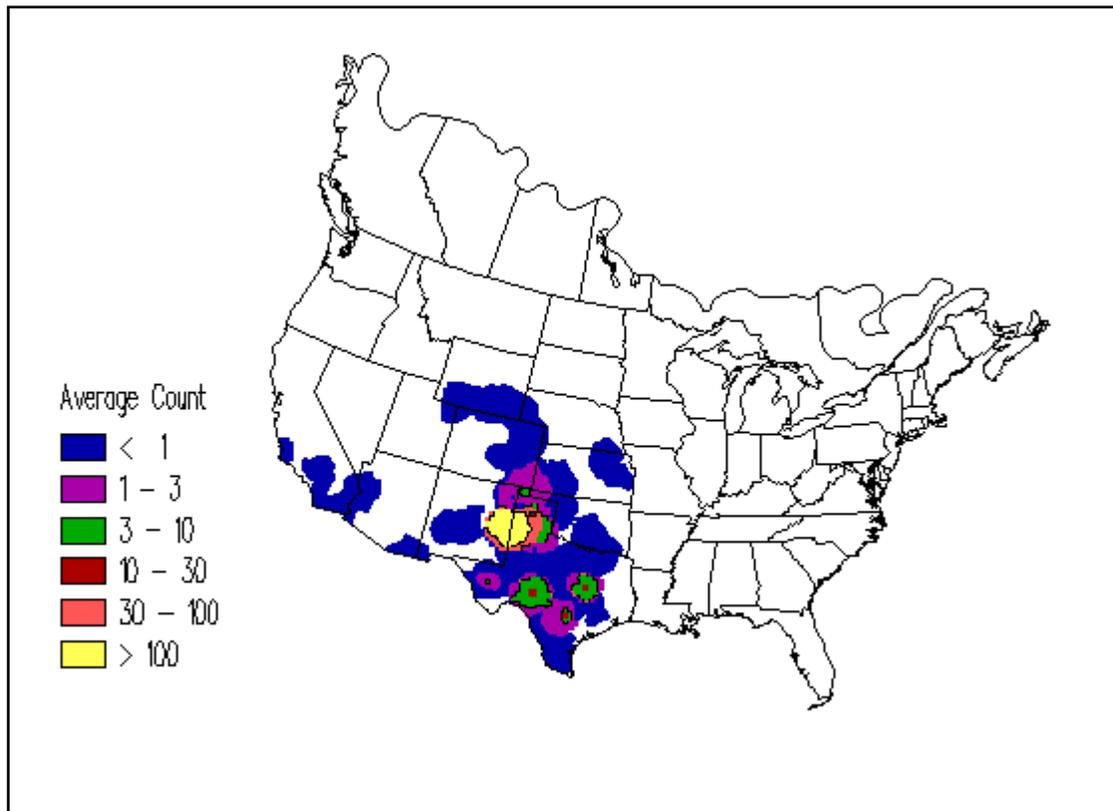


Figure 3. Relative winter season distribution and abundance (average number of birds per count circle) of McCown's longspur based on Christmas Bird Count data, 1982 to 1996.

The most significant population declines occurred long before the initiation of the BBS. Declines were most apparent during the first decades of the twentieth century. Between 1905 and 1930 longspurs disappeared from most of their range in the state of North Dakota (Stewart 1975). Similar declines were apparent on the winter range during this period, especially in portions of Arizona and Texas (Phillips et al. 1964), and another sharp decline was apparent in the Texas panhandle after 1940 (Oberholser 1974). Ligon (1961) reported “far fewer” longspurs in late fall in the late 1950s “than formerly,” both in New Mexico and western Texas. As late as 1893, Ernest Thompson Seton reported “countless multitudes” of McCown’s longspurs in northeastern New Mexico in late fall (Bailey 1928).

On the Pawnee National Grassland in Colorado, breeding longspur densities in heavily grazed pastures (60 percent of annual aboveground primary production consumed by cattle) were estimated to be 46.9 and 40.8 pairs per 100 acres in 1969 and 1970, respectively (Giezentanner 1970b), 75.6 *birds* per 100 acres (Wiens 1971), and 81.5 *birds* per 100 acres (Porter and Ryder 1974). In a lightly grazed pasture (20 percent of annual aboveground primary production consumed by cattle), densities were 13.6 and 40.8 pairs per 100 acres in 1969 and 1970, respectively (Giezentanner 1970b). Overall densities on the Pawnee National Grassland (including pastures with no longspurs) were 11.7 and 14.3 pairs per 100 acres in 1969 and 1970, respectively (Giezentanner 1970b). Hanni et al. (2003) reported densities of 24.8 birds per km² on the Pawnee National Grassland.

Densities on occupied sites on the eastern Pawnee National Grassland from 1997 and 1999 were 0.904 ± 0.58 (*n* = 10 sites), 0.704 ± 0.53 (*n* = 11), and 1.09 ± 0.54 birds/ha (*n* = 6), respectively (Skagen personal communication 2004). Including sites where longspurs did not occur, densities were 0.57 ± 0.64 birds per ha (*n* = 16 sites) and 0.48 ± 0.55 (*n* = 16) in 1997 and 1998, respectively. Notably, McCown’s longspurs did not occur on any of 10 Conservation Reserve Program (CRP) sites surveyed. Densities did not differ in either 1997 or 1998 between fragmented (a 9 km² block of 45 percent grassland and 55 percent agricultural and CRP lands) and intact (a 9 km² block of 100 percent grassland) sites: 1997, intact = 0.68 ± 0.78 birds/ha, fragmented = 0.45 ± 0.48 birds/ha, *P* = 0.504; 1998, intact = 0.44 ± 0.53 birds/ha, fragmented = 0.52 ± 0.60 birds/ha, *P* = 0.785) (Skagen personal communication 2004).

In Saskatchewan, Maher (1973) reported 79 individuals per 100 acres. In Wyoming, density estimates were 76.6 ± 15.0 pairs per 100 acres (3-year

average) on the Laramie Plains and 126 ± 0.0 pairs per 100 acres on the Cheyenne Plains (Finzel 1964).

On the wintering grounds, McCown’s has occurred only sporadically at most CBC sites. In Colorado, the species is unusual in winter, having been recorded in only seven years of CBCs (high count = 270; through 2002). In Kansas, McCown’s was reported in 23 years, with a high count of 801 individuals in 1993 on the Cimarron National Grassland (National Audubon Society 2002). Only the Friona, Texas site reported this bird each year of the census with the highest count being 105.2 individuals per hour of count effort (Root 1988). On the Buffalo Lake National Wildlife Refuge (Texas) CBC, an annual average of 1008 McCown’s were recorded between 1973 and 1993 (Seyffert 2001). Grzybowski (1982) reported a density of 62 birds per 100 ha on a lightly grazed plot in the Muleshoe National Wildlife Refuge (Texas), where it was the second most abundant species. McCown’s has been recorded during all seven years (1997 to 2003) of the Ejido San Pedro CBC (Chihuahua, Mexico; Dieni et al. 2003).

Knowledge of this species’ distribution in Colorado is still increasing, as occurrences are being reported where it was not known previously, including El Paso, Washington, Elbert, Kit Carson, and Lincoln counties (Kuenning 1998; Versaw personal communication 2004). It is unknown whether these newly reported populations are range expansions or merely first discoveries of historical populations. McCown’s occurred in 2 percent of Colorado Breeding Bird Atlas (CBBA) blocks; CBBA estimates ~23,000 to 127,000 breeding pairs in Colorado (Kingery 1998). McCown’s is now being monitored by the Rocky Mountain Bird Observatory (Leukering personal communication 2004).

Population trend

The BBS trend estimates map (**Figure 4**) suggests an increasing trend for most regions within the U.S. and a decreasing trend for Canada (Sauer et al. 2001). However, these data are based on few routes (*n* = 62), and the average relative abundance of McCown’s longspurs (<16 individuals per route) is low. For the period from 1966 to 2000, the only statistically significant (*P* < 0.05) trend estimates are for the Wyoming Basin physiographic stratum (7.7 percent annual increase; **Figure 5**), Wyoming (7.8 percent increase; **Figure 6**), Alberta (8.2 percent decrease), and Canada (20.7 percent decrease) (Sauer et al. 2001). Most BBS trend estimates for regions within USFS Region 2 and USFWS Region 6 are positive, but statistically

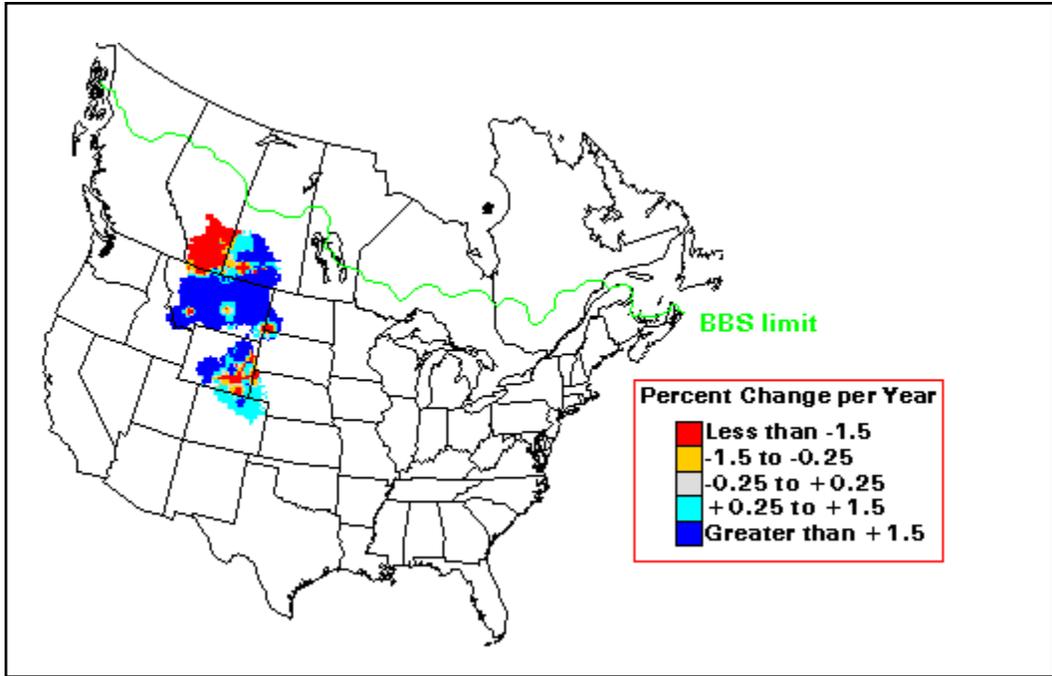


Figure 4. Breeding Bird Survey trend (average percent population change per year) for McCown's longspur, 1966-1996.

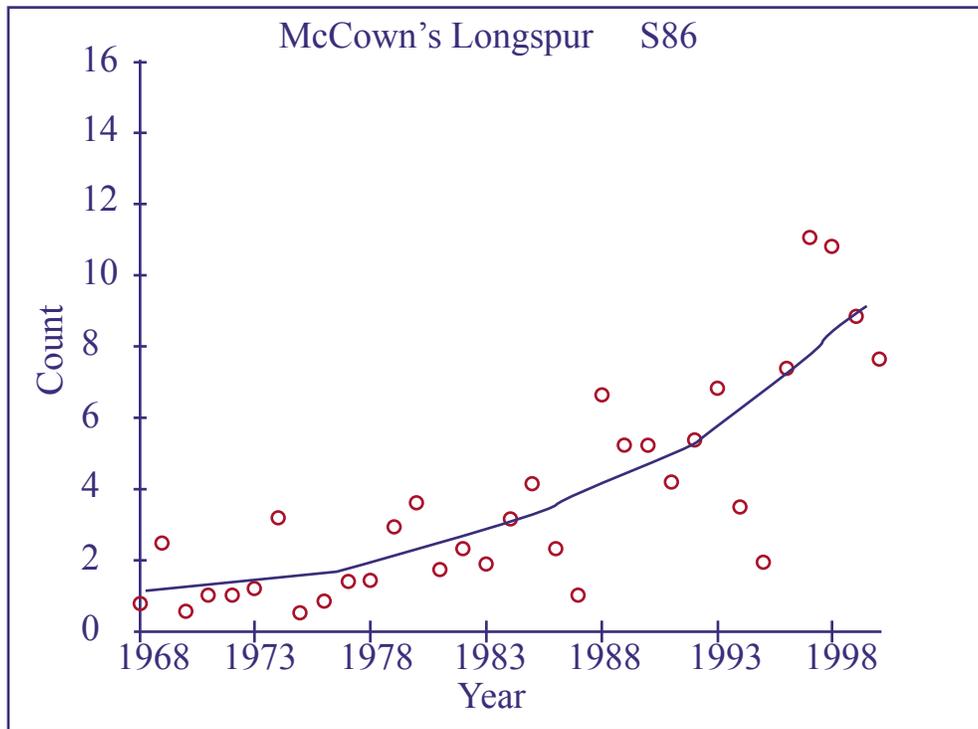


Figure 5. McCown's Longspur trend (average number of Birds per route) for the Wyoming physiographic stratum (S86), 1968 to 2000.

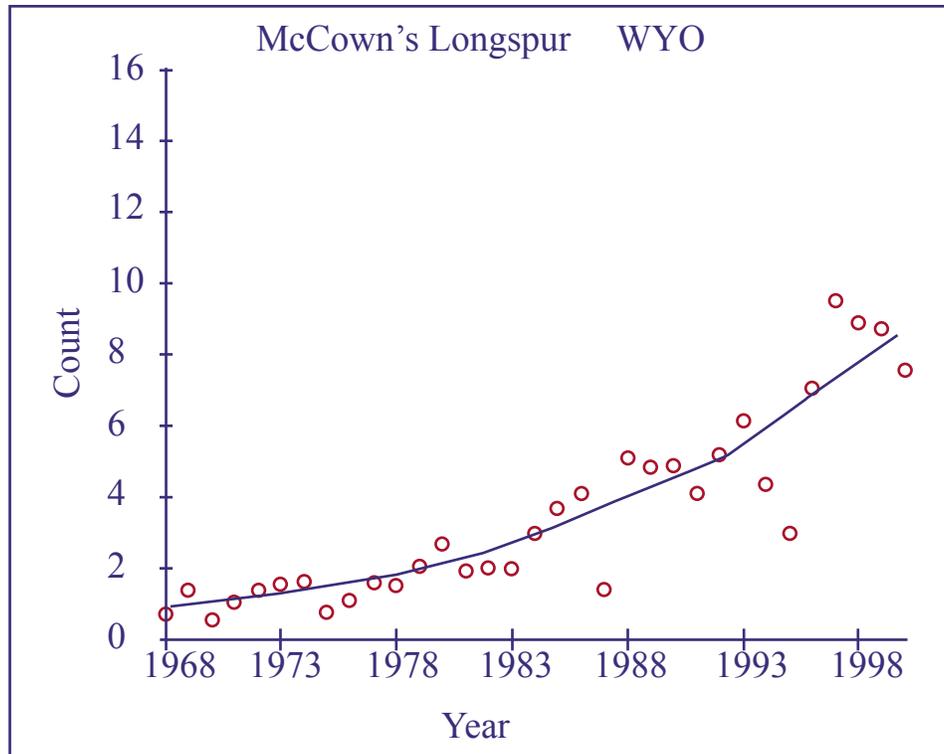


Figure 6. McCown's longspur trend (average number of birds per route) for Wyoming, 1968 to 2000.

insignificant. Trends for the entire U.S. are also positive, but insignificant, whereas the surveywide estimate, which includes the U.S. plus Alberta and Saskatchewan, is negative and non-significant. Thus, BBS data are not particularly revealing regarding population trends of McCown's longspurs. The unpredictable occurrence and erratic fluctuations of McCown's in certain areas of the breeding range (With 1994a) may explain the uncertainty of BBS results.

At a more regional scale, McCown's longspurs were present on an average of 9.71 ± 1.39 percent of the BBS routes run in Physiographic Region 36 (shortgrass prairie) in Colorado from 1988 to 1997, at an average abundance of 2.88 ± 0.74 individuals per route. The Rocky Mountain Bird Observatory's species monitoring plan (Leukering et al. 2000) lists the population trend of the McCown's longspur as "uncertain" in Colorado. Colorado populations are predicted by at least one model to be extirpated due to global climate change within 75 to 100 years (Price 2000).

Activity pattern

McCown's longspurs depart their wintering grounds in late February and March with migration extending into early to late April (With 1994a). Migrating stragglers may be encountered as late as May

(Cruickshank 1950). They arrive on the breeding range in flocks in late March (Colorado) to April (Wyoming, Montana, North Dakota) to mid- to late April and early May (Alberta, Saskatchewan) (With 1994a). Males precede females (by about two weeks in Wyoming) (Mickey 1943). Fall departure dates from the breeding grounds are variable, extending from August to late September (Saskatchewan, Montana). A few individuals may linger until early to mid-October (Saskatchewan, Colorado). Early arrival dates on the wintering grounds occur from late September (New Mexico), to early October (Arizona), to late October (Texas) (With 1994a). They arrive in Mexico by November (Howell and Webb 1995).

McCown's longspurs apparently migrate in flocks in the spring (DuBois 1937) and forage communally until territory establishment (Mickey 1943). "Large flocks" amass during the southern migration to the wintering grounds (Bent 1968), reportedly increasing in size during the southward migration. Immature birds flock with adults at the end of the breeding season and migrate with them to the wintering grounds. Flocks are also reported on the wintering grounds; thus the birds are not territorial during winter (With 1994a). Inclement weather may affect spring arrival dates, as longspurs arrived several weeks late at a Saskatchewan site during an especially cold and snowy spring (Felske 1971).

The breeding season extends from mid-March to August rangewide (Mickey 1943, Giezantner and Ryder 1969, Felske 1971, Creighton 1974, Salt and Salt 1976, Greer 1988, With 1994a), but in some locations a few McCown's longspurs may remain on the breeding grounds as late as mid-November (Johnsgard 1980). Most young fledge by mid-July; attempts to produce second broods may account for extended residence in some areas.

Habitat

Habitat associations

McCown's longspurs breed in shortgrass prairie, especially where vegetation coverage is sparse due to low soil moisture or heavy grazing, or where it is interspersed with shrubs or taller grasses. Blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) are the dominant grasses in nesting areas (DuBois 1935, Cassel 1952, Creighton 1974). These are often interspersed with cactus (e.g., *Opuntia polyacantha*) and a limited cover of midgrasses (e.g., *Aristida longiseta*, *Stipa comata*) and shrubs (e.g., *Gutierrezia sarothrae*, *Chrysothamnus nauseosus*, *Artemisia frigida*). McCown's use grasslands with little litter (Felske 1971) and low vegetation cover (DuBois 1935, Creighton 1974), such as that provided by true native shortgrass prairie or heavily grazed mixed-grass prairie. McCown's prefer to breed in heavily grazed areas (Bradley personal communication), and they respond positively to livestock grazing (Bock et al. 1993). In Colorado, individuals often use sparsely vegetated hillsides with southern exposures for displaying and nesting (Giezantner 1970a and b, Felske 1971, Creighton 1974).

While historically agricultural lands were avoided (Dubois 1935, Mickey 1943), McCown's longspurs may use cultivated lands today, especially in the northern parts of their breeding range. These lands include small-grain stubble fields, minimum- and conventional-tilled lands, and summer fallow fields (Felske 1971, Stewart 1975). In southern Saskatchewan, McCown's longspurs were found in equal abundances in tame and native pastures (Duncan and Davis *in press*). In Alberta and Saskatchewan, McCown's longspurs were more abundant in cropland than in Permanent Cover Program (PCP) grasslands (McMaster and Davis 1998). (PCP was a Canadian program that paid farmers to seed highly erodible land to perennial grassland cover; it differed from CRP in the U.S. in that PCP allowed annual haying and grazing). Early-season abundance of McCown's longspurs nesting in cropland fields in

south-central Alberta showed a positive correlation with percent bare ground, and productivity appeared to be negatively correlated with vertical forb density (Martin *in prep.*). McCown's also nest in heavily grazed mixed-grass prairies.

Wintering ground habitats are open with sparse vegetation, including shortgrass prairie, overgrazed pastures, plowed fields, and dry lakebeds. At the Muleshoe National Wildlife Refuge in Texas McCown's longspurs are most abundant on lightly grazed pastures (a *Bouteloua-Buchloe* matrix interspersed with other grass species including *Sporobolus*, *Hilaria mutica*, *Erioneuron pilosum*, *Gutierrezia sarothrae* and *Castilleja*) (Grzybowski 1982).

Microhabitat

McCown's breeding territories on the Pawnee National Grassland averaged 66.1 percent short grass and 23.5 percent bare ground, with an average vegetation height of 5.2 ± 3.7 (SD) cm ($n = 162$ point locations; Creighton and Baldwin 1974). Territories ($n = 97$) in Wyoming were 22.9 ± 12.55 percent short grass, 38.1 ± 13.79 percent bare ground, 27.1 ± 9.32 percent mid-grass, and 1.0 ± 1.77 percent cactus (Greer and Anderson 1989). In southeastern Wyoming, preferential placement of territories on areas with a high percent of bare ground was attributed to microclimate effects such as early warming and drying of nest sites (Greer 1988). Percent vegetation coverage within 5 cm of the ground was higher in occupied territories than in unoccupied territories in Wyoming, and occupied territories tended to have fewer cow pies, less lichen, and lower forb coverage than unoccupied areas (Greer 1988, Greer and Anderson 1989).

Vegetation characteristics appeared unrelated to prey biomass on territories in a Wyoming study (Greer and Anderson 1989); thus, vegetation structure provides a poor indication of territory quality to longspurs, although longspurs may be sensitive to ground temperatures and/or ground moisture in selecting territories (Felske 1971).

First territories in Saskatchewan were established on barren hillsides in heavily grazed and cultivated areas, generally on southern exposures. These sites likely become snow-free earlier in the breeding season and are favored by the grasshopper, *Aeropedellus clavatus*, which is a primary food item fed to young longspurs. Additionally, territories on the southern slopes were smaller and more densely packed than those on the top of the hill. Later in the breeding season

(July), territories were established in flat, less heavily grazed areas (Felske 1971).

McCown's longspur nests are either placed in the open or beside bunch grasses, cactus, shrubs, or cow or horse dung pats (DuBois 1935, Mickey 1943, With and Webb 1993). Nearly half of the nests (47.5 percent, $n = 40$) in one study were placed beside grass clumps, and the remainder were beside shrubs (Mickey 1943). On the Pawnee National Grassland, nests were associated with: *Opuntia* (35 percent), *Bouteloua gracilis* (20 percent) and *Gutierrezia* (10 percent) ($n = 34$ nests; Creighton and Baldwin 1974); *Aristida longiseta* (32 percent), *Opuntia polyacantha* (19 percent), *Gutierrezia sarothrae* (13 percent), and *Stipa comata* (13 percent) ($n = 31$ nests; With and Webb 1993); *Opuntia* (59 percent) and *Gutierrezia* (18 percent) in a more disturbed pasture ($n = 22$ nests; With 1994a). Nests are often oriented to the north of sheltering vegetation on the Pawnee National Grassland ($x = 5.8 \pm 6$ degrees; $n = 78$ nests; With and Webb 1993). This orientation did not provide protection from prevailing winds, but McCown's ground-level nests were protected nevertheless, as nest-cup wind velocities were at least an order of magnitude less than ambient wind velocities. Early-season nests were completely shaded from solar radiation 43.9 \pm 36.8 percent of daylight hours ($n = 5$ nests), but they were exposed to solar radiation at midday when sunlight was most intense, thus providing a thermal advantage in wet and cold weather (With and Webb 1993). Nests constructed later in the season, however, were not placed beneath shrubs or taller cover as might be expected, and they received little protective cover from solar radiation (With and Webb 1993).

Home range

McCown's longspur territory size ranges from 0.6 ha in southeastern Wyoming ($n = 74$; Greer and Anderson 1989), 0.5 to 1.0 ha in Saskatchewan (Felske 1971), and 1.1 to 1.4 ha ($n = 14$; Wiens 1970, 1971) and 0.93 ha ($n = 20$) on the Pawnee National Grassland in 1991 (With 1994a). In southeastern Wyoming, an increase in density of breeding pairs between years did not cause territory size to decrease, suggesting that there is an optimal limit to territory size (Greer 1988). In another Wyoming study, however, Mickey (1943) reported that territories decreased in size as densities of males increased. McCown's longspurs are not territorial on the wintering grounds.

Spatial patterns, landscape mosaic, juxtaposition of habitats

McCown's longspurs appear to prefer large expanses of shortgrass prairie. Area sensitivity has been well established, and habitat fragmentation is generally thought to be one of the primary causes of avian population decline. Small fragments of grasslands cannot support species that need interior habitats or large expanses of grasslands (Samson 1980, Johnson and Temple 1986), and grassland birds are more likely to occur on large patches of grassland than on small ones (Illinois: Herkert 1994; Maine: Vickery et al. 1994). Herkert et al. (2003) found higher nest predation in small (<100 ha) than in large (>1000 ha) prairie fragments in five mid-continental states. O'Connor et al. (1999) reported that grassland bird species are more influenced by habitat patch variables and less by landscape composition than other bird species. However, few studies have addressed patch size and fragmentation effects on McCown's longspur. One study still in progress did not find differences in either 1997 or 1998 between fragmented (a 9 km² block of 45 percent grassland and 55 percent agricultural and CRP lands) and intact (a 9 km² block of 100 percent grassland) sites: 1997, intact = 0.68 ± 0.78 birds/ha, fragmented = 0.45 ± 0.48 birds/ha, $P = 0.504$; 1998, intact = 0.44 ± 0.53 birds/ha, fragmented = 0.52 ± 0.60 birds/ha, $P = 0.785$) (Skagen, personal communication).

Habitat availability relative to occupied habitat

Some authors have reported large areas of unoccupied habitat. McCown's territories did not saturate the habitat in a Wyoming study (Greer and Anderson 1989), and Felske (1971) also found that ideal nesting habitat in Saskatchewan was apparently available, but not occupied. Factors on the wintering grounds may have contributed to breeding ground declines and the disappearance of breeding birds even from suitable native shortgrass prairies (Stewart 1975). "Ample" habitat remains in North Dakota, for example, but the reasons for the gradual disappearance of McCown's from that state are not apparent (Bent 1968).

Food habits

The diet of McCown's longspurs consists primarily of grass and forb seeds and insects, including grasshoppers, moths, beetles, and ants. Prey are

obtained from the ground (54.0 percent; e.g., stalking grasshoppers), in the air (33.4 percent; e.g., flushing insects from the ground), and by gleaning insects on plants (14.2 percent) (Baldwin and Creighton 1972). Stomach content analysis ($n = 312$) revealed that seeds (*Chenopodium*, *Carex*, *Avena sativa*, and *Triticum aestivum*) constituted the bulk of the adult diet for breeding longspurs in Saskatchewan (Maher 1974a). The female diet was comprised of 64 to 74 percent seeds and 5 to 14 percent ants during the May to August period, and grasshoppers constituted 23 percent of the diet in August. The male diet was 70 to 89 percent seeds, with minor percentages of arthropods from nine different taxa during the May to August period (Maher 1974a). Three grasshopper species were consumed by adults during the breeding season: *Aeropedellus clavatus*, *Camnula pellucida*, and *Encoptolophus sordidus*.

In a study on the Pawnee National Grassland in Colorado, more animal food (78 percent) than plant items (22 percent) constituted the diet of adult longspurs ($n = 24$) from May through July (Baldwin 1973). The occurrence of arthropods in the diet (percent dry weight) was dominated by Acrididae (27 percent), Curculionidae (13 percent), Scarabidae (13 percent), and Carabidae (10 percent). Seeds of *Aristida* (36 percent), *Polygonum* (25 percent), and *Buchloe* (16 percent) dominated the plant items in the diet. Daily caloric requirement was calculated as 37.4 kcal per bird-day (Baldwin 1973).

The young are fed all or mostly insects (Ehrlich et al. 1988, With 1994a). In a Wyoming study, mostly moth larvae and grasshoppers (Acrididae: *Arphia pseudonietana*, *Camnula pellucida*, *Melanoplus femurrubrum* [*femurrubrum*], and *Trimerotropis* spp.) were fed to nestlings (Mickey 1943). In Saskatchewan, grasshoppers comprised 62 to 85 percent of the total diet during two years of sampling ($n = 99$; Maher 1974a). In June, grasshoppers comprised 50 to 70 percent of the nestling diet, in July 80 to 90 percent, and in August 90 to 95 percent. Eleven different species of grasshoppers were fed to nestlings, the major species being *M. femurrubrum*, *Encoptolophus sordidus*, and *M. femurrubrum* (*femurrubrum*). Orthopterans comprised 82 to 92 percent of the prey biomass, and most of the prey items were 5 to 24 mm in length. On the Pawnee National Grassland in Colorado, the composition of the nestling diet by dry weight was 47 percent grasshoppers, 37 percent beetles, 4.5 percent lepidopterans, and 3.5 percent hymenopterans (Creighton and Baldwin 1974).

McCown's are primarily granivorous during winter (Grzybowski 1982). Their diet includes seeds

of knotweed, sunflower, goosefoot, and needlegrass, as well as some grain. Berries may also be taken (Oberholser 1974).

The relative value of food items, the conditions that may lead to variation in food value, the degree of flexibility in diet, and the role that diet and dynamics of food resources may play in species behavior are unknown.

Breeding biology

Phenology of courtship and breeding

Courtship and territorial establishment begin soon after birds arrive on their breeding grounds, late March to early May, depending on latitude. Males sing and display throughout incubation, but with less intensity than prior to mating; males sing even less when feeding young. Singing and courtship are reduced during rain or excessively windy conditions, and pair formation and initiation of nesting may depend on weather (With 1994a). Rapid singing may occur during territorial defense (Mickey 1943). Singing abates near the end of the breeding season as pair bonds dissolve and flocks begin to form.

Egg laying generally begins in early May with peak dates of first completed clutches about 12 May to 3 June on the Pawnee National Grassland (Baldwin and Creighton 1972); median clutch initiation is 6 June in Saskatchewan ($n = 67$ nests; Maher 1973). Clutch initiation spans about 14 weeks on the Pawnee National Grassland (With 1994a). Eggs may hatch as early as the second week of May and fledglings could be present as early as the third week of May on the Pawnee National Grassland (With 1994a). In Saskatchewan, the earliest fledglings were encountered 26 May, and the last young fledged 16 August, with a median fledging date of 27 June (Maher 1973). Second broods may be initiated as soon as three weeks after successful fledging of the first brood. The earliest date for a presumed second brood on the Pawnee National Grassland was 24 June (With 1994a).

Behavior of courtship and breeding

Courtship and territorial establishment begin with aerial flight displays and flight songs. Songs are usually issued in flight but may occasionally be given from shrubs, a fence, or even the ground; singing may also occur while foraging or in the presence of the female during courtship or mate guarding (DuBois 1937). Aerial displays are often performed over incubating females, and the descent may end near a foraging

female (With 1994a). During on-the-ground displays, the male may raise one wing to display the white lining to the female and he may accompany this display with song (DuBois 1937, Mickey 1943). In pre-copulatory displays, the male rapidly circles the female, sometimes singing and displaying his white wing lining (DuBois 1937). The female bows low and flutters her wings in response to these displays if she is receptive, and copulation invariably follows (With 1994a).

Female McCown's longspurs probably select the nest site and then build the nest alone in shallow depressions scraped in the ground (With 1994a). The female collects nesting material on territory (Mickey 1943) and is often accompanied by the male. The nest is an open cup with the rim of the nest flush with the ground. Nests are constructed of coarse grass stems and blades (plus lichen, shredded shrub bark, and weed stems) and are lined with finer grasses plus hair, wool, and/or feathers. Nests average 8.6 cm outer diameter, 6.4 cm inside diameter, and 5.1 cm in depth (DuBois 1935, Mickey 1943). Nests can be completed within a few days (one record of five days from the beginning of building to egg laying); some nests are apparently hastily built with eggs laid in the nest cup before the lining has been added (Felske 1971).

The period between nest construction and egg laying is variable (five days to two weeks). Eggs are usually laid on successive days and in the morning, before 0700 (DuBois 1937, Felske 1971). Damaged eggs may be removed from the nest but are not replaced. Entire clutches lost to weather or predators result in renesting in a different location on territory (With 1994a). Males may guard females during egg laying by perching atop nearby shrubs, and females may exhibit "restlessness" prior to egg laying by flying in circles above the nest just before returning to the nest and depositing an egg (Mickey 1943).

Only females develop a brood patch and incubate; incubation begins when the clutch of two to four eggs, usually three, is completed. However, during wet, cold weather, females have been observed to begin incubating sooner (Mickey 1943). The incubation period is 12 d. Females usually do not flush from the nest unless in danger of being stepped on (Mickey 1943). Males do not generally feed incubating females on the nest, but they may do so during inclement weather (DuBois 1923, With 1994a). Off-nest feeding bouts of females last about 8 min ($n = 9$ bouts from three different females); bout duration undoubtedly depends on ambient temperature (With 1994a). Males are vigilant at the nest during incubation, perching and

singing on shrubs and other structures near the nest (Mickey 1943) and concentrating foraging activities in the vicinity (<20 m) of the nest (With 1994a).

Hatching of the entire clutch is generally accomplished within 24 h, but it may take up to two days if the female began incubating before completing the clutch. Either males or females dispose of eggshells, as these are missing from the nest after the eggs hatch (Mickey 1943). The newly hatched young are altricial, covered with a buff-colored down, and their eyes are closed. By day five after hatching they appear alert, by day eight they are active, and by day nine they exhibit the "fear response" when disturbed. Nestlings gain an average of 1.5 to 1.8 grams per day in mass and 0.6 cm per day in body length (Mickey 1943, Felske 1971, Strong 1971). Nestlings fledge at about 70 percent of adult body mass in Colorado (Strong 1971) and at about 80 percent in Saskatchewan (Felske 1971).

Both parents brood the nestlings, but females brood during most of the first two days after hatching. The young are brooded less from day three on, as the adults spend increasingly more time foraging for their young (Mickey 1943). Nestlings are brooded during the night until they are well feathered at about day six following hatching. Adults alternately shelter the young from the sun, with the adult straddling the nest with wings partly spread (DuBois 1923).

Both parents feed the young. In Colorado, males spent 28 to 32 percent of the day foraging for young during the nestling period (Creighton and Baldwin 1974) and foraged >20 m from the nest 63.9 ± 17.6 percent of the time ($n = 5$ males; With 1994a). Adults give a food call when approaching the nest with prey, to which the young respond with a twittering begging call (Mickey 1943). The proportions of food provisioning by males and females are unknown. In Saskatchewan, adults averaged 2.25 visits per hour to the nest and brought 4.1 items per visit (Maher 1974a).

Young leave the nest at 10 days (With 1994a), although a range of 7 to 11 days has been reported (DuBois 1937, Mickey 1943, Maher 1973). At 10 days, young cannot fly, but they can run and flutter their wings if pursued. At 11 to 12 days, they are able to fly short distances (Mickey 1943). Recently fledged young seek refuge beside or beneath vegetation and remain there until fed by adults or disturbed. Young disperse on fledging and do not necessarily associate with siblings. Adults may divide broods, with parents sequentially feeding particular offspring or being pursued by a subset of a brood (With 1994a). Young remain dependent on

adults for at least three weeks (based on the time interval between nest departure of first broods and the initiation of second clutches). Immature birds flock with adults at the end of the breeding season and migrate with them to the wintering grounds. Young birds apparently do not return to natal breeding areas as extensive banding of nestlings ($n = 74$) on the Pawnee National Grassland has failed to document any returns (With 1994a).

Breeding behavior, site fidelity, limitations of site availability on breeding

It is not known if pairs reunite in subsequent seasons or if individual males or females return to previous breeding territories. Evidence of adult site tenacity is scant. On the Pawnee National Grassland, two banded adult females were not seen in following years, but two banded males did return to the same pasture where they were banded, but they occupied different territories (Ryder 1972). That McCown's longspurs are somewhat nomadic suggests that region wide distributional shifts in both the summer and winter are responses to unsuitable habitat conditions.

Demography

Genetic issues

No geographic variation or subspecies have been described (With 1994a). Sibley and Pettingill (1955) reported a hybrid between McCown's and chestnut-collared longspurs. McCown's longspurs are monogamous, with monogamy likely enforced by mated females, as suggested by observations of agonistic responses to intruding females attempting to associate with the territorial female's mate (With 1994a). Extra-pair copulations have not been reported in this species, congruent with the fact that males associate closely with females before egg laying and do not tolerate the presence of other males on the territory (With 1994a). Suspected egg dumping has been reported only once in this species (Felske 1971).

The continued fragmentation of the shortgrass prairie may have genetic consequences for this species. Fragmentation isolates populations, increases the likelihood of local extinctions, decreases the probability of colonization, and genetically isolates populations. This leads to increased probabilities of inbreeding and genetic drift, and a lowering of genetic diversity. Fragmentation can potentially turn continuous populations into "metapopulations of semi-independent demes" that gradually disappear (Risser 1996).

Recruitment, survival, immigration, age at reproduction

McCown's longspurs probably breed at one year of age although this has not been documented. Birds continue to renest throughout the breeding season if previous attempts are not successful. Second broods are apparently possible but may be limited by female energy reserves (Felske 1971). These may be initiated as soon as three weeks following fledging of first broods. Second broods have been reported in north-central Colorado, Montana, and southeastern Wyoming (DuBois 1935, Strong 1971, Greer 1988). The earliest date for initiation of a presumed second brood on the Pawnee National Grassland was 24 June (With 1994a).

The clutch size is two to four, occasionally five, and rarely six eggs (Nice 1931, DuBois 1935, Mickey 1943, Bent 1968, Strong 1971, Maher 1973, Porter and Ryder 1974, With 1994a). The modal clutch size is either three or four eggs, depending on the region (With 1994a).

Five different studies reported hatching success (number of nestlings per number of eggs), ranging from 54 to 70.9 percent (**Table 2**). Fledging success (number of fledglings per number of nestlings) in Colorado was reported as 42 percent (Creighton and Baldwin 1974) and 38 ± 47.6 percent (With 1994a), and as 45 to 54 percent over three years in Saskatchewan (Felske 1971). Other estimates were higher (Colorado, 75 percent, Strong [1971]; Wyoming, 77 percent, Mickey [1943]) because the proportion of young fledged across all nests was used rather than the average proportion of young that fledged per nest. Mean reproductive success (number of fledglings per number of eggs) ranged between 32.0 and 46 percent; the number of fledglings produced per nest was between 1.1 and 3.5; and the number produced per successful nest was between 2.0 and 3.5.

Using the Mayfield estimate (Mayfield 1975), daily survival estimates (eggs and nestlings combined) on the eastern Pawnee National Grassland for the years 1997, 1998, 1999, and 2001, were 0.962 ($n = 16$ nests), 0.938 ($n = 23$), 0.942 ($n = 10$), and 0.987 ($n = 8$), respectively (Skagen personal communication 2004). Nest success (proportion of nests fledging >1 young) was reported as 0.423, 0.270, 0.283, and 0.750 for the same four years, respectively.

There have been no studies of extensively marked populations and no long-term studies. Therefore,

Table 2. Reproductive success for McCown’s longspurs.

Location	Hatching success (number of nestlings per number of eggs)	Fledging success (number of fledglings per number of nestlings)	Reproductive success			Source
			(number of fledglings per number of eggs)	Number of fledglings produced per nest	Number of fledglings produced per successful nest	
Colorado	54 percent ($n = 53$ nests)	75 percent ($n = 53$ nests)	40.4 percent	1.3	2.4	Strong 1971
Colorado	62.1 \pm 43.8 percent ($n = 69$ nests)	38 \pm 47.6 percent ($n = 76$ nests)	32.0 \pm 43.5 percent ($n = 73$ nests)	1.1 \pm 14.7 ($n = 77$ nests)	2.7 \pm 0.9 ($n = 31$ nests)	With 1994a
Colorado	70.9 percent ($n = 34$ nests)	42 percent	—	—	—	Creighton and Baldwin 1974
Saskatchewan	58 to 64 percent ($n = 203$ eggs)	45 to 54 percent	33 percent	1.6	2	Felske 1971
Wyoming	60.1 percent ($n = 45$ nests)	77 percent ($n = 45$ nests)	46 percent ($n = 45$ nests)	1.6 ($n = 45$ nests)	3.5 ($n = 45$ nests)	Mickey 1943

there are no estimates of annual fecundity or lifetime reproductive success. However, based on 17 females in a Colorado study whose presumed renests and/or second nests were found in close proximity to first nests, With (1994a) reports that 16 out of 17 females produced at least one fledgling. Over half of the females (nine out of 17) attempted a second brood but fewer than half of these (four out of nine) were successful in producing offspring. Thus, about 25 percent (four out of 17) of the females successfully reared second broods. These 17 females undertook an average of 2.5 ± 0.87 nesting attempts, and the average female was successful 54 ± 0.30 percent of the time. In Saskatchewan, females attempted 1.5 to 1.8 clutches per female (Maher 1973) and 1.3 to 1.4 nests per female (Felske 1971).

There have been no studies of extensively marked populations and no band encounters or returns reported to the USGS Bird Banding Laboratory. Thus, there is no information on lifespan, survivorship, or immigration/emigration between populations for this species (With 1994a). The proportion of the population that breeds and the possible existence of “floaters” in McCown’s populations are also unknown.

Life cycle diagram and demographic analysis

The studies of fecundity and survival (e.g., Nice 1931, DuBois 1935, Mickey 1943, Krause 1968, Strong 1971, Maher 1973, Creighton and Baldwin 1974, Porter and Ryder 1974, With 1994a) provided the basis for formulating a life cycle graph for McCown’s longspur that comprised two stages (censused at the fledgling stage and “adults”). No estimates of survival were

available for this species, so data for chestnut-collared longspurs were used as the basis for estimated survival rates. Because of the paucity of survival data, our initial variant (Variant 1 – which we will refer to as the “equal survival” variant) assumed that first-year and “adult” survival were equivalent ($P_{21} = P_a = 0.57$) and assigned a survival value that yielded a population growth rate (λ) of 1.0. This “missing element” method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. An alternative model (Variant 2 – “low first-year survival”) assumed that first-year survival ($P_{21} = 0.35$) was considerable lower than was “adult” survival ($P_a = 0.74$). From the resulting life cycle graph (**Figure 7**), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of input terms: P_i describing survival rates, and m_i describing number of female fledglings per female (**Table 3**). **Figure 8a** shows the symbolic terms in the projection matrices corresponding to the life cycle graph for the first variant ($P_{21} = P_a = 0.57$). **Figure 8b** and **Figure 8c** give the corresponding numeric values for the two variants. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the fledgling number used was half the total annual production of fledglings, assuming a 1:1 sex ratio. Note also that the fertility terms (F_i) in the top row of the matrix include both a term for fledgling production (m_i) and a term for the survival of the mother (P_i) from the census (just after the breeding season) to the next birth pulse almost a year later. The population

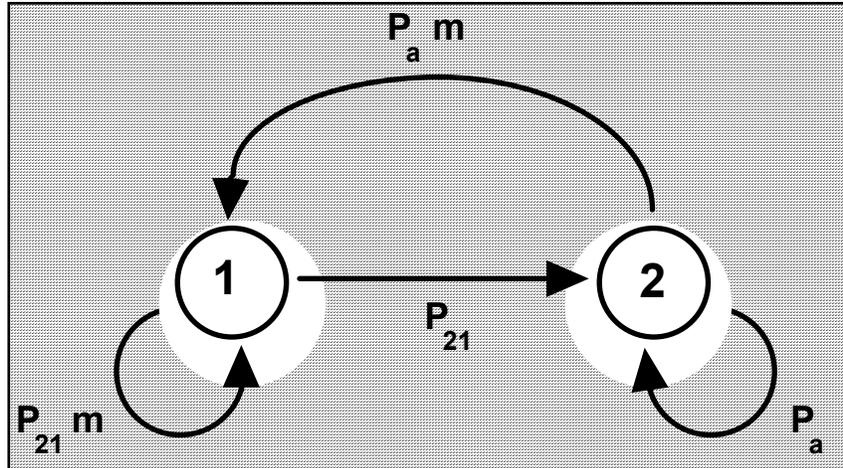


Figure 7. Life cycle graph for McCown’s longspur. The numbered circles (“nodes”) represent the two stages (first-year birds and “adults”). The arrows (“arcs”) connecting the nodes represent the vital rates – transitions between age-classes such as survival (P_{ji}) or fertility (the arcs pointing back toward the first node).

Table 3. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for McCown’s longspur.

Parameter	Numeric value	Interpretation
M	0.765	Number of female fledglings produced by a female
P_{21}	0.57 or 0.35	First-year survival rates under the two variants
P_a	0.57 or 0.74	Survival rate of “adults” under the two variants

	1	2
1	$P_{21}m$	$P_a m$
2	P_{21}	P_a

Figure 8a. Symbolic values for the projection matrix of vital rates, A (with cells a_{ij}) corresponding to the McCown’s longspur life cycle graph of **Figure 7**. Meanings of the component terms and their numeric values are given in **Table 1**.

	1	2
1	0.44	0.44
2	0.57	0.57

Figure 8b. Numeric values for matrix Variant 1, assuming equal first-year and “adult” survival rates.

	1	2
1	0.27	0.56
2	0.35	0.74

Figure 8c. Numeric values for matrix Variant 2, assuming low first-year survival rate.

growth rate was 1.006 for both variants, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and it should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on λ of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph [Figure 7] and the cells in the matrix, **A** [Figure 8]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to λ , which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of survival (P_i) and fertility (F_i) transitions. Second,

sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but it could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing (λ) of an endangered species or which are the “weak links” in the life cycle of a pest. **Figure 9** shows the “possible sensitivities only” matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the biologically impossible sensitivity of λ to the transition from Stage 2 “adult” back to being a Stage 1 first-year bird).

	1	2
1	0.433	0.567
2	0.433	0.567

Figure 9a. Possible sensitivities only matrix, S_p for the equal survival Variant 1 matrix (blank cells correspond to zeros in the original matrix, **A**). The population growth rate of McCown’s longspur is most sensitive to changes in “adult” survival and fertility (Cell s_{22} = Cell s_{12} = 0.567).

	1	2
1	0.266	0.348
2	0.561	0.734

Figure 9b. Possible sensitivities only matrix, S_p for the low first-year survival Variant 2 matrix (blank cells correspond to zeros in the original matrix, **A**). Under this variant, the population growth rate of McCown’s longspur is most sensitive to changes in “adult” survival (Cell s_{22} = 0.734) followed by changes in first-year survival (Cell s_{21} = 0.561).

The summed sensitivity of λ to changes in survival is equal to that for changes in fertility under the equal survival Variant 1 model ($P_{21} = P_a = 0.57$). Under the lower first-year survival model ($P_{21} = 0.35$ vs. $P_a = 0.74$) of Variant 2, survival is of greater importance (68 percent of the total sensitivity). Under either variant, “adult” survival is of considerably greater importance than is first-year survival (**Figure 9**). The major conclusion from the sensitivity analysis is that adult survival rates (both variants) or adult fertility rates (Variant 1) are most important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 percent to 40 percent). On the other hand, an absolute change of 0.5 in fertility may be a very small proportional

alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1 percent). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for McCown’s longspur are shown in **Figure 10**. The population growth rate was most elastic to changes in “adult” survival for both variants ($e_{22} = 32$ percent [Variant 1] or 54 percent [Variant 2] of total elasticity on arc P_{22} , the self-loop from the second node back to the second node in **Figure 7**). Next most elastic were first-year survival and “adult” reproduction ($e_{12} = e_{21} = 24.6$ percent [Variant 1] or 19.5 percent [Variant 2] of total elasticity). Least important was reproduction by first-year birds (18.8 percent or 7.1 percent respectively of total elasticity). The sensitivities and elasticities for McCown’s longspur were generally consistent in emphasizing “adult” transitions with the elasticities strongly emphasizing adult survival. Thus,

“adult” transitions, particularly survival rates, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable age distribution (SAD, **Table 4**) describes the proportion of each age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary, or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For McCown’s longspur at the time of the post-breeding annual census (just after the end of the breeding season), fledglings represent 43.3 percent of the population (regardless of model variant used). Reproductive values (**Table 5**) can be thought of as describing the value of a stage as a seed for population growth relative to that of the first (newborn or, in this case, fledgling) stage (Caswell 2001). The reproductive value of the first stage is always 1.0. An “adult” female individual in Stage 2 is “worth” 2.1 fledglings under the low first-year survival model of Variant 1, but only as valuable as a fledgling (1.0) under the equal survival Variant 1. The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The “adult” females are important stages in the life cycle. The cohort generation time for this species was 2.3 years (SD = 1.8 years) under Variant 1 and 3.8 years (SD = 3.3 years) under the low first-year survival Variant 2.

	1	2
1	0.188	0.246
2	0.246	0.321

Figure 10a. Elasticity matrix, **E** (remainder of matrix consists of zeros) for the equal survival Variant 1 matrix. The population growth rate of McCown’s longspur is most elastic to changes in “adult” survival ($e_{22} = 0.321$), followed by second-year fertility and first-year survival ($e_{12} = e_{21} = 0.246$).

	1	2
1	0.071	0.195
2	0.195	0.538

Figure 10b. Elasticity matrix, **E** (remainder of matrix consists of zeros) for the low first-year survival Variant 2 matrix. The population growth rate of McCown’s longspur is most elastic to changes in “adult” survival ($e_{22} = 0.538$), followed by second-year fertility and first-year survival ($e_{12} = e_{21} = 0.195$). Under this variant, first-year reproduction is relatively unimportant.

Table 4. Stable age distribution (right eigenvector). At the census, 43 percent of the individuals in the population should be fledglings. The rest will be older “adult” females in their second year or older.

Stage	Description	Proportion	Mean age (\pm SD) Variant 1	Mean age (\pm SD) Variant 2
1	Fledglings (to yearling)	0.433	0 \pm 0	0 \pm 0
2	“adult” females	0.567	2.3 \pm 1.7	3.8 \pm 3.2

Table 5. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive value (second-year females) is highlighted.

Age Class	Description	Variant 1 (equal survival)	Variant 2 (low first-year survival)
1	Fledglings/first-year females	1.0	1.0
2	“Adult” females	1.0	2.15

Stochastic model

We conducted a stochastic matrix analysis for McCown’s longspur. We incorporated stochasticity in several ways (**Table 6**), by varying different combinations of vital rates, by varying the amount of stochastic fluctuation, and by varying the “base matrix” (the equal survival or low first-year survival variants of **Figure 8**). We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation we used a standard deviation of

one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Under Case 1 we subjected both the fertility arcs (F_{11} and F_{12}) to high levels of stochastic fluctuations (SD one quarter of mean) using the equal survival Variant 1 matrix. Under Case 2 we varied both the survival arcs (P_{21} and P_{22}) with high levels of stochasticity (SD one quarter of mean), again with the Variant 1 matrix. Under Case 3 we again varied survival with high levels of stochastic fluctuation, but using the low first-year survival Variant 2 matrix. Case 4 varied survival with the low first-year survival Variant 2 matrix, but with only half the stochastic fluctuations

Table 6. Results of four cases of different stochastic projections for McCown’s longspur. Stochastic fluctuations have the greatest effect when acting on survival rates for the low first-year survival variant (Case 3).

Input/Output Factors	Case 1 (Variant 1)	Case 2 (Variant 1)	Case 3 (Variant 2)	Case 4 (Variant 2)
<u>Input factors:</u>				
Affected cells	F_{11} and F_{12}	P_{21} and P_a	P_{21} and P_a	P_{21} and P_a
S.D. of random normal distribution	1/4	1/4	1/4	1/8
<u>Output values:</u>				
Deterministic λ	1.006	1.006	1.006	1.006
# Extinctions/100 trials	0	1	70	0
Mean extinction time	N.a.	1,302	1,100	N.a.
# Declines/# surviving populations	7/100	37/99	22/30	5/100
Mean ending population size	2.0×10^8	7.7×10^7	2.0×10^9	1.4×10^8
S.D.	1.3×10^9	5.2×10^8	1.1×10^{10}	4.6×10^8
Median ending size	2.3×10^6	59,831	592	6.2×10^6
Log λ_s	0.0025	0.001	-0.0079	0.0028
λ_s	1.0025	1.001	0.9921	1.0028
percent reduction in λ	0.33	0.49	1.35	0.29

(SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the SAD under the deterministic model. Beginning at the SAD helps to avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $\log \lambda_s$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table 6**) produced two major results. First, only high variability on survival rates using the low first-year survival Variant 2 matrix had strong detrimental effects. For example, 70 of 100 runs led to extinctions with stochasticity affecting both survival rates and acting on the low first-year survival matrix (Case 3). The next greatest effect came from varying the survival rates for the equal survival Variant 1 matrix (Case 2). The difference in the effects of which arc was most important is predictable largely from the elasticities. The population growth rate was most elastic to changes in survival, especially under the low first-year survival variant. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model – the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. Second, the magnitude of stochastic fluctuation has a discernible effect on population dynamics (compare Variants 3 and 4 in **Table 6**). With low level of stochastic variation directed at the low first-year survival variant, no populations went extinct, although 5 of 100 underwent declines (vs. 70 extinctions and an additional 22 declines under the high stochasticity case). These results indicate that populations of McCown’s longspur are somewhat vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance), especially when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. McCown’s longspur, however, may have little flexibility in reducing

variability in first-year survival. Variable early survival is likely to be the rule rather than the exception.

Potential refinements of the models

Clearly, data on survival rates are needed in order to increase confidence in any demographic analysis. The most important “missing data elements” in the life history for McCown’s longspur are for survival rates, which emerge as vital rates to which λ is sensitive as well as most elastic. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Using observed correlations would improve on our “uncorrelated” assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models:

- ❖ Survival accounts for 50 percent of the total “possible” sensitivity under the equal survival Variant 1 matrix, and as 67.8 percent of the total under the low first-year survival Variant 2 matrix. Any absolute changes in survival rates will have major impacts on population dynamics.
- ❖ Survival (P_{21} and P_{22}) account for 56.7 percent (equal survival variant) or 73.8 percent (low first-year survival variant) respectively of the total elasticity. Proportional changes in first-year and especially in “adult” survival will have a major impact on population dynamics.
- ❖ The reproductive value of “adult” females is relatively low under the equal survival variant and higher under the low first-year survival variant. In the latter case, the higher reproductive value of “adults” makes them possible buffers against the detrimental effects of variable conditions.

- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in survival to population dynamics. In comparison to life histories of other vertebrates, McCown's longspur appears slightly less vulnerable to environmental stochasticity (because of the buffering effect of a reservoir of "adult" females and because of the relatively even importance of different vital rates, as assessed by the sensitivities and elasticities).

Ecological influences on survival and reproduction

Within suitable breeding habitat, breeding densities may not be limited by space or food availability. McCown's longspurs did not saturate available breeding habitat in a Wyoming study (Greer and Anderson 1989), and territory size remained constant from year-to-year, despite a 169 percent increase in the number of territories. Neither territory size nor population density was related to prey productivity, suggesting that the habitat was unsaturated. Because nesting success was not related to arthropod productivity and there was only a subtle relationship with vegetation features, Greer and Anderson (1989) concluded that predation, rather than food resources, limits productivity in this Wyoming population. The severe and unstable climate during the breeding season is thought to be responsible for eroding the normally close coupling of arthropod abundance with vegetation. Features other than prey abundance and territory-wide vegetation characteristics may drive habitat selection in longspurs, including microclimate at the nest, predation risk, and more efficient foraging in certain microhabitats (Martin 1986).

Populations may be regulated by weather and nest site microclimate, especially at the beginning of the season. In Saskatchewan, initial territories are often on southern exposures of barren hillsides where the ground temperatures are higher and ground moisture is less (Felske 1971). Later in the season, when temperatures are warmer and the ground is drier, male longspurs set up territories in flatter, more heavily vegetated areas.

Spacing, defense and size of area, and population regulation

McCown's longspurs territories are discrete and are aggressively defended by males against conspecific males and sometimes other females (With 1994a). Pairs nest and generally forage within territory boundaries, although individuals occasionally make long flights

from territories, possibly for water (With 1994a); others doubt that these flights are for either water or food (Mickey 1943). Birds are not territorial during the winter, as flocks form after the breeding season and are reported on the wintering grounds (With 1994a). The role that dominance hierarchies may play in the settlement of males on the breeding grounds is unknown. Pairs often nest in close proximity (Mickey 1943, Felske 1971).

Territory area requirements of McCown's longspurs vary by region. Territory size ranges from 0.6 ha in southeastern Wyoming ($n = 74$; Greer and Anderson 1989), 0.5 to 1.0 ha in Saskatchewan (Felske 1971), and 1.1 to 1.4 ha ($n = 14$; Wiens 1970, 1971) and 0.93 ha ($n = 20$) on the Pawnee National Grassland in Colorado (With 1994a). In southeastern Wyoming, an increase in density of breeding pairs between years did not cause territory size to decrease, suggesting that there is an optimal limit to territory size (Greer 1988). Renests and second brood nests are generally placed near earlier nests (Mickey 1943). The average distance between first and subsequent nests on the Pawnee National Grassland was 30.4 ± 15.7 m ($n = 16$ territories; With 1994a).

Dispersal

Young disperse on fledging and do not necessarily associate with siblings. Adults may divide broods, with parents sequentially feeding particular offspring or being pursued by a subset of a brood (With 1994a). Immature birds flock with adults at the end of the breeding season and migrate with them to the wintering grounds. Young birds apparently do not return to natal breeding areas, as extensive banding of nestlings ($n = 74$) on the Pawnee National Grassland has failed to document any returns (With 1994a). Juveniles either disperse widely from natal breeding grounds and/or suffer high mortality. Evidence of adult site tenacity is scant. Two adult females banded on the Pawnee National Grassland were not seen in following years. Two males in this study did return to the same pasture where they were banded, but they occupied different territories (Ryder 1972).

Source/sink, demographically linked populations

There is no evidence of source-sink dynamics in this species. Because there have been no long-term studies of marked populations and no recoveries of banded individuals, there is no information on the possible linkage of populations or metapopulation dynamics.

Factors limiting population growth

Weather rarely results in total nest failure for McCown's longspurs, but it may reduce clutch size early in the breeding season if the ground becomes saturated and the eggs become chilled (With 1994a). Most (73.3 percent) of the egg loss during a cold, wet spring in Colorado was related to egg chilling rather than to predation ($n = 15$ nests suffering clutch reductions; With 1994a). Nestlings are also susceptible to temperature extremes. Mickey (1943) reported nestling mortality after rain showers in a Wyoming study, and in Colorado six brood reductions out of 77 nests were attributed to wet and cold weather (With 1994a). The impact of climate on prey abundance and availability and the local absence of longspurs during wet years may influence population growth (Bent 1968, With 1994a).

Predation rates on eggs and nestlings are "generally high" (With 1994a). On the Pawnee National Grassland, 38 percent of nests were depredated in the early 1970s (Strong 1971), and 65.6 percent ($n = 32$) and 45.7 percent ($n = 46$) were depredated in 1990 and 1991, respectively (With 1994a). In Wyoming, predators accounted for the failure of 51 percent ($n = 73$ nests) of all nests (Greer and Anderson 1989). In Saskatchewan, egg predation was 19 to 23 percent, and about 30 percent of nestlings were taken (Felske 1971). In another Saskatchewan study, 72 percent of egg mortality and 80 percent of nestling mortality were attributable to predation (Maher 1973). Predation rates may vary within season; 30 percent of nests were depredated before July, and 60 percent were lost to predators after July in Saskatchewan (Felske 1971).

Fragmentation of shortgrass prairie is a problem that is as potentially severe as the conversion of shortgrass prairie to agricultural lands. Fragmentation isolates populations, increases the likelihood of local extinctions, decreases the probability of colonization, and genetically isolates populations, leading to increased probabilities of inbreeding and genetic drift, and lowering genetic diversity. Fragmentation can potentially turn continuous populations into "metapopulations of semi-independent demes" that gradually disappear (Risser 1996).

Community ecology

Predators and habitat use

In a Colorado study, nests in a heavily grazed pasture (60 percent of annual aboveground primary production consumed by cattle) always suffered higher

predation rates (75 percent in 1990 [$n = 12$ nests], 50 percent in 1991 [$n = 18$]) than those in a moderately grazed (40 percent of annual aboveground primary production consumed by cattle) pasture (60 percent in 1990 [$n = 20$]; 42.9 percent in 1991 [$n = 28$]) (With 1994a). However, reproductive success (percent young fledged per number of eggs laid) tended to be higher on the heavily grazed areas (36.7 percent) than on the moderately grazed area (31.9 percent) (With 1994b).

Nests placed near shrubs were two to three times more likely to be depredated than nests associated with short grass, cactus, or mid-grass; 75 to 80 percent of nests placed near shrubs were depredated compared to 52.6 percent ($n = 78$) of all nests (With 1994b). Nests that were successful in producing young had no measurable shrub cover within 1 m. Nests associated with shrubs were thought to be at higher risk of incidental predation by thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) because squirrel activity is concentrated near shrubs (With 1994b).

Known predators of McCown's longspurs include thirteen-lined ground squirrels, short-eared owls (*Asio flammeus*), Swainson's hawks (*Buteo swainsoni*), and loggerhead shrikes (*Lanius ludovicianus*) (Dubois 1937, With 1994a). Suspected predators include Richardson's ground squirrels (*Spermophilus richardsonii*), Wyoming ground squirrels (*S. elegans*), white-tailed prairie dogs (*Cynomys leucurus*), badgers (*Taxidea taxus*), striped skunks (*Mephitis mephitis*), red fox (*Vulpes vulpes*), swift fox (*V. velox*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), and bullsnakes (*Pituophis melanoleucus*) (Dubois 1937, Mickey 1943, Greer and Anderson 1989, With 1994a). In Saskatchewan, egg losses were attributed to deer mice (*Peromyscus maniculatus*), and American crows (*Corvus brachyrhynchos*) were implicated as the major nest predator (Felske 1971). Adult mortality during the breeding season is probably negligible. Felske (1971) reported that adults appeared "to suffer no losses" in a Saskatchewan study.

Competitors (of breeding sites, food) and habitat use

Other species that may use habitat in a similar way and respond similarly to threats, management, and conservation activities include the mountain plover, horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), chestnut-collared longspur, and Sprague's pipit (*Anthus spragueii*). McCown's longspurs join in interspecific flocks in winter with horned larks, Lapland longspurs (*Calcarius*

lapponicus), and Sprague's pipits (Bent 1968, Grzybowski 1982). Breeding McCown's longspurs may occasionally defend their territory or nest against other species, e.g., by chasing lark buntings or horned larks foraging near the nest or encountered within the territory (With 1994a). However, competition may not be an important limiting factor, as Greer (1988) observed high territorial overlap among McCown's and chestnut-collared longspurs and horned larks, and a scarcity of interspecific aggression.

Food habits of McCown's longspur overlap to some extent with those of chestnut-collared longspurs, although chestnut-collared longspurs prefer more mesic habitats and taller vegetation than McCown's longspurs (With 1994a). In Colorado, grasshoppers and beetles comprised 47 percent and 37 percent of the nestling diet by dry weight of McCown's longspurs, and 57 percent and 31 percent, respectively, for chestnut-collared longspurs. Horned larks mostly fed beetles to nestlings (49 percent dry weight; Creighton and Baldwin 1974). In Saskatchewan, grasshoppers comprised 62 to 85 percent, 71 to 75 percent, and 27 to 48 percent of the total diet of McCown's longspurs, chestnut-collared longspurs, and horned larks, respectively (Maher 1974a). The overlap between McCown's and horned larks was greater in July and August, when grasshoppers comprised 80 to 95 percent of McCown's and 68 to 85 percent of horned larks' diet.

The status of McCown's longspur as a host of the brown-headed cowbird (*Molothrus ater*) is not well known (Friedmann 1963, Maher 1973), but no parasitism was observed or mentioned in studies in Colorado (With 1994a), Saskatchewan (Maher 1973), Wyoming (Mickey 1943), or Montana (DuBois 1935, 1937), or in four years of nest monitoring on the Pawnee National Grassland (Dillon personal communication 2004).

Parasites and disease

In Wyoming, ants were "omnipresent" at longspur nests, and a female was observed picking them from nestlings and from the nest. There is no other information on disease or parasite loads for this species.

Envirogram of ecological relationships

The envirogram emphasizes the effects of weather (especially rainfall), humans, and topography on McCown's longspur resource availability, fecundity, survival, phenology, and predation and competition

(**Figure 11**). Climate affects vegetation growth and physiognomy, which in turn is mediated by human impacts of grazing and prairie dog control, which affects longspur food resources and cover. Humans, via oil and gas development, grazing, pesticides, and fire, can severely alter the vegetation, both directly and by fragmenting habitats, which can affect longspur fecundity, survival, and distribution, both on the summering and wintering grounds. Topography, via climate, mediates vegetation structure, which influences both microhabitat and food resources and the abundance and distribution of predators and competitors.

CONSERVATION

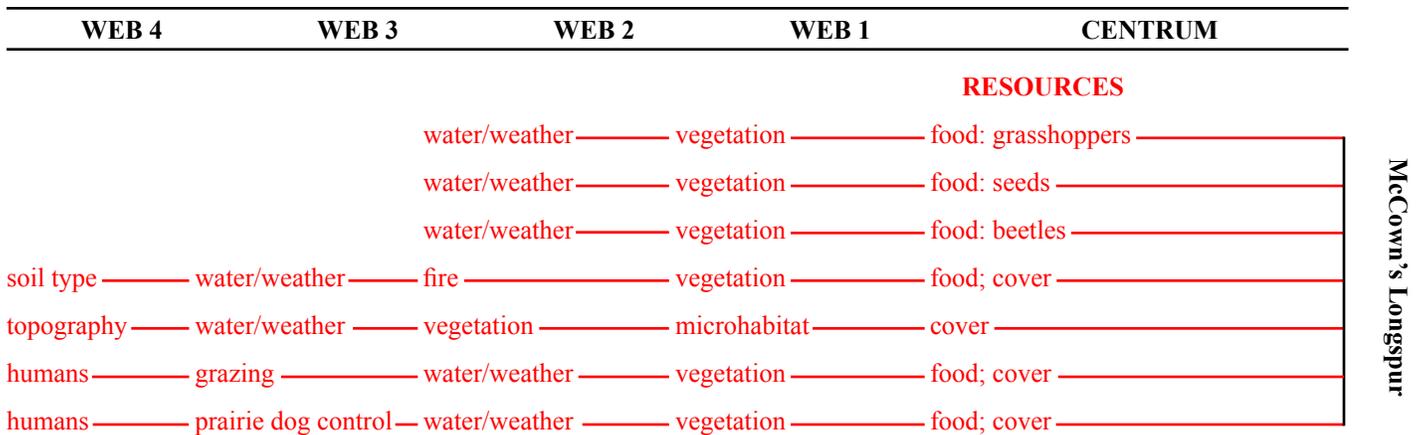
Threats

Each of the threats below is considered only at the local, site-specific scale. Such site-specific threats are not likely to affect population viability across Region 2. It should be understood that larger scale, region wide threats or levels of disturbance, and the accumulation of threats or land use changes over time may constitute a major, negative impact on McCown's longspur populations (Theobald et al. 1997).

Livestock grazing

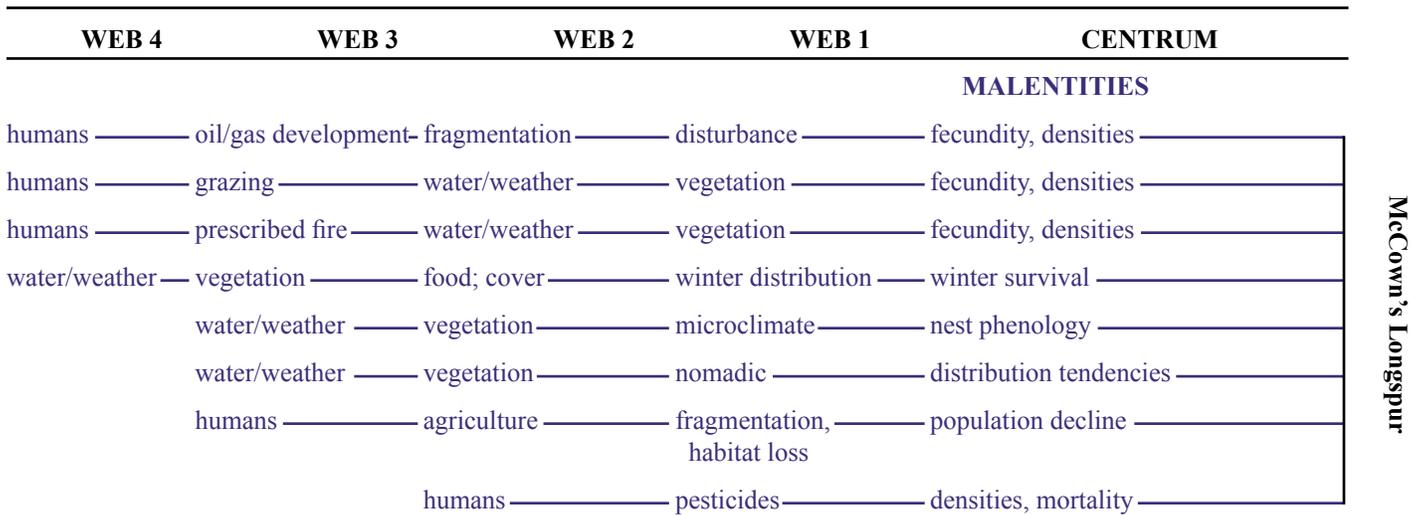
McCown's longspurs are not, with certain exceptions, negatively impacted by grazing. They breed in short grass, especially where vegetation coverage is sparse due to grazing or low soil moisture. In fact, they often prefer to breed in heavily grazed areas (Bradley personal communication) and may respond positively to livestock grazing (Bock et al. 1993). Ryder (1980), for example, found higher densities of this species on heavily grazed pastures than on less intensely grazed ones, and summer-grazed areas were preferred over winter-grazed areas in Colorado shortgrass prairie (Giezentanner and Ryder 1969, Giezentanner 1970a and b, Wiens 1970).

Overgrazing in arid, sparse shortgrass habitats, however, may be detrimental to McCown's (Oberholser 1974, Ryder 1980). Nests in a heavily grazed pasture (60 percent of annual aboveground primary production consumed by cattle) in Colorado always suffered higher predation rates than those in a moderately grazed (40 percent of annual aboveground primary production consumed by cattle) pasture, but reproductive success nevertheless tended to be higher on the heavily grazed area (With 1994b). Grazing as an impact also varies according to soil type. In Montana, Wyoming, Colorado, and Nebraska, for example, McCown's prefer heavily



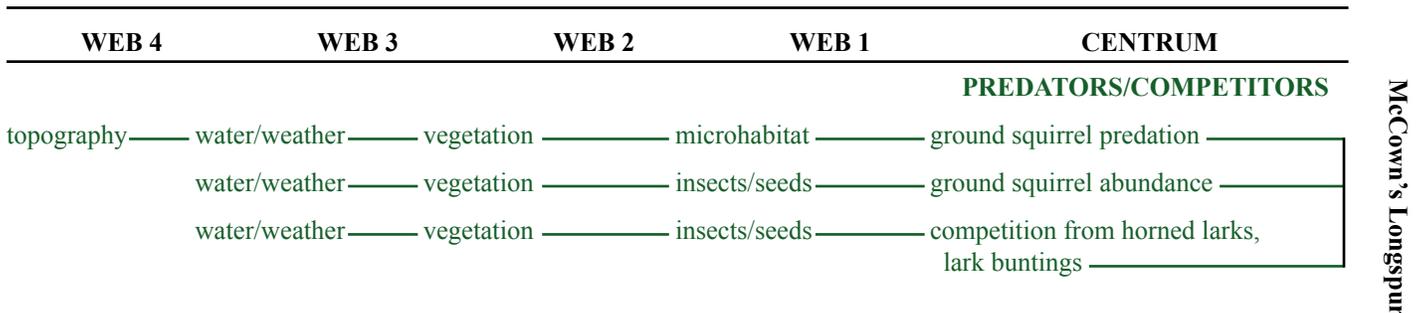
McCown's Longspur

Figure 11a. Resources centrum for the McCown's longspur envirogram.



McCown's Longspur

Figure 11b. Malentities centrum for the McCown's longspur envirogram.



McCown's Longspur

Figure 11c. Predators/competitors centrum for the McCown's longspur envirogram.

grazed areas with aridic boroll soils, but they prefer only moderately grazed areas with aridic ustoll soils (Kantrud and Koligiski 1982).

Oil and gas exploration

Oil and gas exploration can negatively impact wildlife through loss or fragmentation of habitat (well pads, roads, pipelines, storage tanks, power lines, compressor and pumping stations), disturbance (drilling, vehicle traffic), or environmental contamination. New construction for oil and gas exploration—and wind-power development and water well drilling—has intensified in recent years. In the Powder River Basin of western Wyoming, for example, 15,811 oil and gas wells have been approved, and an additional 65,635 are being considered to potentially develop oil and gas reservoirs (Connelly et al. 2004). Habitat loss to such activities has obvious negative impacts on McCown's populations. Secondary impacts have been reported for other species. Ingelfinger (2001), for example, found that roads associated with natural gas development in sagebrush steppe reduced the guild of sagebrush obligates by 50 percent within 100 m of roads. Lyon and Anderson (2003) reported lower rates of greater sagegrouse (*Centrocercus urophasianus*) nest initiation in areas disturbed by the vehicle traffic associated with gas wells. Although there have been no specific studies of the disturbance, environmental contamination, or fragmentation effects of oil and gas activities on longspurs, these are likely negative (Knopf 1996).

Commercial, recreational, scientific and educational threats

The sensitivity of individual McCown's longspurs to human presence near the nest is largely unknown. Some individual (foraging) longspurs permit approach to a distance of 5 to 10 m whereas others flush when approached to within 25 m (With 1994a). DuBois (1935) reports that longspurs are tenacious at the nest site and that they may stay at, or even allow themselves to be lifted off of the nest by an observer, at least during inclement weather (With 1994a). Keeping incubating females from the nest >15 minutes during the construction of nest exclosures during the early part of the breeding season resulted in the partial or total death of clutches (With 1994a). Nest desertion, possibly due to human disturbance, has been suggested by Strong (1971), who observed that 13 percent ($n = 53$) of nests were deserted (Colorado), and by Felske (1971) who reported that 10.8 percent of eggs and 7.5 percent of nestlings that were abandoned in a Saskatchewan

study were due to human interference. Recreation is increasing in Region 2 (USDA Forest Service 2002), and the negative effects of recreation on bird species composition and nest placement in both forests and grasslands have recently been documented (e.g., Miller et al. 1998). Although McCown's sensitivity to human recreational activities is uncertain, nest desertion, altered nest placement, and lower feeding rates of young by adults are likely, depending on the intensity and duration of recreation.

Application of chemicals

Pesticide application may pose a significant threat in local areas within the breeding range. The Plant Protection Act authorizes USDA-APHIS-PPQ to cooperate with federal land management agencies, state agencies, and private landowners to control various insect pest populations on western rangelands. During grasshopper outbreaks, USDA cooperative grasshopper control programs have treated as much as 13.1 million acres (5.3 million ha) of rangeland in a single season (USDA Animal and Plant Health Inspection Service 1987). Although the long-term effects on McCown's longspurs have not been investigated, application of the insecticide toxaphene (chlorinated camphene, combined chlorine content 67 to 69 percent) that was sprayed on 14 June at the rate of 1 lb. per acre (1.12 kg per ha) on a 38.5 acre (15.6 ha) plot on the Pawnee National Grassland resulted in direct poisoning of nestling longspurs (McEwen and Ells 1975). Application of malathion (95 percent O, O-dimethyl phosphorodithioate of diethyl mercaptosuccinate) sprayed at the rate of 8 oz. per acre (560 g per ha) did not produce a similar reduction in population size.

In addition to direct mortality, pesticide applications may also result in reduced food delivery rates, lowered avian densities, and depressed brain acetylcholinesterase activities (Martin et al. 2000). Numbers of the closely related chestnut-collared longspur declined between pre-spray and post-spray censuses with the application of BAY 77488 (phenylglyoxylonitrile oxime O,O-diethyl phosphorothioate), Baygon (*o*-isopropoxyphenyl methylcarbamate), and fenitrothion (O,O-dimethyl O-[4-nitro-*m*-tolyl] phosphorothionate) on rangelands in Wyoming and Montana (various application rates), and total numbers of grassland birds (including longspurs) declined with the application of diazinon (O,O-diethyl O-[2-isopropyl-4-methyl-6-pyrimidinyl] phosphorothionate) (McEwen 1972). Direct mortality due to insecticide spraying was documented for chestnut-

collared adults and/or nestlings on plots sprayed with Baygon and diazinon, and for other grassland birds on plots sprayed with BAY 77488 and fenitrothion.

In an Alberta study of chestnut-collared longspurs, Martin et al. (1998) reported that the application of Decis 5F, a broad spectrum pyrethroid, (1) did not reduce overall biomass fed to nestlings; (2) did not affect the weight of nestlings at fledging; (3) did not reduce clutch size or nestling survival; (4) did result in lower hatching success; and (5) did cause a switch from grasshoppers to alternate insect prey to feed nestlings. In a study of the effects of Decis 5F and Furadan 480F (a carbamate) on chestnut-collared longspurs, Martin et al. (2000) reported that: (1) neither insecticide resulted in a decrease in biomass delivered to nestlings; (2) neither insecticide affected nestling weight or size; (3) neither insecticide affected the number of eggs, nestlings, or fledglings produced per nest; (4) the number of grasshoppers in nestling diets was significantly reduced in Decis-sprayed plots; (5) by two weeks after spraying, adults were foraging almost twice as far from their nests as were birds in control plots to maintain prey delivery rates ($P < 0.05$), and; (6) brain acetylcholinesterase was significantly reduced in most Furadan-exposed birds. Seeds treated with fungicides or other chemicals before planting may also pose a threat, as McCown's feed on seeds and grains in agricultural areas during migration and on the wintering grounds (Oberholser 1974).

Fire and fire suppression

Fire was once an important ecological process of shortgrass prairie ecosystems, influencing plant physiognomy, species composition, and productivity (Brockway et al. 2002). Prairie wildfires are smaller and less frequent today because of (1) the reduction of Native American use of fire after about 1875, (2) land use changes and the conversion of grasslands to croplands, (3) active fire suppression (a common management practice throughout much of Region 2 over the last 100 years), and (4) systematic grazing by cattle and sheep, which reduces available fuel levels. The diminished role of fire in the shortgrass prairie is thought to be responsible for the invasion of less fire-tolerant species and changes in plant species composition and diversity (Brockway et al. 2002). At least some of the declines in abundance and distribution of McCown's longspur may be due to the restriction of uncontrolled grass fires that serve to maintain the stature of its shortgrass breeding habitats (Bent 1968, Oberholser 1974).

Prairie dog removal

Indiscriminant removal or eradication of prairie dogs by both the public at large and by federal agencies may adversely impact McCown's longspurs. Because prairie dogs are considered a keystone species, their removal can result in a cascade of changes, resulting in a rapid decline in species diversity. In Colorado, prairie dog colonies occupy <3 percent of current potential habitat and <1 percent of their pre-settlement habitat (Seidl et al. 2001). Whether or not McCown's longspurs specifically prefer the habitat created by prairie dogs is unknown. This is true for the mountain plover, a McCown's breeding season associate, especially in shrubbier habitats where grasses tend to be naturally higher than in pure shortgrass prairie (Knopf personal communication).

Interactions with exotic species

There are no known interactions of this species with either exotic plants or animals, although prairie restoration efforts that seed degraded grasslands with taller, exotic grasses such as crested wheatgrass (*Agropyron cristatum*) may reduce habitat quality for McCown's longspurs (Samson and Knopf 1994).

Conservation Status of McCown's Longspurs in Region 2

Compared to its historical distribution, the breeding range of McCown's longspur has been "drastically" reduced (Bent 1968). This reduction parallels shortgrass prairie losses to agriculture (30.7 percent in Colorado, 78 percent in Kansas, 65.4 percent in Nebraska, and 12.1 percent in Wyoming) (Knopf and Rupert 1999) and concurrent historical observations of declines in wintering populations (Oberholser 1974). Remaining populations show significant increasing BBS trend estimates for the period from 1966 to 2000 in some strata of Region 2 (Wyoming Basin: 7.7 percent annual increase; Wyoming: 7.8 percent increase; both $P < 0.05$; Sauer et al. 2001), and increasing, but insignificant trends in others (Colorado, High Plains, and Great Plains Roughlands physiographic strata, and USFWS Region 6 [includes USFS Region 2 states plus Utah, Montana, and North Dakota]). Despite BBS trend estimates, the Natural Heritage Program's rank for McCown's in the two states in Region 2 where breeding commonly occurs is "vulnerable" (Wyoming) and "imperiled" (Colorado). The Rocky Mountain Bird

Observatory's species monitoring plan (Leukering et al. 2000) lists the population trend of the McCown's longspur as "uncertain" in Colorado. Because of historic declines in numbers prior to the initiation of the BBS, continuing habitat losses to agriculture and development, and concerns over habitat fragmentation, the species is listed as a species of management concern by a variety of conservation organizations (see Management Status and History). Additionally, it has been added to the Regional Forester's Sensitive Species List (Revised 2003).

The McCown's longspur is, in a sense, a habitat specialist—a bird that "responds to not easily discernible environmental changes" (Bent 1968) and that is restricted to shortgrass prairie.

Viability of McCown's could be impaired throughout Region 2 by continued fragmentation of habitats, which have altered natural expanses of shortgrass prairie to a mosaic of pastures variably grazed by cattle and fragmented by agricultural activities and human development (O'Connor et al. 1999). The negative impacts of accelerating oil and gas development are unknown, but associated habitat loss and fragmentation almost certainly impair viability.

An unknown portion of the McCown's historical decline may be related to the removal of native herbivores and the suppression of prairie wildfires. McCown's responds positively to livestock grazing in some situations (Bock et al. 1993), negatively in others.

Because much of the McCown's longspur range falls within Region 2 and because McCown's is restricted to shortgrass prairie, risks in Region 2 parallel continent-wide risks. Continued loss of shortgrass prairie to agriculture and urban expansion, fragmentation of longspur habitats, indiscriminant use of pesticides, prairie fire suppression, and oil and gas development all put the McCown's longspur at risk. Its relatively nomadic nature, however, suggests vagility in terms of natural or anthropogenic habitat disturbances; region wide distributional shifts in both the summer and winter suggest that the species has the capability of moving from regions of unsuitable habitat to more preferable habitats, when necessary.

Management of McCown's Longspurs in Region 2

Implications and potential conservation elements

Consequences of natural events and management

McCown's longspurs of the shortgrass prairies evolved under intense, but uneven grazing by bison (*Bison bison*), pronghorn (*Antilocapra americana*), and prairie dogs, resulting in a heterogeneous, patchy grassland landscape. Annual variations in precipitation and rainfall, and occasional wildfires also impacted the abundance and distribution of longspurs at various geographic scales. In general, prairie management today should mimic the historical natural disturbance regime to take advantage of pre-selected adaptive traits of prairie endemics (Samson and Knopf 1994). However, cattle have replaced bison, prairie dogs occupy 2 percent of their historic area (Summers and Linder 1978), and fire suppression and altered grazing regimes have reduced the frequency and extent of prairie fires on the shortgrass prairie. To conserve McCown's longspurs, land managers should seek to replicate the native, historic shortgrass prairie condition on the breeding and wintering grounds. To achieve this goal, managers have available to them two primary management tools – prescribed fire and grazing by cattle (Bock et al. 1993).

Prioritizing potential management actions; desired environmental outcomes

Preferred environmental conditions. A summary of the environmental conditions preferred by McCown's longspurs includes:

- ❖ shortgrass prairie dominated by buffalograss and blue grama
- ❖ 23 to 66 percent short grass cover
- ❖ 24 to 38 percent bare ground
- ❖ limited cover of mid-grasses and shrubs

- ❖ little litter cover
- ❖ low forb cover
- ❖ an average vegetation height of about 5 cm
- ❖ a preference for heavily grazed areas
- ❖ no tall exotic grasses
- ❖ no trees.

Exotics. Early attempts to rehabilitate grasslands included seeding with exotic crested wheatgrasses imported from Siberia, and planting trees to control wind erosion (implemented by the Civilian Conservation Corp from 1938 to 1941) (Samson and Knopf 1994). Tall exotic grass species do not provide suitable habitat for this McCown's longspurs, and prairie restoration efforts that seeded degraded grasslands with taller, exotic grasses such as crested wheatgrass, may have reduced habitat quality for this species (Samson and Knopf 1994). Trees are not a historical element of the shortgrass prairie landscape. Trees may result in an increase in cowbird parasitism and in predation by providing perches for cowbirds and avian predators such as crows, grackles, and jays.

Prairie dogs. Prairie dog control by both the public at large and by state and federal agencies has reduced prairie dog populations by 98 percent. Considered a keystone species, prairie dogs are thought to influence the entire grassland community either directly or indirectly, including McCown's longspurs. Prairie dog removal can result in a cascade of changes, resulting in a rapid decline in species diversity. There has been no research on whether or not McCown's longspurs specifically prefer the habitat created by prairie dogs. Such preference has, however, been demonstrated for the mountain plover, a McCown's breeding season associate, especially in shrubbier habitats where grasses tend to be naturally higher than in pure shortgrass prairie (Knopf personal communication 2004).

Fire. The fragmentation of the shortgrass prairie by agricultural conversion has prevented uncontrolled wildfires, and those wildfires that do occur are often contained to the smallest area possible (Bent 1968). Little is known about the short- or long-term effects of burning on McCown's longspur habitats and populations, but fire is thought to serve in maintaining

the stature of breeding habitat (Bent 1968, Oberholser 1974). Prescribed burns can be used in shortgrass prairie to remove woody vegetation, cactus, and accumulated litter and to improve grazing conditions for livestock, but the grasses recover slowly, requiring two to three years with normal precipitation (Wright and Bailey 1980). Dormant-season burning may be the preferable method for restoring fire in shortgrass prairie ecosystems where fire has been excluded for a prolonged period of time (Brockway et al. 2002).

Grazing. Grazing management today tends to spread grazing intensity evenly, producing a comparatively homogeneous landscape. PIF recommends grazing short grasses at moderate intensity in the summer, and grazing taller grasses at moderate to heavy intensity. In areas where grass is too tall or thick for McCown's longspurs, grazing can improve habitat by providing shorter, sparser vegetation (Giezantner 1970b, Stewart 1975, Kantrud and Kologiski 1982, Bock et al. 1993). Heavily grazed areas with aridic boroll soils and moderately grazed areas with aridic ustoll soils appear to be ideal longspur nesting habitat in portions of Montana, Wyoming, Colorado, and Nebraska (Kantrud and Kologiski 1982). In Alberta, McCown's longspurs prefer continuously grazed (season-long) native pastures, and they are fairly common in native pastures grazed in early summer (Prescott et al. 1993, Prescott and Wagner 1996). They infrequently occupy spring-grazed (late April to mid-June) pastures of crested wheatgrass, and they avoid deferred grazed (grazed after 15 July) native pastures. In north-central Alberta, McCown's longspurs use moderately to heavily grazed grasslands on sites that are drier and sandier than those used by chestnut-collared longspurs (Wershler et al. 1991). McCown's longspurs nesting in Alberta and Saskatchewan were found to favor season-long grazed native pasture over areas managed with complementary grazing (early-season grazing on crested wheatgrass with cattle rotated through several native-grassland paddocks for the remainder of the summer; Dale and McKeating 1996). McCown's longspurs did not breed on idle mixed-grass prairie in Saskatchewan, and they preferred heavily grazed pastures over lightly or moderately grazed pastures (Felske 1971). Summer-grazed areas were preferred over winter-grazed areas in Colorado shortgrass prairie (Giezantner and Ryder 1969, Giezantner 1970a and b, Wiens 1970). Overgrazing may be detrimental, however, particularly in arid, sparse shortgrass (Oberholser 1974, Ryder 1980).

Tools and practices

Inventory and monitoring of populations and habitat

Broad-scale information on avian population status includes that of the BBS, CBC, and MAPS programs. These have been discussed in the “Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies” section. At a broad geographic scale, the BBS data provide the information necessary to detect continental trends in distribution and long-term changes in abundance. BBS results may be used as a guide to local or regional management decisions, with several caveats. BBS results are often inconclusive due to difficulties associated with the interpretation of index counts (Sauer 2000). Many species (especially less common species) and habitats are inadequately sampled, and these BBS data do not reliably predict population trends at fine geographic scales (Sauer 2000). Because habitat information is not recorded, BBS data have only limited utility for determining avian response to environmental change or management actions. CBC surveys on the wintering grounds (Colorado and Kansas in Region 2, and primarily New Mexico, Texas, and northern Mexico farther south) may provide insight into long-term, wintering-population trends in distribution and in abundance. Annual variation in observer effort and areal coverage within count circles, the participation of inexperienced observers, and inadequate sampling of habitats can compromise the interpretation and limit the utility of CBC data. The more recently established MAPS program, which collects information on avian productivity, survivorship, and distribution, was begun only in 1989, and demographic information is only beginning to become available.

At smaller, regional scales, point count techniques (variable circular plots: e.g., Reynolds et al. 1980, Hutto et al. 1986, Ralph et al. 1995) or line transect count techniques (Burnham et al. 1980) are recommended to detect population changes of McCown’s longspurs in response to management, natural disturbance, or climate change. Only males sing, most often in flight (With 1994a), and thus they are easily detectable. Because of an early spring migration compared to most passerines, and a typical decline in singing and courtship as the breeding season progresses, monitoring activities for this species should begin relatively early. Monitoring could begin shortly after males (about two to three weeks after) and females (about one week after) arrive on the breeding grounds, i.e., Colorado: 3rd week in April; Wyoming and Montana: 2nd week in May; Alberta and Saskatchewan: mid-May. Monitoring

could continue as long as the estimated clutch initiation span (14 weeks), although with declining detectability as more and more pairs fledge young and singing and courtship activities diminish. Both line transect and point count distance sampling data may be analyzed with the Windows-based computer package, DISTANCE (Buckland et al. 2001, Thomas et al. 2002). The territory flush technique (Wiens 1969) and spot mapping (International Bird Census Committee 1970) may also be employed at smaller scales. To monitor breeding productivity, to assess breeding habitat conditions, and to estimate densities at small scales, the BBIRD protocol is often used (Martin et al. 1997). For an overview and details on estimating bird numbers, see Ralph and Scott (1980).

Vegetation and habitat should be characterized in terms of both horizontal and vertical structure. Techniques (see e.g., Rotenberry and Wiens 1980, Wiens 1989) should include estimates of horizontal cover (Daubenmire frames: Daubenmire 1959) and estimates of vertical structure (e.g., Robel et al. 1970) by employing vertical rods (counting vegetation contacts) and cover boards (estimating vertical coverage class values within 5-cm intervals, for example). Horizontal patchiness may be determined by using the coefficient of variation of vertical structure across horizontal distance (variation in vegetation contacts and coverage class values, above; see Rotenberry and Wiens 1980). Long-term avian population monitoring coupled with vegetation data will provide information on long-term avian population trends, habitat relationships, and the effects of land use.

Management tools

The historical impact of grazing by bison, prairie dogs, and pronghorn as an ecological force established the precedent of using cattle grazing manipulations as the primary wildlife habitat management tool to manage shortgrass prairies. The key management goal for McCown’s longspurs is to provide short, sparsely vegetated grassland blocks of adequate size. Mixed-grass areas or areas where the grass is too tall or too thick can be made suitable for breeding McCown’s longspurs by implementing moderate to heavy, or season-long grazing (Dechant et al. 1999). Areas where vegetation is already sparse and short from overgrazing should be protected, especially in areas of low precipitation. Prescribed prairie burns may be appropriate for historically burned areas where fire has been suppressed. New construction for oil and gas exploration, wind-power development, and water well drilling should be restricted during the breeding

season; this is already done in some areas in Colorado, Wyoming, and Utah (Knopf 1996).

Management approaches that address conditions that cause the McCown's longspur to be at risk include:

- ❖ providing areas of adequate size to support multiple McCown's longspur territories (0.5 to 1.5 ha per territory, depending on geographic location), as pairs often nest in loose colonies (Mickey 1943, Wiens 1970, Felske 1971, Greer 1988, Greer and Anderson 1989, With 1994a)
- ❖ providing areas of short, sparse vegetation with little litter and low forb cover (DuBois 1935, Felske 1971, Maher 1973, 1974b, Stewart 1975, With 1994a, Martin *in prep.*)
- ❖ using prescribed burning in late summer or early fall to reduce shrub density and structure in historically burned areas where fire has been suppressed (Bent 1968, Oberholser 1974, With 1994a)
- ❖ protecting rangeland from overgrazing and rehabilitating overgrazed habitats (Oberholser 1974), especially in areas of low precipitation (Ryder 1980)
- ❖ grazing areas where grass is too tall or too thick for breeding McCown's longspurs (Giezantner 1970a and b, Stewart 1975, Kantrud and Kologiski 1982)
- ❖ restoring the inherent heterogeneity of native grazing communities and encouraging larger grazing allotments
- ❖ discouraging prairie dog control, especially on public lands
- ❖ avoiding the establishment of non-native grass species
- ❖ encouraging an increased use of bison to create varied habitat mosaics
- ❖ seeding with native shortgrass species, such as blue grama and buffalograss, when rehabilitating shortgrass prairie

- ❖ seeding CRP lands with native seed, rather than cool-season grasses, to provide additional habitat for shortgrass specialists such as the McCown's longspur (Knopf and Rupert 1999)

- ❖ limiting insect control where McCown's longspurs breed to avoid impacting their primary nestling food base, grasshoppers

- ❖ avoiding fragmentation of shortgrass habitats and seeking opportunities to reduce fragmented habitats where they occur.

Information Needs

Distribution

McCown's longspurs are not adequately sampled in the BBS; the data, especially at finer scales, are too sparse to allow meaningful analysis of regional trends. At a continental scale, long-term population trends on the breeding grounds are less ambiguous. CBC data suggest that wintering ground abundance and distribution are highly variable from year to year, but our knowledge of the mechanisms driving wintering grounds shifts is depauperate.

Species response to habitat change

The influences of landscape factors on reproductive success require more investigation. The consequences of an increasingly fragmented landscape on longspur abundance and reproductive success are virtually unknown. Studies of reproductive success and prey and predator responses in fragments of various sizes are needed. Minimum patch size requirements in different habitat types and physiographic regions within McCown's range are largely unknown. Special emphasis should be placed on the role, effects, and utility of fire and various grazing regimes in rehabilitating and maintaining longspur habitats. In non-native and altered landscapes, the effects of different amounts and species of non-native grasses on longspur reproductive success and pattern of use should be examined. Winter ecology and habitat requirements are largely unknown. Seeding techniques for grassland reclamation, restoration, and enhancement should be developed and tested.

Movement patterns

The extent of natal philopatry and adult site fidelity and dispersal are virtually unknown, limiting our knowledge of population demography.

Prey response to habitat change

Studies of prey response (especially of grasshoppers, a key nestling food) to different grazing regimes, drought and climate change, and prescribed burning are needed.

Demography

Basic information on annual fecundity and lifetime reproductive success is lacking. Long-term studies of marked populations are required for better estimates of recruitment, survival, immigration, and emigration. Genetic studies of small, isolated populations are needed to determine levels of genetic diversity and gene flow.

Population monitoring

Methods to monitor populations are well known (see Tools and Practices, above).

Restoration methods

Restoration methods, including prescribed fire, grazing management, and prairie reclamation are available.

Research priorities in Region 2

The Colorado PIF Bird Conservation Plan (Colorado Partners in Flight 2000) outlines six research priorities for the central shortgrass prairie:

- ❖ the interplay of precipitation, habitat condition, and population distributions at the landscape level
- ❖ the effects of prescribed burning on bird populations
- ❖ the effects of different grazing regimes
- ❖ the identification of key migratory stopover and wintering areas
- ❖ the effects of prairie dog hunting and sport hunting on bird populations
- ❖ patch-size effects and area sensitivity of shortgrass prairie birds.

Additionally, the impacts of new construction for gas and oil exploration, wind-power development, and water well drilling should be investigated.

Additional research

McCown's longspur wintering ecology is poorly understood, as are the historic factors affecting longspurs on their winter range.

DEFINITIONS

Bird Conservation Regions — ecologically distinct regions in North America with similar bird communities, habitats, and resource management issues within which bird conservation efforts are planned and evaluated, as endorsed by the North American Bird Conservation Committee. See [Figure 12](#).

Physiographic Area — Partners in Flight planning units defined on the basis of biotic communities and bird distribution; used in bird conservation planning. See [Figure 13](#).

Physiographic Stratum — Breeding Bird Survey regional areas defined on the basis of similar vegetation, soil, and physiographic features and used in the analysis of bird species' population trends and relative abundance (Robbins et al. 1986). Based on Bailey's ecoregions (Bailey 1993). See [Figure 14](#).

USDA Forest Service Region 2 — Wyoming, Colorado, South Dakota, Nebraska, and Kansas. See [Figure 1](#).

U.S. Fish and Wildlife Service Region 6 (Mountain-Prairie Region) — Wyoming, Colorado, South Dakota, Nebraska, Kansas, Montana, Idaho, and Utah.

U.S. Fish and Wildlife Service Region 2 (Southwest Region) — Arizona, Oklahoma, New Mexico, and Texas.

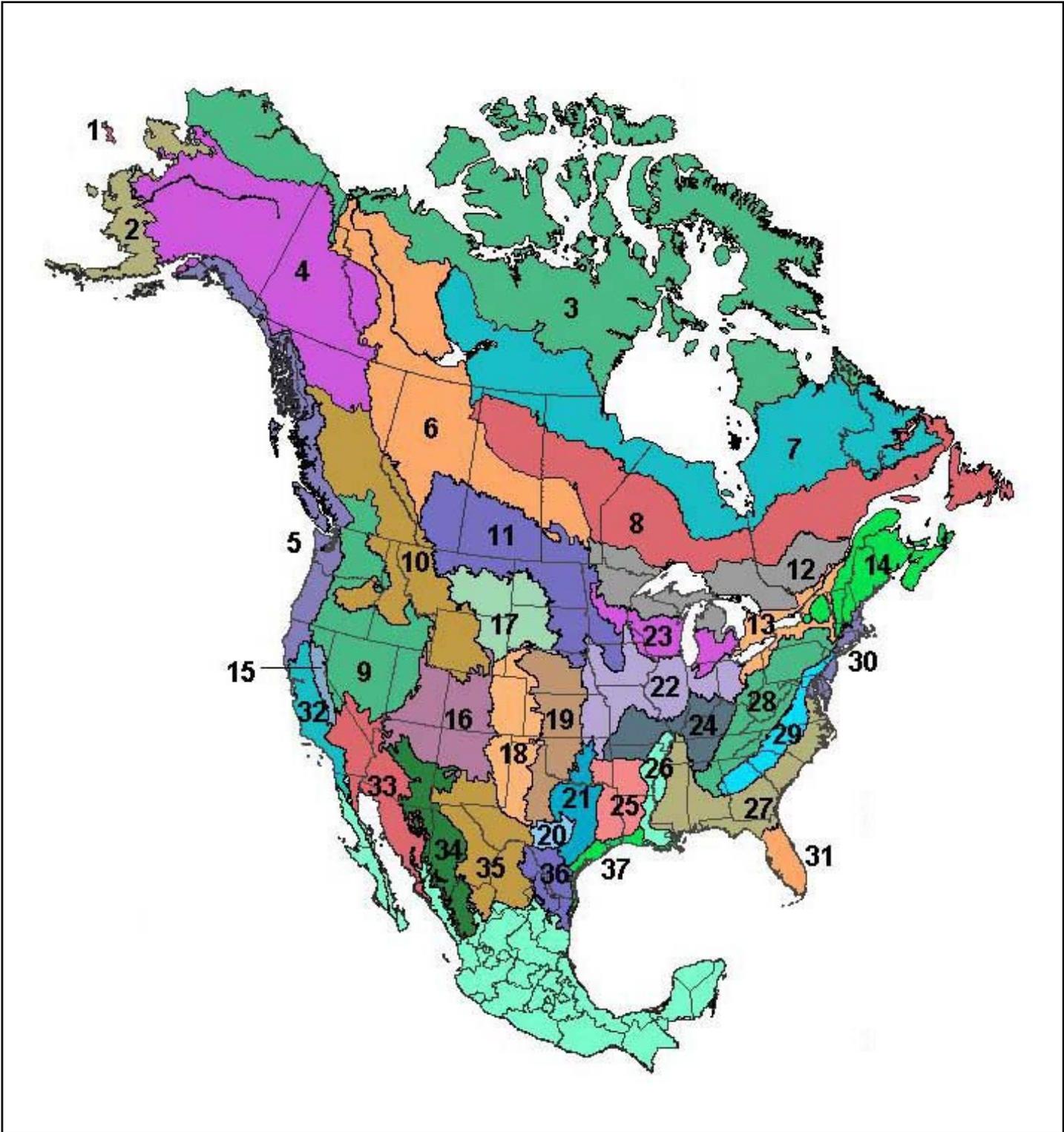


Figure 12. Bird Conservation Regions of the United States. McCown’s longspurs occur in regions 11 (Prairie Potholes), 17 (Badlands and Prairies), and 18 (Shortgrass Prairie).

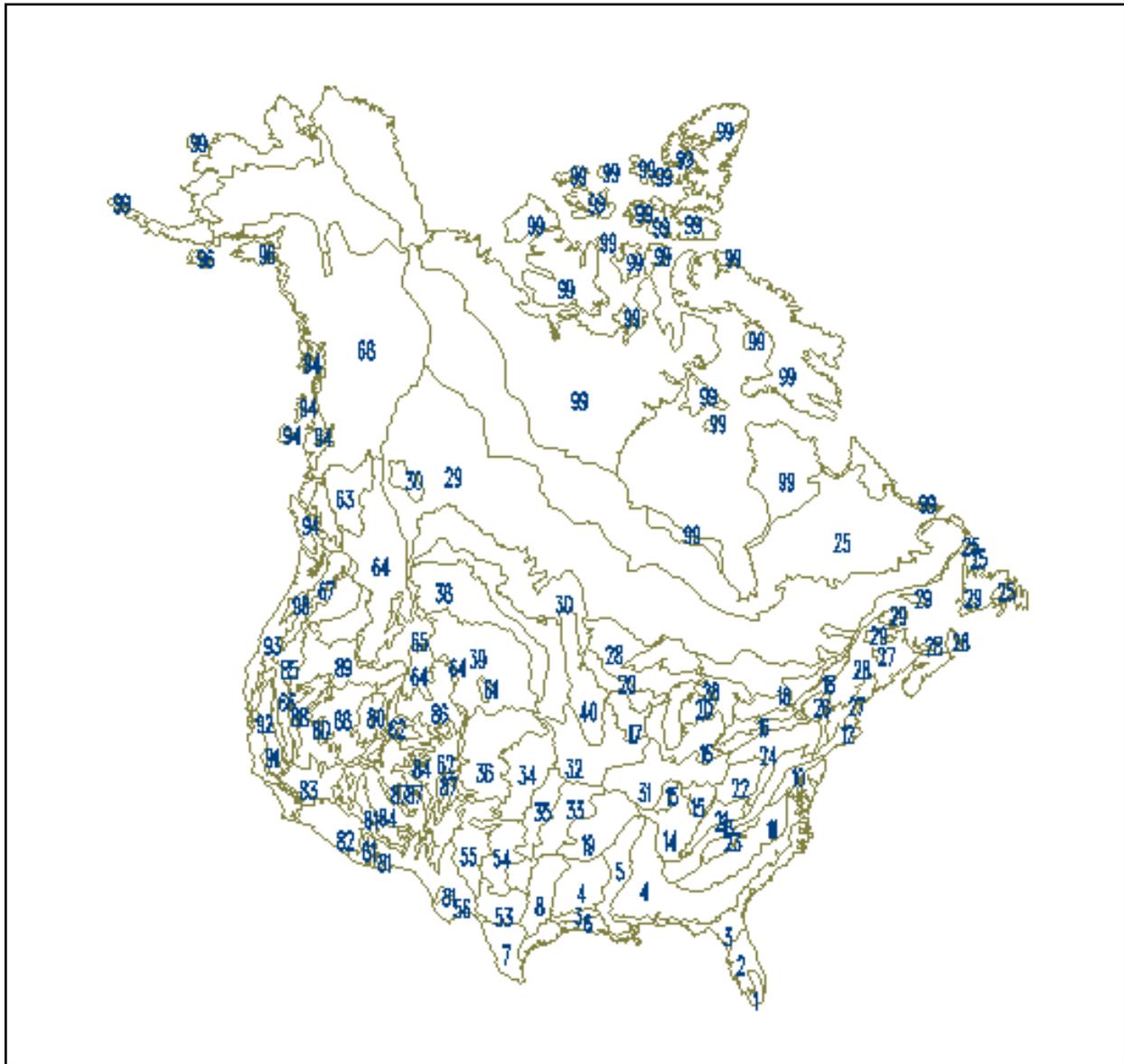


Figure 13. Breeding Bird Survey strata. McCown's Longspurs occur in strata 36 (High Plains), 37 (Drift Prairie), 38 (Glaciated Missouri Plateau), 39 (Great Plains Roughlands), 65 (Dissected Rockies), and 86 (Wyoming Basin).

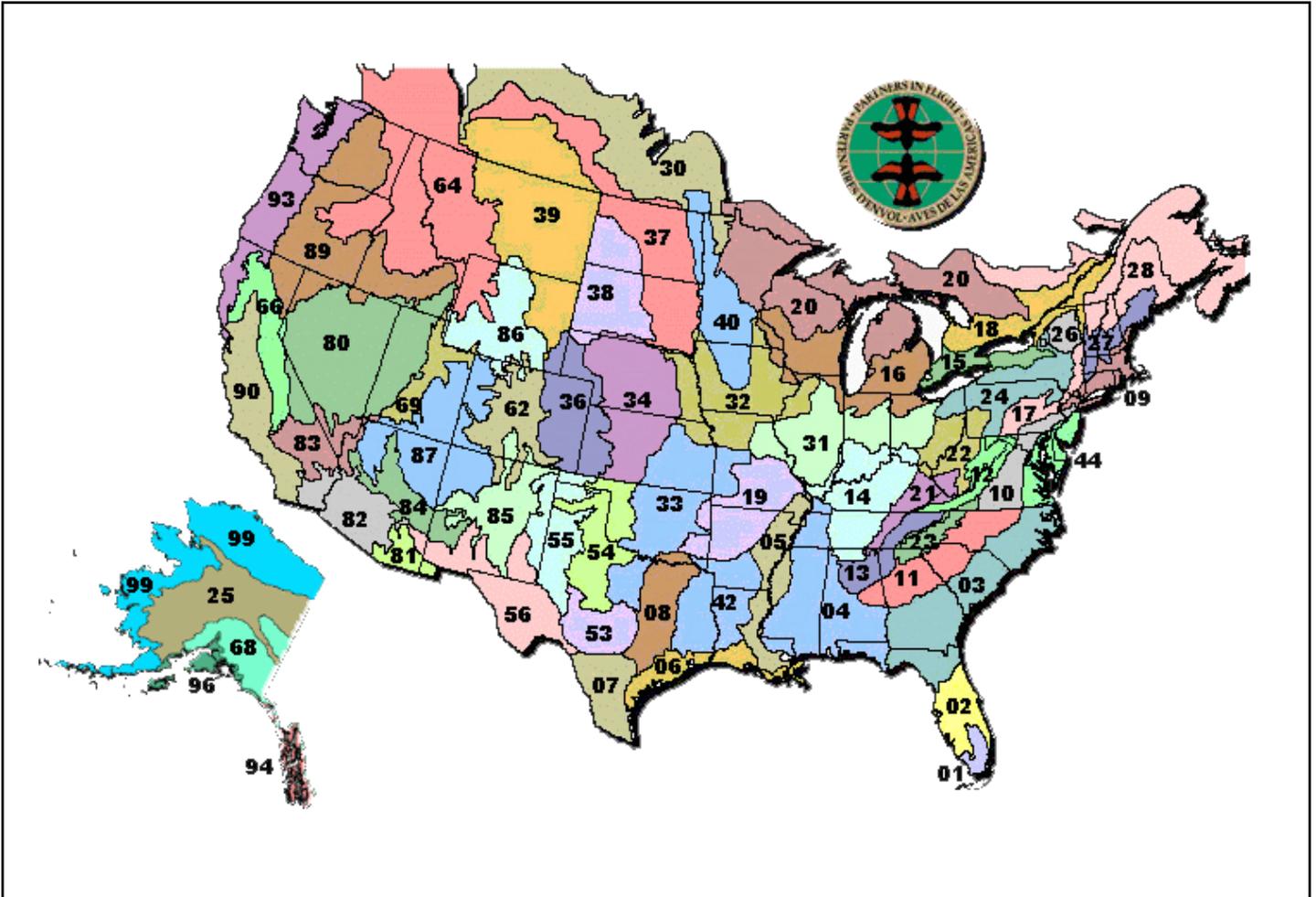


Figure 14. Physiographic Areas, as defined by Partners in Flight. McCown’s longspurs occur chiefly in areas 36 (Central Shortgrass Prairie), 39 (Northern Shortgrass Prairie), and 86 (Wyoming Basin).

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